Lichen Flora of the Greater Sonoran Desert Region

edited by:
T. H. Nash III,
B. D. Ryan,
C. Gries and F. Bungartz

Volume 1

Lichen Flora of the Greater Sonoran Desert Region

Volume I (the pyrenolichens and most of the squamulose and macrolichens)

Thomas H. Nash III

Bruce D. Ryan

Corinna Gries

Frank Bungartz

Lichens Unlimited

Arizona State University

Tempe, Arizona

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PREFACE

Because no comprehensive, modern lichen flora is available for any region of North America outside of the Arctic and because the taxonomic literature is so diverse and scattered, a comprehensive lichen flora for the Sonoran region has been planned, and this is the first of two anticipated volumes. In general, most lichens are independent, symbiotic organisms formed by a mycobiont and one or more photobionts (green algae and/or cyanobacteria). In reality not all groups are fully lichenized (e.g. the Caliciales) and biological relationships can be quite complex. In some cases it is becoming apparent that lichenization may have been lost. Furthermore, there are a few examples of parasitic lichens growing on other lichens. In this flora groups are treated in full, including both lichenized and non-lichenized taxa and parasitic ones. In addition, a few purely fungal genera are included because they are frequently investigated by lichenologists and are likely to be collected as lichens. In volume II we intend to treat the lichenicolous fungi as well.

The target region (NW Mexico and SW USA) covers almost 600,000 km^2 including the whole Sonoran Desert and adjacent regions up the mountain crests of Arizona, southern California and the Sierra Madre Occidental. Although we have collected in the region since the early 1970's, the impetus for developing the flora came from a major field expedition to Arizona and Baja California in Dec., 1988, to Jan., 1989. Well over 30 people participated in this excursion and many of them have become core contributors to the flora. Although the rare individual may gain sufficient expertise in a lifetime to write a flora, the philosophy behind this flora is that an assemblage of individual monographers will provide more thorough analyses.

Because there are relatively few lichen systematists (fewer than 10 active people in all of North America) and because lichens are relatively cosmopolitan (many species occur on multiple continents), it made sense to build an international team - now totaling over 60 scientists (see our home page for a list – http:// mgd.nacse.org/Arizona/) from 15 countries). Because a specialist will find many more species of the group than a generalist is likely to find, a concerted effort was made to take the specialists into the field. To revise a group it is also essential that the specialist understands the inherent variability of his group in the field. Accordingly, 14 major expeditions were mounted and almost every contributor participated in at least one expedition.

When working with an assemblage of people this large, a major practical difficulty is coordinating schedules to produce the final product. It proved impossible to have everyone conform to one deadline. In fairness to those who have already completed their contribution, it was decided to publish the flora in two volumes. The result lacks the full coherence that would be desirable, but it should still be helpful because it provides the first modern revision for many groups for any region of North America outside of the arctic. The first volume covers most of the pyrenolichens, many of the squamulose, foliose and fruticose lichens and approximately half of the Lichinaceae.

The decision to go to two volumes made it impossible to develop a comprehensive glossary because terminology used by future authors cannot be fully anticipated. Accordingly, more extensive introductory information is provided to facilitate the use of the flora by beginning lichenologists.

T. H. Nash III November, 2001

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In the ASU herbarium major assistance has been received from Beth Kantrud in her tenure as an associate curator and subsequently by Maria de los Angeles Herrera Campos, Frank Bungartz and Bruce D. Ryan. In addition, numerous undergraduate students, including Rhett Billingsley, Jennifer Biringer, Dennis Cook, Elizabeth Glover, Travis Robbins, Kim Roser, Robin Schoeninger and Betsy Ullstrup, have worked in the herbarium with an emphasis on the Sonoran project.

In the field gaining access to many Mexican localities has been facilitated by Maria Herrera de los Angeles Campos and the Instituto de Botanico, Universidad Nacional Autonoma de Mexico. Numerous park and forest service employees have facilitated collecting access to their regions in the US. These include Nancy Brian at the Grand Canyon National Park, Sarah Chaney at the Channel Islands National Park, Grace Smith of the US Naval Air Weapons Station on San Nicolas Island and the late Jennifer Stone of Southwest Division of Naval Facilities Engineering Command for San Clemente Island. Co-ordination of trips to the Channel Islands in southern California has been facilitated by Mrs. Charis Bratt of the Santa Barbara Museum (now Santa Barbara Botanical Garden), both for group expeditions and for many individual scientists and students.

Development of the database of Sonoran specimens that is now accessible over the world wide web has been developed by Dr. Corinna Gries with recent collaboration from Robin Schoeninger and Frauke Ziemmeck (http://cochise.asu.edu/collections/index.html). An integral part of the specimen database is formed by the longitude and latitude values for each location. Many of these coordinates were researched by Dr. William Davis (Tempe). For making the database searchable over the internet the collaboration of Sherry K. Pittam and F. Joseph Hanus under the direction of Dr. C. Pancake at Oregon State University (National Science Foundation grant ACIR 9523629) has been essential. On-going database activities at Arizona State University are supported by two NSF grants (BDI-9983132 and BRC-0096982).

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CONTRIBUTORS TO VOLUME 1

Dr. Teuvo Ahti,
University of Helsinki, Helsinki, Finland

Dr. Andre Aptroot,
Central Bureau for Fungal Cultures, The Netherlands

Dr. Lars Arvidsson,
Gothenburg City Museum, Gothenburg, Sweden

Dr. Othmar Breuss,
Natural History Museum, Vienna, Austria

Dr. Burkhard Büdel,
University of Kaiserslautern, Kaiserslautern, Germany

Mr. Frank Bungartz,
Arizona State University, Tempe, Arizona

Dr. José Maria Egea,
University of Murcia, Murcia, Spain

Dr. John A. Elix,
Australian National University, Canberra, Australia

Dr. Theodore L. Esslinger,
North Dakota State University, Fargo, North Dakota

Dr. David J. Galloway,
University of Otago, Dunedin, New Zealand

Dr. Corinna Gries,
Arizona State University, Tempe, Arizona

Dr. Martin Grube,
Karl Franzens University, Graz, Austria

Dr. Samuel Hammer,
Boston University, Boston, Massachusetts

Dr. Dr. Per Magnus Jørgensen,
University of Bergen, Bergen, Norway

Dr. Klaus Kalb,
Lichenological Institute, Neumarkt, Germany

Dr. Ingvar Kärnefelt,
University of Lund, Lund, Sweden

Dr. H. Thorsten Lumbsch,
University of Essen, Essen, Germany

Dr. Helmut Mayrhofer,
Karl Franzens University, Graz, Austria

Dr. Bruce McCune,
Oregon State University, Corvallis, Oregon

Dr. Roland Moberg,
Uppsala University, Uppsala, Sweden

Dr. Thomas H. Nash III,
Arizona State University, Tempe, Arizona State University

Dr. Per Luigi Nimis,
University of Trieste, Trieste, Italy

Dr. Christian Printzen,
University of Bergen, Bergen, Norway

Dr. Bruce D. Ryan,
Arizona State University, Tempe, Arizona State University

Mrs. Robin T. Schoeninger,
Arizona State University, Tempe, Arizona

Dr. Matthias Schultz,
University of Kaiserslautern, Kaiserslautern, Germany

Dr. Harrie G. M. Sipman,
Botanical Garden, Berlin, Germany

Dr. Anders Tehler,
Natural History Museum, Stockholm, Sweden

Dr. Arne Thell,
Botanical Garden, Hamburg, Germany

Dr. John W. Thomson, Jr.,
University of Wisconsin, Madison, Wisconsin

Dr. Einar Timdal,
University of Oslo, Oslo, Norway

Dr. Pilar Torrente,
University of Murcia, Murcia, Spain

Dr. Mauro Tretiach,
University of Trieste, Trieste, Italy

Mr. Martin Westberg,
University of Lund, Lund, Sweden

Dr. Clifford M. Wetmore,
University of Minnesota, St. Paul, Minnesota

Dr. Isao Yoshimura,
Kochi Gakuen College, Kochi, Japan

INTRODUCTION

Circumscription of the Study Region

by T. H. Nash III & C. Gries

The geographic region (almost 600,000 km^2) treated in this flora (Fig. 1) is defined as all of Baja California (both states), the northern half of Sinaloa (Mazatlan and route 40 to Durango forming the southern boundary at approximately 23°N), all of Sonora, the Sierra Madre Occidental region of Chihuahua (primarily a belt roughly 100 km wide running along the border with Sonora) all of Arizona, and the southern eight counties in California (San Diego, Orange, Los Angeles, Ventura, Santa Barbara, San Bernardino, Riverside and Imperial Counties). The northern portion of the region lies at approximately 35°N in California and 37°N in Arizona.

On the basis of our book's title, Lichen Flora for the Greater Sonoran Desert Region, the region defined above is intimately related to the Sonoran Desert. In fact if one takes Forest Shreve's definition of the Sonoran Desert (Fig. 1), then approximately 60% of the geographic region defined above would be included. The utility of the flora is greatly expanded by utilizing the larger geographic area. For example, the upper elevational limit of the Sonoran Desert is approximately 1000 m, but within the region as a whole elevations up to 3660 m can be found. By including the upper elevations we include many forested, montane regions and even some alpine areas in the case of the San Francisco Peaks near Flagstaff, Arizona. This more than doubles the number of lichen species treated.

The greater Los Angeles-San Diego region is included because many of the coastal lichen species occurring there have geographic distributions that extend well into the Sonoran Desert region to the south (both Baja California and Sonora). In addition, that region is historically important because of the early work of Hasse (1913). Within Arizona an alternative, physiographic boundary of the Mogollon Rim, the southern boundary of the Colorado Plateau that runs from north of Prescott ESE to the New Mexican border, might have been selected, but the political boundaries are of greater utility when dealing with collections. To the south the northern part of Sinaloa falls outside of Shreve's (1964) definition of the Sonoran Desert, but much of it is included in the Sonoran Desert by Robichaux (1999).

Fig. 1. The geographic region treated in this Flora (light gray: Sonoran Desert as defined by Shreve (1964); dark gray: additionally investigated in this research.

The whole region actually does have relatively natural boundaries. For example, much of the eastern boundary is formed by the crest of the Sierra Madre Mountains, which have major biological affinities with the mountains of southeastern Arizona. To the west and partially in the south the Pacific Ocean is a natural boundary. To the north the central valley of California is a boundary to the west and the Great Basin Desert (Nevada and parts of Utah) in the Basin and Range Physiographic Province (Fenneman 1931) provides an approximate boundary to the east. Along the Pacific coast the northern boundary ends in Santa Barbara County because a major shift in ocean currents occurs there with very cold ocean currents from the north terminating at Point Concepcion and warmer water occurring to the south.

Climate

Precipitation

Deserts are by definition dry places and the Sonoran Desert is no exception with annual precipitation varying from less than 70 mm in parts of central Baja California

and the northern rim around the Gulf of California to approximately 250 mm at the upper elevation boundary (Jaeger 1957). In general precipitation increases with elevation and the wettest region (the White Mountains in east, central Arizona) receives over 1000 mm per year. The pattern of precipitation within a year varies across the region, primarily as a function of latitude and position relative to the Pacific Ocean. During the winter months westerly winds from the Pacific Ocean predominate throughout the region and periodic cyclonic storms occur, particularly in the northern region. Although the high mountains of southern California and northern Baja California create a rain shadow effect, some winter precipitation typically occurs in northern part of the Sonoran Desert region. In contrast, southern California and northern Baja California are extremely dry during the summer months when the westerly winds have moved to more northerly latitudes.

Summer precipitation frequently as thunder storms dominates the southern part of the region and also occur in eastern and central Arizona. Throughout the tropics precipitation typically occurs when the sun is at the zenith and maximal convection of moist air occurs, and this pattern occurs along the southern boundary in the summer. In addition, occasional major tropical storms sometimes move into the region in late summer from the Pacific Ocean to the south. A second source of summer precipitation is moist air from the Gulf of Mexico that arrives in SE Arizona in early July and creates what is locally known as the monsoon season. The warming of the central part of North America in summer draws moist air from the Gulf of Mexico inland, and part of this moist air follows the Rio Grande Valley westward into New Mexico and ultimately reaches as far as central Arizona. The overall result is that the northeastern part of the Sonoran Desert has a bimodal (summer and winter) annual precipitation pattern, California has a winter dominated pattern of precipitation and the southern portion of the region in Mexico has a summer dominated precipitation pattern.

Fog and Dew

From a lichen's perspective the occurrence of fog and dew, particularly along the Pacific coast, may provide a greater moisture source than precipitation. Fog frequently occurs in the summer months along the Pacific coast when temperature differentials between the land and sea are maximal. It is probably most frequent between central Baja California and southern California, although a second fog bank occurs in the Gulf of California, and it affects the southern coast of Sonora and northern coast of Sinaloa. In addition, dewfall occurs almost on a daily basis adjacent the western coasts. The result of dew and fog is a spectacular development of lichen communities where biomass almost rivals that of the vascular plants (Nash et al. 1979). In contrast, fog and dew are very infrequent along the east coast of Baja California and lichens are rare and infrequent. Inland fog is even less frequent. For example, in Phoenix, Arizona, the airport experiences fog only approximately once every two years (Nash et al. 1982).

Temperature

An extreme range of temperatures occur throughout the region. Deserts are, of course, well known for their hot climates and the Sonoran Desert is one of the three hot deserts of North America with summer temperatures exceeding 50°C (122°F) and winter temperatures as low as -9°C in the north. However, frost is relatively infrequent in winter and almost never occurs along the coast and in most of the southern portions of the region. Mean July temperatures exceed 30°C throughout much of the Sonoran Desert region and mean January temperatures lie between 10 and 20°C throughout the whole region (Jaeger 1957). Along the immediate coast of California and northwestern Baja California summer temperatures are substantially ameliorated by the occurrence of fog and cloudy conditions such that the mean July temperatures fall below 20°C. In general temperatures decrease with increasing elevation. Above 2200 m mean July temperatures are mostly below 20°C and mean January temperatures are frequently below 0°C. Within Arizona alone both the lowest and highest daily temperatures for the whole U.S.A. are sometimes reported.

Geology and Geomorphology

The Greater Sonoran Desert as defined earlier, covers several geologic provinces with the actual Sonoran Desert being in the southern part of the North American Basin and Range Province (Fenneman 1931). This province

stretches from northern Mexico across much of Arizona and Nevada, parts of California and Utah, and into southern Idaho. It is characterized by broad, low elevation valleys rimmed by long, narrow, parallel mountain ranges oriented NE to SW. In the Sonoran Desert the valleys are filled with hundreds of meters of gravel and sand carried down from the mountains. The mountain sides show topological features characteristic for arid regions, in which sediments are not moved far from the mountains due to the lack of water. Alluvial fans develop where streams flow intermittently out of the mountains. Where alluvial fans merge to engulf the base of the mountain in an apron of boulders, gravel and sand, it is called a "bajada", a term widely used in the Southwest from Spanish days. The mountain ranges increase in elevation and the valleys become narrower to the east and north in the Central Arizona Highlands. In the north this transition zone leads up to the Colorado Plateau Province beginning at the sharp rise of the Mogollon Rim and stretching into Utah, Colorado and New Mexico. This province is characterized by colorful rock formations in flat-lying sedimentary strata, flat-topped mountains (called "mesas"), steep cliffs and deep canyons. To the west the Sonoran Desert is bounded by the Pacific Ocean, the Sierra San Pedro Martir, and southern California's Laguna Mountains, which are loosely connected to the Sierra Nevada. The southern limits of the Sonoran Desert are defined by the Pacific Ocean and the Gulf of California while in the southeast the Sierra Madre Occidental borders the Sonoran Desert. This tall mountain range consists of a series of closely spaced volcanic sierras and plateaus that locally coalesce to form one of the world's largest volcanic fields. This topography, resembling a shallow bathtub, is open to the Gulf of California and is partly responsible for the extremely arid climate of the Sonoran Desert.

The geologic history of the Greater Sonoran Desert is determined by the fact that this area is located at the edge of one of the major tectonic plates, the North American Plate, that stretches from the Mid-Atlantic Ridge to the Pacific shore and from Alaska to the Caribbean. During earth's history this plate has been attached to other plates, broken off again and moved into different directions. Its movements relative to the Pacific Plate are of interest here as they have created the major features we see today. This long, narrow and arc-shaped zone of structural instability is characterized by thick sequences of sedimentary and volcanic rocks that have been folded, faulted, metamorphosed, and intruded by plutons. It is the leading edge of a moving plate where volcanism, earthquakes, granitic batholiths, regional metamorphism, and mountain building occurred. Basalts, rhyolites, dacites and andesites are some of the most common rock types of the region reflecting a rich history of volcanism in eons past. Limestone and gypsum are relatively rare, found mainly on the Colorado Plateau and in some areas where erosion and sedimentation from the Plateau occurred (e.g. the Verde Valley, Arizona). More common in the deserts are local secondary $CaCO_3$ deposits called "caliche".

The oldest rocks found in the Sonoran Desert region, Precambrian gneiss and schist in the bottom of the Grand Canyon, suggest that it was located at the southwestern edge of North America for more than 1.7 billion years. The Precambrian era saw several cycles of mountain building, faulting and uplifting followed by phases of erosion with marine and near-shore sedimentation. Active volcanism contributed layers of volcanic rocks, intrusions of dykes, sills and large granitic batholiths, all of which has undergone millions of years of weathering, erosion or metamorphism but still can be found as cores of mountains, that are sometimes exposed, in the desert and Central Highland ranges and at the bottom of the Grand Canyon.

Following the Precambrian came the Paleozoic or 'quiet' time (about 600 – 230 million years ago). Most of the Precambrian mountains were eroded down to a nearly featureless landscape. No records of active volcanism have been found for this time, only massive erosion and sedimentation. Marine sandstone, siltstone and limestone alternate with continental delta and desert sand dune deposits, suggesting changing elevation and submersion of the continent. It is assumed that the current North American and Pacific Plates were not moving relative to each other and became part of the Permian supercontinent Pangea. Located at mid latitude, we can picture shallow tropical seas in which invertebrate groups underwent major evolutionary and adaptive radiation, with some barren desert islands protruding from this ocean. Only the end of the Paleozoic saw terrestrial plant and animal life developing.

The beginning of the Mesozoic era (230 – 63 million years ago) is marked by a change in motion as the supercontinent, Pangea, started to break up. The North Ameri-

can Plate began to move westward against the Pacific Plate forcing the thinner and heavier oceanic crust of the Pacific Plate under the continent in a subduction zone. This caused the edge of the continental crust to crumple and buckle and mountains to rise, first forming the Sierra Nevada (Cordilleran Orogeny). These movements were accompanied by active volcanism, which was very explosive and spewed vast quantities of volcanic rocks, and ash as can be seen today in several thousand meter thick layers of tuff and breccia. This silicic volcanism was rich in silica, aluminum, potassium and sodium and can be seen today in the light colored rhyolite of the Tucson Mountains. The lower volcanic complex of the Sierra Madre Occidental is also dominated by andesitic volcanism. In other places magma pushed up and cooled into large granitic batholiths far below the surface with metamorphism of the host rocks resulting from the thermal effect of the intruding magma, e.g. chief portion of the Sierras in Baja California and most of the core of the peninsula. The sea invaded one last time from the north before uplift and igneous activities intensified again. Uplift, folding and faulting created mountains in what is now the Basin and Range Province. The third and most intense phase of mountain building and intrusions, the Laramide Orogeny, gave rise to the Rocky Mountains and began at the end of the Mesozoic era when the continental crust overrode a particularly active area of the oceanic crust and collided with island like microcontinents. Mountain ranges originating from this compression type of mountain-building phase are oriented NW-SE.

The Cenozoic era (63 millions year ago to today) with mammals and angiosperms spreading across the landscape began while the Laramide Orogeny was still in full swing. Conditions were just right for mineral rich solutions to rise and deposits rich in copper, silver, gold and other minerals to come to the surface and subsequently to be eroded. A quiet period without active volcanism but extensive erosion separates the Laramide Orogeny from the following Mid-Tertiary and its Basin and Range Orogenies, both of which were a different type. As the North American plate overrode the East Pacific Rise, the Pacific plate started to move NW now pulling the Greater Sonoran Desert Region apart rather than pushing into it. A major fault zone developed in the area of the Basin and Range Province to accommodate the stretching and a new phase of tension type mountain building started. Explosive volcanism once again spread thick layers of ash across southern Arizona and northern Mexico and can now be observed in the Superstition and Chiricahua Mountains. The upper volcanic complex of the Sierra Madre Occidental is related to this phase of volcanism and consists of extensive siliceous ignimbrite sequences up to 1000 m thick and spanning the whole province. As major uplifting and volcanism occurred during the Mid-Tertiary Orogeny, the Rocky Mountains, the Sierra Madre Occidental, the Great Basin and the Colorado Plateau increased their respective elevations. Through 600 million years of folding, tilting, faulting and mountain-building in all the surrounding areas, the Colorado Plateau has stayed as a stable and coherent block of the earth's crust. It is divided by faults, monoclines and the Grand Canyon into a number of smaller plateaus, all of which have experienced uplifting to various degrees during this time in earth's history, but no major tilting, crumpling or folding occurred during the Cenozoic. This phase of increasing elevation across the Sonoran Desert region set the stage for development of today's desert climate as air movement became blocked by high mountain ranges. During the Basin and Range Orogeny a less explosive volcanism dominated and block faulting created mountains of a different type. As the crust pulled apart, basins between the mountain ranges began to subside leaving behind long, narrow fault block ranges oriented NE-SW and perpendicular to the mountains that originated during the Laramide Orogeny. Only the highest parts of these mountain blocks can be seen today with large basins in between filled with sediments. The volcanism of this time until recently is of basalt type with thin fast lava flows that are dark colored and cover large areas, as can be seen in the Pinacate field and around the San Francisco Peaks. The movement of the Pacific plate relative to the North American plate is also responsible for the opening of the Gulf of California, which began about 8 million years ago as the continent finally yielded to the stretching and the rift started to gradually open. This rift zone continues north through the Salton Sea and along the legendary San Andreas Fault in California, along which coastal California and Baja California together with the Pacific plate move NW away from the North American continent.

Vascular Plant Vegetation

Sonoran Desert

Paleontological investigations suggest that the Sonoran Desert is about 8 million years old. Evolutionary adaptations to a harsher, non-tropical climate probably began during mid-Tertiary, when major uplifting of the Rocky Mountains and the Sierra Madre Occidental started to block moist tropical air. Deciduous plants developed in response to extended dry seasons. Along the lower, dry edges of this deciduous tropical forest a new biome, the tropical thorn-scrub, evolved and is thought to be the ancestral biome for many of the modern Sonoran Desert plant species. A drying trend about 15 to 8 million years ago is considered responsible for bringing about the actual Sonoran Desert flora. The ancestral desert expanded and contracted with changes in climate and modern biotic communities have developed only since the most recent expansion about 9000 years ago in Arizona, California and northwestern Mexico.

At lower elevations the region is, of course, dominated by the Sonoran Desert, which was extensively investigated by Forest Shreve in the initial half of the twentieth century. He defined the desert as occurring throughout most of Baja California (excluding the Cape region in the southern tip and the NW corner that has greater affinities to coastal regions of southern California) and lowland areas (roughly up to 1000 m) of Sonora and adjacent parts of Arizona and California (Fig. 2). The vegetation is a rich mixture of succulents (of all sizes), small trees, shrubs and ephemerals that constitute approximately 40% of the region's species richness. In fact the luxuriousness of the region's flora has led some botanists not to classify it as a desert at all (e.g. Walter 1965). Shreve (1950) established that some floristic commonality occurred within the region in so far as a few species, such as *Bursera microphylla* (elephant tree, corote, copal) and *Larrea tridentata* (creosote bush), occurred throughout the whole Sonoran Desert. However, major changes in the dominant vegetation occur across the Sonoran Desert, and consequently Shreve (1950) recognized seven major subdivisions (Fig. 2):

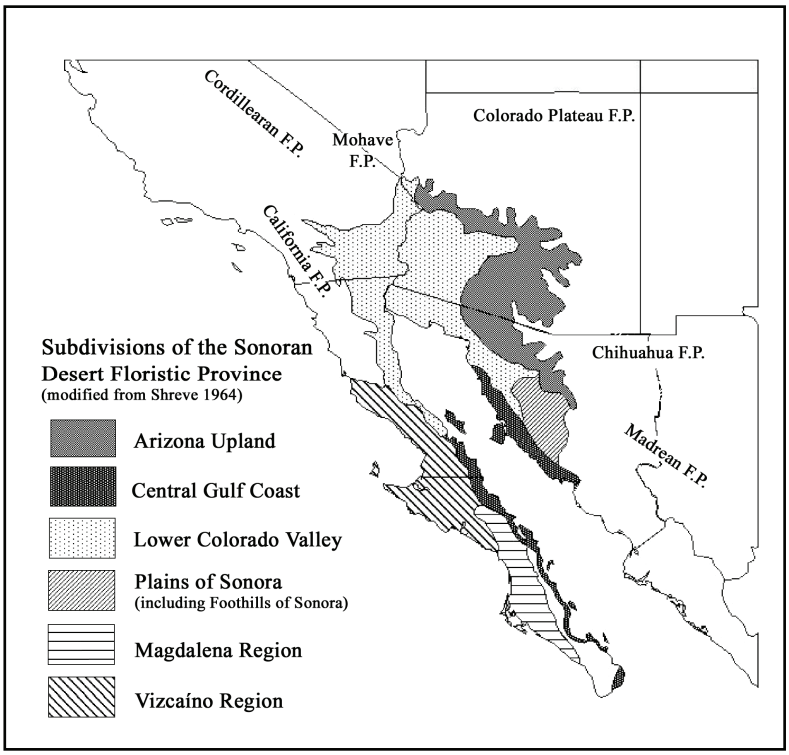

Fig. 2. Floristic Provinces (F.P.) of the Greater Sonoran Desert Region.

(1) In the "**Arizona Upland**", along the northeast, roughly between 200 and 1000 m. *Ambroisia deltoidea* (bursage) is the dominant shrub, *Cereus gigantea* (saguaro) the dominant cactus, and small trees, such as *Cercidium microphyllum* (palo verde) and *Olynea tesot*a (ironwood), commonly occur as well. This "Saguaro-Palo Verde forest" is the only subdivision that experiences frequent hard frosts, which excludes many species from further south.

(2) The "**Lower Colorado Valley**" in the north surrounds the upper end of the Gulf of California and extends northwards along the lower parts of the Colorado and Gila River. The region extends from below sea level to roughly 200 (max. 400) m. *Larrea tridentata*

and *Ambroisia dumosa* are the dominant shrubs. This is the driest subdivision of the Sonoran Desert with perennial vascular plants in some places restricted to riparian areas.

(3) The "**Plains of Sonora**" are located in central Sonora, both N and S of Hermosillo, the capital of the state. This flat plain has some small mountain ranges from roughly 100 to 750 m. *Encelia farinosa* (brittlebush) is the dominant shrub and *Olynea tesota* the most common small tree. Conspicuous cacti include *Lamaerocereus thurberi* (organ pipe) and *Lophocereus schottii* (senita).

(4) The "**Foothills of Sonora**" are sometimes regarded as part of the Plains of Sonora (and therefore not shown in Fig. 2). The Foothills extend in southern and eastern Sonora from sea level to approximately 1000 m in the Sierra Madre Occidental. This floristic region is a transition area of thorn forest with many small trees (*Bursera* spp., *Cercidium sonorae*, *Jatropa cordata*, *Ceiba acuminanta*, etc.) and some large columnar cacti like *Pachycereus pectin-aboriginum*.

(5) The "**Vizcaíno Region**" of north central Baja California extends from the Pacific Ocean to roughly 500 m. *Yucca valida* (patililllo) dominates the aspect of the landscape together with the shrubs *Bursera microphylla* (torote, copal) and *Ambrosia chenopodifolia* (huizapol). Leaf succulents such as *Agave* spp. (century plants) and *Dudleya* spp. (siempreviva) are quite common and the small tree *Pachycormus discolor* (copalquín) is largely confined to this region. The two tallest plants of the desert region, *Fouquieria columnaris* (boojum tree) and the giant cactus *Pachycereus pringlei* (cardon) also occur together in part of this region.

(6) The "**Magdalena Region**" of south central Baja California extends from the Pacific Ocean to roughly 500 m. *Pachycereus* spp. (cardon) appears to be the dominant, although the shrubs *Fouquieria diguetii* (palo adán), *Jatropha cinerea* (lomboy blanco) and *Bursera laxifolia* (torote, copal) are more common. The vegetation becomes relatively dense thoughout much of the range and numerous medium sized cacti are present (*Machaerocereus gummosus*, *Lamaerocereus thurberi*, *Opuntia* spp.).

(7) The "**Central Gulf Coast**" is a lowland region on both sides of the Gulf of California from sea level to roughly 300 m. *Bursera* spp. and *Jatropha* spp. (leatherplant) are dominant small trees. In a narrow region along the coast of Sonora *Fouquieria columnaris* (boojum) and *Pachycereus pringlei* (cardon) reappear.

Other vegetation types

At lower elevations at approximately 1000 m, a small portion of the Chihuahuan Desert extends into SE Arizona in limestone regions. In the NW corner of Arizona and extending across to San Bernardino County, California, the southern portion of the Mohave Desert is situated. Neither desert is as structurally complex as the Sonoran Desert. Although all three deserts have an abundance of *Larrea tridentata*, they differ markedly in species composition. For example, *Yucca brevifolia*, *Y. schidigera* (soap tree), and *Ambrosia dumosa* (burro bush) are dominants in the Mohave Desert and *Holocarpha virgata* (tar bush) is abundant in the Chihuahuan Desert. In California and NW Baja California a fire-adapted, shrub dominated community called chaparral occurs commonly from sea level to approximately 1200 m. Frequently it is divided into (1) "soft" chaparral (dominated by *Artemisia californica*, coastal sagebrush) at lower elevations and (2) "hard" chaparral (*Adenostema fasciculatum* [chamise], *Ceanothus spp.* [buckbrush], *Rhamnus* spp., [buckthorn], *Rhus* spp., [sumac], and *Arctostaphylos* spp. [manzanita]), that also extends into western Arizona where winter precipitation also dominates. Intermixed with the chaparral in California, oak woodlands (especially *Quercus agrifolia*, [Californian live oak]) are also common, particularly in canyons. In Sinaloa and extending into southern Sonora a tropical thorn forest is abundant near sea level. Small trees (e.g. *Acacia* spp., (acacia) and *Ipomoea arborea,* (morning glory tree) grow upwards to 10 m in height and provide continuous vegetation cover. Also common are cacti, of which *Pachycereus pecten-aboriginum* (cawe) is the most prominent. Along the immediate coast small patches of mangrove vegetation (*Avicennia* sp., [black

mangrove]) can occasionally be found on both sides of the Gulf of California.

With increasing elevation a marked zonation pattern of vegetation is evident throughout the whole greater Sonoran region. For example, in SE Arizona, where summer rains occur commonly, desert grasslands immediately above the deserts, and at the highest elevation an alpine vegetation is found. But alpine areas are limited to the higher peaks in Arizona. In general conifers dominate the higher elevations, although oak forests (over 20 species of oak with dominants changing in different geographical areas) also occur extensively below the conifers, particularly in the Cape Region, Sierra Madre Occidental and SE Arizona. At mid-elevations above the oaks, pines (over 10 species) dominate. For example, the largest North American *Pinus ponderosa* (ponderosa pine) forests occur in central Arizona. In the upper montane region of Arizona and the Sierra Madre Occidental, *Pseudotsuga menziesii* (Douglas fir) forests are quite common above the pine forests. In Arizona at even higher elevations (3000-3300 m) spruce (*Picea engelmannii,* Engelmann's spruce) and fir (*Abies lasiocarpa*, subalpine fir) forests can be found and these are floristically similar to the Rocky Mountain region to the north and east. In Sinaloa in the upper reaches of major canyons *Abies religiosa* (sacred fir) forests can occasionally be found within the oak/pine forests. In the high mountains of southern California and northern Baja California montane pine forests (with an understory of *Quercus* spp.) also occur and in moister areas *Libocedrus decurrens* (incense cedar) is relatively common. *Pseudotsuga menziesii* (Douglas fir) does not occur there, but a second species, *P. macrocarpa* (bigcone Douglas fir), occurs infrequently in lower montane areas. In the northern part of the study region a short stature (less than 10 m) Pinyon-Juniper forest (short needle *Pinus* spp. and *Juniperus* spp.) occurs immediately below the *P. ponderosa* forests. On some of the Pacific islands at upper elevations pine forests also occur (e.g. on Cedros and Santa Cruz Island) and *Cupressus* (cypress) forests (e.g. on Guadalupe Island). Special vegetation occurs in riparian areas along river drainages where the more favorable moisture regime allows a wide variety of deciduous tree species to grow. In the deserts *Populus fremontii* (Fremont cottonwood) is quite common and in Sinaloa and adjacent parts of Sonora *Taxodium mucronatum* (bald cypress) occurs occasionally. In lower montane to montane areas *Platanus* spp. (Sycamore), *Fraxinus* sp. (ash), *Acer* spp. (maple), *Juglans* spp. (walnut), *Alnus* sp. (alder) and *Cupressus arizonicus* (Arizona cypress) all occur.

History of Lichenology in the Region

by T. H. Nash III

Historically H. E. Hasse, a physician who worked at the Soldier's Home (near the current UCLA campus) between Santa Monica and Los Angeles, is doubtlessly the most important lichenologist to have investigated a portion of the region's lichen flora. Over a period of 30 years starting in the mid-1880's he collected throughout southern California, but with an emphasis on areas readily reachable by horseback (e.g. the Santa Monica Mountains). He corresponded extensively with A. Zahlbruckner (Vienna, Austria), the most prominent lichenologist of his time, and developed a profound understanding of the region's lichen flora, that culminated in his floristic treatment (Hasse 1913) for southern California. The coastal flora was particularly rich and from a lichenological perspective contained a relatively large number of endemics. Hasse's investigations became a major cornerstone of Fink's (1935) Lichen Flora of the United States.

In contrast, most of the rest of the region was relatively poorly investigated for lichens until recently. For example, Fink's flora recognized no more than a couple dozen lichen species from Arizona, an area for which almost 800 species are known today (Nash et al. 1998). The first major paper dealing with Arizonan lichens was published by Darrow (1950), who investigated the epiphytic lichens of southern Arizona while based in Tucson. Later Weber (1963) investigated the Chiricahua Mountains (SE Arizona) and published the first floristic treatment dealing with all lichen groups for an area in Arizona. To the south Sonora and Sinaloa were until recently almost unknown lichenologically except for a small paper by Herre (1944). Vehicular access to much of Baja California has only been available in recent decades and consequently much lichen material is limited to recent collections, although some of the more prominent species were included in early monographs, such as Darbishire's (1898) investigation of *Roccella*.

Morphology and Anatomy of the Lichen Thallus

by B. D. Ryan, F. Bungartz and T. H. Nash III

The **thallus** (pl. thalli) of a lichen is the vegetative and assimilative body, composed of a lichen fungus, the **mycobiont** and the photosynthetic partner called **photobiont**. The photobiont can either be an **alga** or a **cyanobacterium** (or both). The fungal partner usually belongs to the sac-fungi or **ascomycota**. In the Greater Sonoran Desert Region only one genus of lichens which belongs to the **basidiomycota** has been found. Characters of this genus (*Dictyonema*) will be discussed under the treatment of the genus. Our discussion here focuses on the ascomycetous lichens. Like the **mycelium** of non-lichenized fungi, this fungal part is composed of thread-like **hyphae**, forming a less differentiated structure than the thallus of bryophytes or vascular plants. In most cases the thallus develops a morphology different from that assumed either by the mycobiont or photobiont when grown separately. Usually the mycobiont is the dominant partner (often contributing 80-90% of the biomass of the lichen, but in a few tropical genera the photobiont is dominant (e.g. *Coenogonium*). The boundary between lichenized and non-lichenized fungi is not always clear, as a few species may only be facultatively lichenized or the algae may not be fully integrated into a thallus, although most lichens are well integrated symbiotic organisms. In addition, a few non-lichenized fungi occur in the same microhabitats as lichens and are often collected by lichenologists. Those traditionally treated in lichen floras are also included in this flora. **Lichenicolous fungi** are non-lichenized, growing on lichens as parasites, saprophytes or epiphytes. They share the thallus and usually the photobiont of the **host** lichen. Very few lichens are lichenicolous and the degree to which they are independent from their host requires further investigation.

Morphology of the Lichen Thallus

Most commonly lichen growth forms are referred to as **crustose** (crust-like), **foliose** (leaf-like) or **fruticose** (shrub- or beard-like). However, there are many intermediate forms, which are frequently indicated with the prefix sub-, e.g. subfoliose or subfruticose. Gelatinous lichens are often treated as a separate group, even though they generally assume a crustose, foliose or fruticose growth form as well. Another common way to distinguish growth forms is according to thallus size as either **micro-** or **macrolichens**. This designation is rather subjective. Not all microlichens are crustose and some crustose lichens can be rather large.

In the development of a lichen thallus it is generally assumed that lichens first establish an undifferentiated **prothallus**, a thin layer of undifferentiated mycelium, upon which an algae-containing secondary thallus later develops. In crustose and foliose lichens this undifferentiated prothallus may persist, and it is then commonly referred to as **hypothallus**. Often the hypothallus has a different color and texture from the fully differentiated lichenized thallus. It may be white, reddish, or blue-black, and is usually visible only as a rim or line along the outline of the main thallus.

Most lichens, especially the larger ones, are distinctly separate from their substrate, but many smaller ones occur partially or wholly within the substrate. A rich terminology has developed to describe thallus to substrate relationships, such as **epi-** (on), **endo-** (within), **chasmo-** (hidden) or **crypto-** (buried) with the suffix referring to the substrate. **Epiphytic** lichens grow on other plants, **epilithic** ones on rock and **epigaeic** ones on soil. **Chasmolithic** lichens grow hidden between the mineral grains of the upper rock surface. **Endolithic** ones grow inside the upper rock layers, whereas **cryptoendolithic** ones grow buried deep below the rock surface. **Endophloeic** lichens grow inside the outer layers of bark.

Substrate preferences are described with the following terminology: **corticolous** lichens grow on bark, **lignicolous** ones on wood; **saxicolous** lichens, on rock, and **terricolous** ones, on soil.

Crustose thalli

Strictly **crustose** lichens consist of a strongly adherent crust within or on the substrate. Because of their intimate contact they cannot usually be removed without damaging the thallus or removing part of the substrate as well. These lichens lack a distinct lower surface and associated structures. Internally the thallus is often poorly differentiated. However, there are many intermediates with foliose or fruticose forms, where parts of the thallus be-

come ± independent from the substrate and show the tendency to develop a lower cortex.

Among crustose lichens several growth forms are commonly distinguished (Fig. 3):

Leprose lichens represent the least organized growth form. Their thalli are a powdery to finely granular mass of algal cells and fungal hyphae. They are never delimited by cortical layers and resemble an extensive crust of poorly differentiated lichen soredia (see vegetative propagules).

Crustose lichen thalli can be classified as **continuous** if they have few or no distinct breaks or divisions. However, most crustose thalli are not continuous. **Rimose** thalli are irregularly cracked, chinked or fissured. In a strict sense this term only refers to incomplete, rather narrow and shallow fissures, extending irregularly in all directions. These fissures are sharp-edged and the side walls are not delimited by cortical layers. The thallus may further break apart into clearly delimited **areoles**. These lichen thalli are then referred to as **rimose-areolate**.

Truly **areolate** thalli derive from an independent, isolated development of individual areoles. These areoles are initially scattered and therefore always sharply divided. The thalli often resemble a mosaic or jigsaw puzzle. However, adjacent areoles may become grouped and even coalesce and then the distinction from rimose-areolate thalli becomes less evident.

Areolate thalli may further be distinguished according to the shape of the individual areoles. **Bullate** thalli are composed of inflated, swollen areoles. The surface of **verrucose** areoles is warty and **granular** thalli are entirely composed of irregularly spherical grains called **granules**.
Crustose thalli may be **indeterminate**, i.e. not sharply delimited and often scattered. These lichens generally have no consistent outline or well-defined margin but they represent an irregular aggregation of indistinct confluent thalli. They are referred to as **effuse** if they are ± uniformly structured across, for example if the fruiting bodies are evenly spread over the entire surface of the thallus.

In contrast, **determinate** crustose lichens have a well-delimited margin. They can either be characterized as **irregular** without a distinct shape or **orbicular** with an approximately circular outline. Determinate crustose lichens may be **zonate** with a distinctly sterile outer area and a fertile central region. In **radiate** thalli the outer sterile part

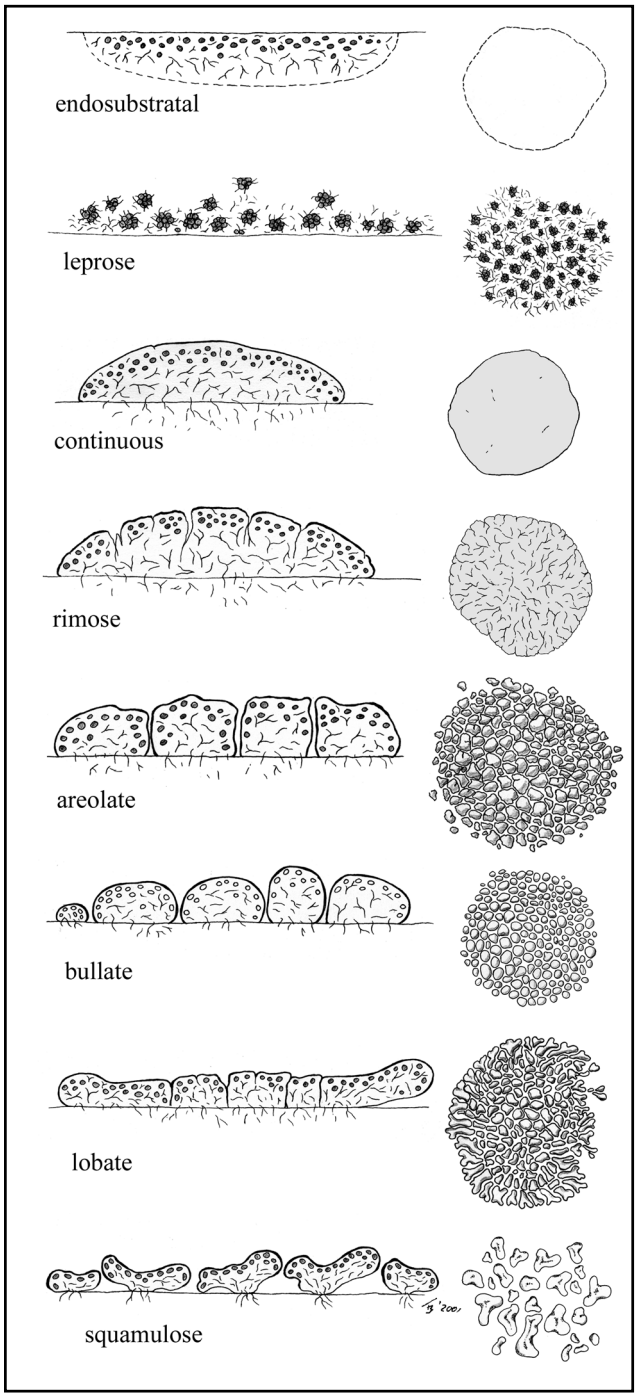

Fig. 3. Crustose growth forms showing cross-section (left) and surface view (right).

is radially structured, often showing the tendency to form lobes and thus transitions to foliose forms.

Crustose lichen thalli as well as individual areoles are frequently surrounded by a conspicuous hypothallus. On very hard rock surfaces, particularly quartz, these hypothalli may become **dendritic** (producing a tree-like branching pattern), a growth pattern which is particularly common in the crustose lichen genera *Lecidea*, *Rhizocarpon* or *Buellia*.

All these terms are not necessarily exclusive. Many crustose lichens show transitions of growth forms across their entire thallus and surface structures often intergrade with the overall growth form. The thallus center of crustose lichens is often more highly developed than the thallus margins. In **pulvinate** lichens the center grows into exuberant, elevated cushions. Thallus areas which lack cortical layers are often entirely composed of delicate threads. This surface structure is referred to as **byssoid**. **Floccose** thalli also lack cortical hyphae but irregularly break apart in large clusters. Eventually the whole center of the thallus may disintegrate becoming detached from the substrate.

Areoles which are irregularly scattered often become minutely lobed and these scales are more accurately referred to as **squamules**. In **lobate** thalli marginal areoles are more developed than central ones. Both squamulose and lobate lichen thalli represent transitions to foliose lichens and will therefore be discussed in more detail among intermediate growth forms.

Foliose thalli

Foliose lichens are "leaf-like", usually dorsiventrally oriented with a distinct upper and lower surface (Fig.4 and 5). This structure is often associated with internal differentiation and foliose thalli are generally ± flattened in cross-section. Foliose lichens can usually be removed intact from their substrate even though they are commonly attached by distinct **holdfasts** like rhizines, hapters or other attachment organs.

Rhizines are root-like attachment organs of strongly conglutinated hyphae originating in the lower cortex. They range from short and barely differentiated to thread-like and intricately branched. Usually they are smooth and solid, but sometimes can be fibrous or tomentose. **Rhizinose strands** are less conglutinated and more irregular than rhizines and extend more deeply into the substrate.

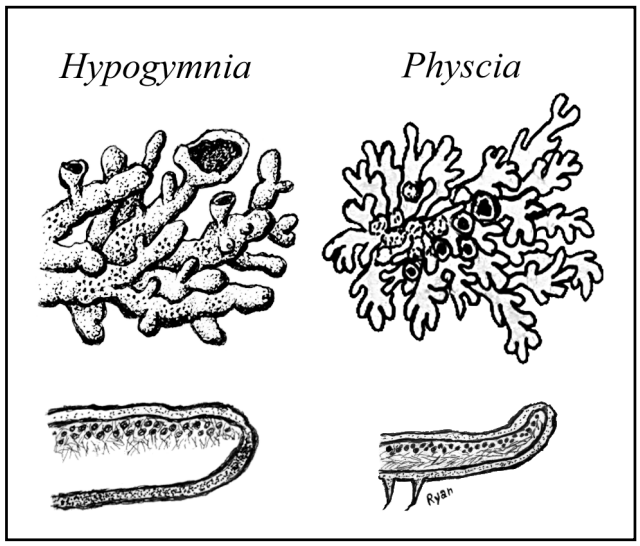

Fig. 4. Variation in thallus morphology of small foliose lichens (not drawn to scale: *Physcia* has 1-2 mm wide lobes, *Hypogymnia* has slightly wider, inflated lobes).

Rhizoids are individual hyphae anchoring the thallus in the substrate. **Hapters** are scattered or tufted holdfasts, which attach the thallus at distinctly confined areas.

Most foliose lichens are attached to their substrate across their whole lower surface but the degree of adherence to the substrate can vary from tightly to loosely **adnate** (= appressed).

A few foliose lichens (e.g. *Pannaria* spp.) develop on a **hypothallus**, which is a mat of non-lichenized fungal mycelium below the main thallus. Usually this hypothallus is dark brown to blue-black.

Most foliose lichens are approximately circular in outline and typically divided into separate **lobes** radiating from the thallus center. Lobes can be narrow or broad but the length-width ratio is generally low. Usually lobes are crowded or contiguous towards the center of the thallus and more distinct along the periphery. Some foliose lichens are finely divided and **microphylline** (minutely foliose), or **panniform**, i.e. composed of or covered by small, often elongate, ± tightly imbricate **lobules**.

Regular branching, in which the lobes repeatedly follow the same pattern of division can generally be distinguished from irregular branching, where branching does not follow any definite pattern (Fig. 6). If the branching lobes are of equal size the resulting regular pattern is **iso-**

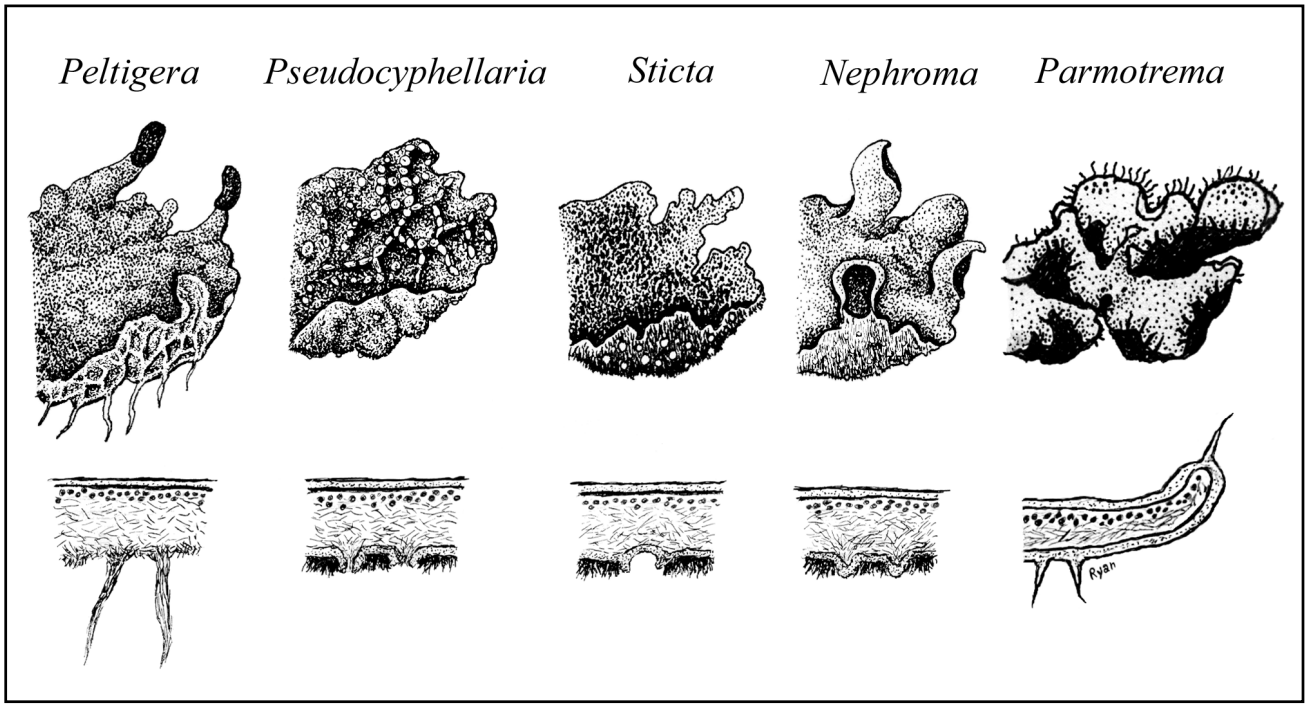

Fig. 5. Variation in thallus morphology of large foliose lichens (not drawn to scale: *Peltigera*, *Pseudocyphellaria*, *Sticta* and *Nephroma* are large cyanolichens with several cm wide lobes; *Parmotrema* is a green algal lichen with lobes usually less then a cm wide).

tomic. **Anisotomic** lobes are the result of regular branching into lobes of unequal size. Regular branching into two lobes of approximately equal size and length is referred to as **dichotomous**.

Lobe shape may vary considerably from **linear**, very narrow and elongated with parallel margins to **regular** with a broad and rounded outline and no parallel margins. Transitions are usually referred to as **sublinear** or **subirregular**.

Ligulate lobes are strap-shaped, flattened and generally very narrow and elongated. Their width is about the same from the thallus center to the lobe tip, The tips are often blunt, squarish and forked in twos. **Lingulate** lobes are tongue-shaped, **spathulate** lobes spatula- or spoon-shaped, with gradually widened and flattened blunt ends. **Flabellate** lobes are fan-shaped, in the form of a semicircle (Fig. 7). Lobe apices can be **truncate**, i.e. ending abruptly with blunt tips or more or less squared off. In contrast **rotund** tips are rounded in outline (Fig. 7).

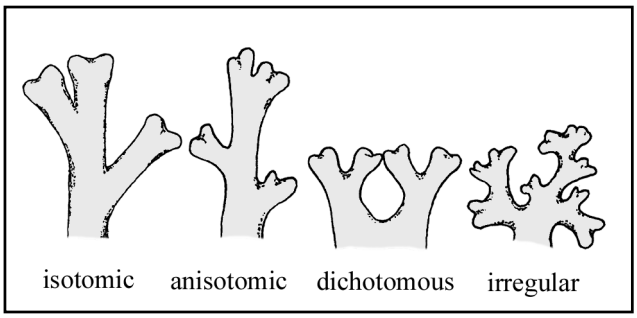

Fig. 6. Branching patterns in foliose lichens.

Margins of lobeswhich are smooth and without notches, lobes or teeth can be described as **entire**. **Irregular** margins are uneven. **Flexuous** margins are regularly bent in alternating directions. Their bending is more or less gradual and rounded. **Crenate** margins have rounded teeth. **Incised** lobe margins are deeply notched. **Dissected** lobes are divided or cut-up, into many tiny lobules sharply and deeply divided whereas **laciniate** (dim. lacinulate)

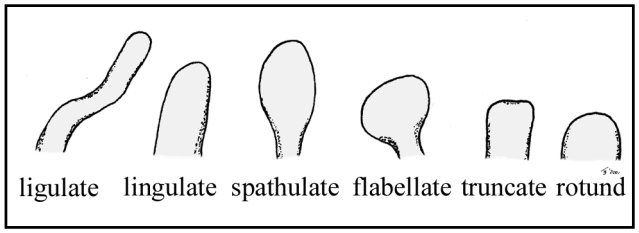

Fig. 7. Lobe shapes.

margins are irregularly divided into ± numerous often narrow and rounded lobules. **Lacerate** margins appear irregularly torn into ragged sections of unequal size (Fig. 10).

The axil between two lobes is generally referred to as the lobe **sinus**. **Sinuous** lobes are irregularly and shallowly waved in one dimension.

Recurved lobes are turned either up- or downwards. The term is usually applied to lobe tips of foliose lichens that turn back upon themselves, often exposing the medulla and/ or a sorediate undersurface. **Reflexed** lobes are turned and ± bent backwards along their margins. **Crisped** (Fig. 8) are intricately waved in both vertical & horizontal planes like the margins of kale. **Revolute** lobes are rolled outwards or downwards and **involute** lobes are rolled inward. Both form a ± tubular shape. Like involute or revolute lobes, **cucullate** lobes are also folded lengthwise but their lob margins become fused for some part along the lobe length. **Corniculate** are only partly rolled up and tapering towards the end, like in *Leptogium corniculatum*. **Inflexed** lobes are ± strongly curled downwards and **deflexed** lobes are abruptly bent downwards.

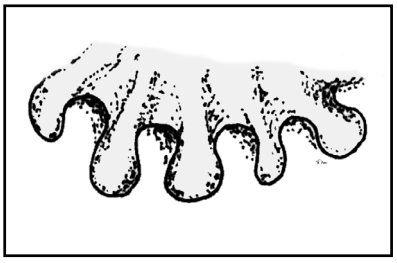

Fig. 8. Crisped thallus lobes.

The tips and/or the sinuses of lobes may have long hair-like projections called **cilia**. Unlike **rhizines** cilia project from the margin of the lobes or occasionally on the upper surface and not from the lower side. This distinction may be less evident in lichens where rhizines extend right to the lobe margins but cilia generally do not function as attachment organs. Cilia are usually long and thin, but in the genus *Bulbothrix* they are swollen at the base, a condition referred to as **bullate**.

A unique variation on the foliose growth form are **umbilicate** lichens, attached only at one central point by a short stalk called the **umbilicus** (Fig. 9, e.g. *Dermatocarpon* and *Umbilicaria*). Umbilicate lichens can be **polyphyllous**, with numerous subunits, but most commonly they are **monophyllous** consisting of a single ± orbicular lobe. Some monophyllous umbilicate lichens like *Omphalora arizonica* may become quite large.

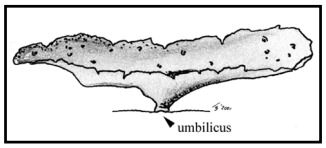

Fig. 9. An umbilicate thallus

Rhizine-like structures can frequently be observed on

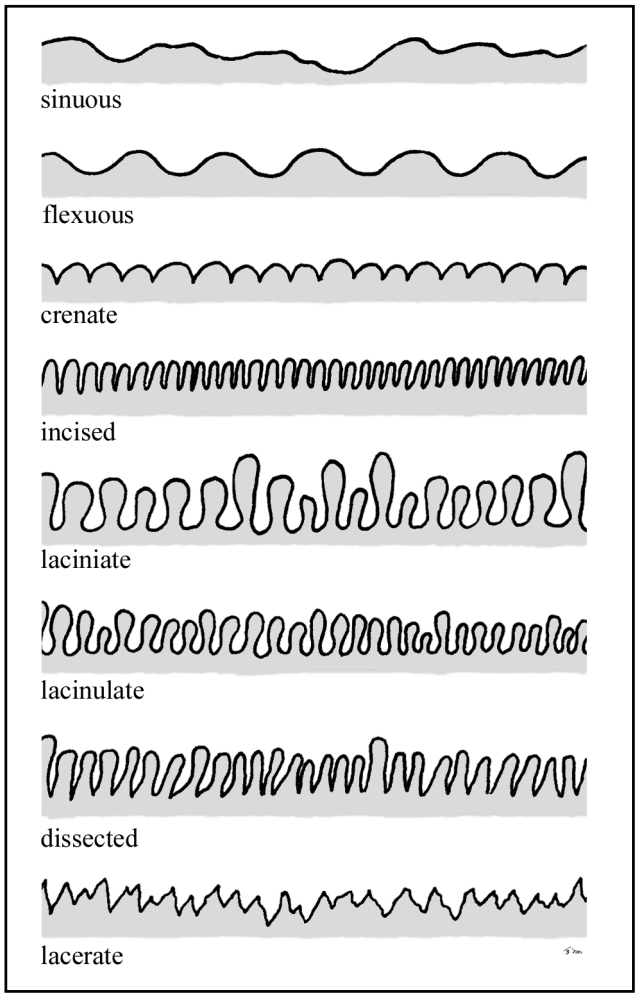

Fig. 10. Shapes of lobe margins.

the lower side of umbilicate thalli belonging to *Umbilicaria* or *Dermatocarpon* These structures do not function as attachment organs. They are therefore called **rhizinomorphs**. On the lower side of some thalli belonging to these genera plate-like, flattened lamellae called **trabeculae** may also be abundant. Like rhizinomorphs these trabeculae are formed from cells of the lower cortex. On the lower side of some *Umbilicaria* thalli granular structures composed of one to several pigmented, thick-walled fungal cells can be seen. These **thallospores** probably function as vegetative propagules of the mycobiont. They differ from other asexual lichen propagules by lacking photobiont cells. Thallospores are not produced in specialized conidiomata although they are often called **thalloconidia**. The umbilicate lichen genus *Lasallia* is characterized by **pustules**, large convex, blister-like bulges on the upper side, each corresponding to a depression in the lower surface.

Fruticose thalli

Fruticose lichens are bushy, shrub-like, tree-like, beard-like, or stalked (Fig. 11 and 12). They are usually attached to the substrate by a single holdfast. The branches of fruticose lichens are usually **circular** or **angular** in cross-section. In some groups branches may be more or less flattened and dorsiventrally orientated (e.g. *Ramalina*) but their internal structure is nevertheless ± radially symmetrical with a cortex on both sides and an algal layer all around the central medullary hyphae. These growth

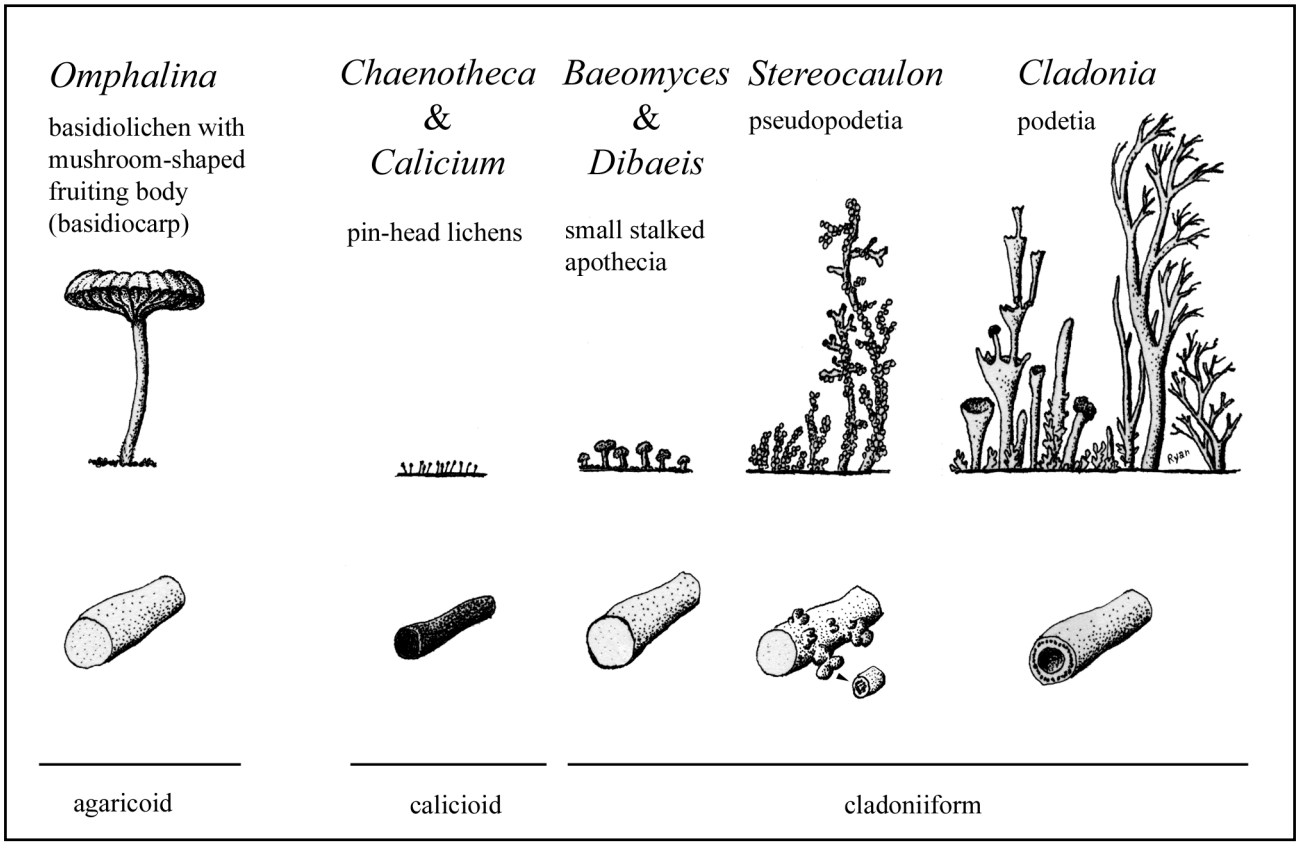

Fig. 11. Variation in thallus morphology; lichens with an erect fruticose, secondary thallus and a crustose or squamulose primary thallus (not drawn to scale: *Cladonia* and *Stereocaulon* can be several cm tall, Stalked fruiting bodies of *Dibaeis* and *Baeomyces* are less than a few mm and calicioid lichens are fractions of mm tall; The basidiocarps of *Omphalina* is usually less than 3 cm tall).

habits represent somewhat intermediate forms with foliose lichens.

Fruticose thalli are either ± **erect** or ± **pendent** (= **pendulous**). **Erect** lichens forming dense tufts or cushions are **caespitose**. **Decumbent** lichens are resting flat on the substrate, growing along the surface of the substrate and forming low cushions or rosettes. **Pendulous** lichens hang from their substrates and show little or no upright growth (Fig. 12). Lichens with many stout and thick branches at the base but acquiring a more slender and pendulous appearance at the tip are often referred to as **subpendent.**

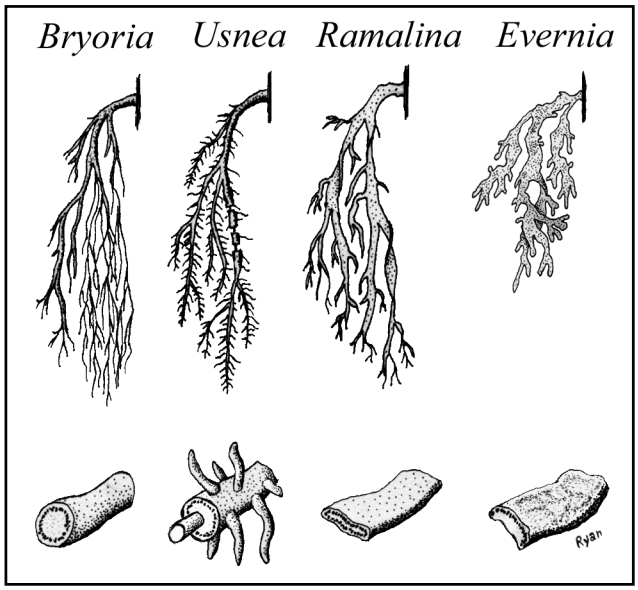

Fig. 12. Variation in thallus morphology of pendulous fruticose and subfruticose lichens.

The centers of branches usually have loose or dense hyphae, or in rare cases may be hollow. The genus *Usnea* is characterized by a **central strand** of densely and tightly interwoven hyphae. This central strand can easily be observed if the main thallus branches are gently pulled apart. The outer layers of the thallus thus break apart and the central strand is exposed.

Branches of fruticose lichens can be **subulate**, i.e. elongate and gradually tapering from a wide base to a sharp point like in *Cladonia subulata*. **Terete** branches are also elongate but they are ± evenly circular in cross-section. Terete branches are generally narrow and cylindrical and only very gradually tapering towards their tips. **Tortuous** branches are irregularly bending and twisting throughout. **Torulose** branches are cylindrical but with regular swellings at intervals. They are referred to as **moniliform** if they have a regularly beaded appearance. **Ventricose** branches are irregularly inflated or swollen in the middle or along one side. **Angulate** branches have distinct angles or corners as seen in cross section. These corners usually form sharp ridges running lengthwise on the outside of the branch. **Complanate** branches are flattened or at least compressed and **alate** branches have wing-like extensions along either side. They often have thin, angular ridges, e.g., in *Usnea*.

Like in foliose lichens branching patterns of fruticose lichens may be regular or irregular. **Furcate** ramifications are regularly forked into branches of approximately equal length. Furcate ramifications are often **dichotomous** with two regular and ± equal portions, as in the letter "Y". **Polychotomous** branching patterns refer to ramifications simultaneously divided into more than two branches. They can usually be found at the apex of a node. Trichotomous refers to equal branching of 3's and tetrachotomous to equal branching of 4's (Fig. 13).

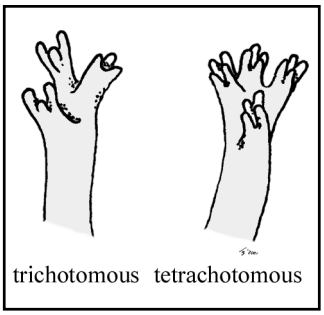

Fig. 13. Branching patterns in some fruticose lichens.

The overall branching pattern of a fruticose lichen may be **isotomic** if all side branches are equal in size and diameter. This results in a thallus without a single, distinguishable main axis. If the overall branching pattern is **anisotomic,** shorter and thinner side branches can be distinguished from a main stem or trunk. **Divergent** branches grow away from one another, usually spreading apart at a wide angle. They are referred to as **divaricate** if they branch perpendicularly. **Squarrose** lichens have sparse to numerous, generally short, ± perpendicular lateral branches. When densely and finely branched these lichens look like a pipe-cleaner or test-tube brush. **Filamentous** branching patterns result in a vine-like growth as in many species of *Bryoria* or some species of *Usnea*, where a short main stem is soon divided into subsymmetrical

branches, from which long secondary branches hang down almost parallel to each other. In contrast, **strigose** thalli of *Usnea* bear dense, short, hair-like projections and the whole thallus appears much more tufted.

A rich terminology describes the branching structures particularly in the genus *Usnea*. The **trunk** is the basal part or main stem of the thallus, which extends from the holdfast to the primary branches. **Branch segments** can generally be of various orders, e.g. primary (or main), secondary, tertiary, etc. The **ultimate segments** are the smallest terminal to lateral divisions. **Branchlets** are small, juvenile branches arising laterally from main branches. They are usually longer than **fibrils,** which are short, simple branchlets perpendicular to the main branches. A **spine** is a stout process with a sharp point and a **spinule** a small spine, constricted at the base where it may easily break off and function as a vegetative propagule.

The term **filamentous** not only refers to branching patterns. It is frequently applied to the growth form of fruticose lichens, which are entirely composed of very thin threads or hair-like strands. These fine threads usually grow ± prostrately on the substrate. Filamentous lichens are somewhat unusual because their overall structure is determined by threads of photobiont cells closely surrounded from mycobiont hyphae (e.g. some members of the Lichinales, *Coenogonium*, or *Cystocoleus*). More generally, however, the term has also been applied to *Pseudephebe pubescens*, where the filamentous structure is defined by the mycobiont.

Very small fruticose lichens are often referred to as **dwarf-fruticose** or **fruticulose**. Like caespitose lichens they usually grow in dense tufts or cushions but are much more minutely divided into slender branches – e.g. *Polychidium* and many members of the Lichinales, such as *Synalissa.*

Intermediate growth forms

Lichens are grouped as crustose, foliose and fruticose largely for convenience. There is no strict segregation of these morphologies and many intermediate forms can be observed.

Crustose thalli, that are lobed along their margins, show several transitions to foliose ones. **Effigurate** lichens are only obscurely lobed; whereas **placodioid** (= placoid) thalli are characterized by distinct, marginal lobes. **Rosulate** lichens have marginal lobes which are closely attached to the substrate These lobes are thickly crowded, distinct and sharply divided, but they rarely overlap. Many species of *Caloplaca* subg. *Gasparrinia* and *Lecanora* sect. *Petrasterion* belong to this group. In a strict sense only **lobate** lichens develop truly distinct, marginal lobes that are ± independent from the substrate and can therefore easily be removed. These lobes often overgrow one another, and often the central part of thallus becomes lobate as well. This can be observed in *Lecanora* subg. *Placodium*, especially the *Lecanora muralis* complex.

Subfoliose lichen thalli are only attached centrally by a few adhesion spots, that are easily loosened. They typically lack rhizines which are often found in foliose thalli. The central part of their thalli is often **lobulate**, i.e. crowded by minute, overlapping lobes. Marginal lobes of subfoliose lichens are frequently ascending and their medulla sometimes becomes very loose to hollow. This can be observed in *Lobothallia* species, *Lecanora garovaglii* s. l., and some species of *Brodoa* and *Xanthoria*.

The mere presence or absence or even the degree of the development of a lower cortex is taxonomically not significant and many closely related groups show transitional forms where the lower cortex is well or only poorly developed.

Areoles of crustose lichens that are not closely aggregated may become minutely lobed and these scales are more accurately referred to as **squamules**. Typically two growth patterns of **squamulose** lichens can be distinguished: (1) individual squamules may be attached only along one edge and tightly overlap like shingles of a roof. These squamulose lichens typically form densely **imbricate** thalli of minute squamules. On burnt wood and acidic bark some species of *Hypocenomyce* are quite common examples of this growth pattern. (2) More abundant in the Sonoran Desert is another growth pattern of squamulose lichens where individual squamules are typically attached with most of their lower surface and often widely scattered across open soils. Their squamules are often broadly rounded and typically less than 5 mm in diameter. They frequently form extensive mats composed of numerous squamules tightly attached to or even imbedded in their substrate. These mats can reach several cm across and occasionally even cover half a square meter. *Catapyrenium, Placidium, Psora* and *Toninia* are some of the more common lichen genera of squamulose soil lichens. They

often associate with free-living cyanobacteria and bryophytes to form extensive soil crusts which were probably much more abundant in the Sonoran Desert before the introduction of cattle.

Squamules, which are attached to the substrate with their lower side, exhibit transitions to the umbilicate growth form. **Gomphate** squamules have distinctly elevated margins but are still attached with a relatively broad central area whereas **peltate** squamules are minutely umbilicate ones attached only by a small holdfast. Individual squamules of peltate lichens are typically less than 0.5 cm across and therefore much smaller than the large thalli of umbilicate lichens. *Peltula* is a common genus of mostly soil (or rock) inhabiting, squamulose, gomphate and peltate species. In larger genera like *Gypholecia* and many species of *Rhizoplaca* the transition between peltate and umbilicate is less distinct and within large populations one can find extremes that would fit either the crustose or foliose category.

The squamulose growth form also intergrades with dwarf-fruticose lichens. Thalli that consist of rounded, ± erect and swollen squamules are referred to as **toniniiform**. Their squamules are often hollow and may also be interpreted as strongly inflated, bullate areoles. Thalli of toniniiform lichens are at most indistinctly radiate at their border as in many *Toninia* species or *Lecanora cavicola*. In **dactyliform** lichens individual squamules become finger-like and elongated. **Caulescent** forms are **substipitate**, i.e. their inflated squamules are becoming stalked. **Frutescent** forms represent transitions to fruticose lichens.

Subfruticose lichens are intermediate between the foliose and fruticose growth form. Lobes of subfruticose lichens are usually rather narrow and abundantly branched but ± flattened or channeled in cross-section. A distinct upper side with an algal layer and a lower side without may be distinguished. The lobe margins often curl for as much as one third of their length. Otherwise subfruticose lichens are usually prostrate and broadly attached at the center. Root-like holdfasts are often sparse or absent and frequently of intermediate length. Some taxa with ± distinctly dorsiventral thalli are usually included under foliose lichens, while other taxa with a more erect or pendulous growth habit are commonly treated as fruticose lichens. Subfruticose species of *Tuckermannopsis* are usually treated as foliose. *Pseudevernia* has species which are treated as foliose as well as ones which are generally regarded to be fruticose. *Evernia prunastri* and *Evernia-strum* species are commonly interpreted as fruticose lichens even though their branches are clearly dorsiventral with upper and lower sides.

Lichens that combine more than one growth form

Many lichens combine more than one growth form. **Cladoniiform** lichens have a basal granular or squamulose **primary thallus**. This primary thallus usually extends horizontally on the substrate and gives rise to erect stalks or branches referred to as the **secondary thallus**. The granular primary thallus may soon disappear and only the secondary thallus persists whereas the squamulose primary thallus persists even after the secondary thallus is fully developed.

In *Cladonia* itself the stalks of the secondary thallus are called **podetia.** They are usually hollow and are derived from the formation of reproductive structures like apothecia or pycnidia. Podetia therefore always bear either pycnidia or apothecia at their tips. In many *Cladonia* species podetia are cup-shaped bearing apothecia or pycnidia along the cup margin. Other *Cladonia* species have shrub-like podetia which may or may not bear squamules.

In taxa like *Dibaeis, Baeomyces* and *Stereocaulon* the upright stalks are **pseudopodetia** because they are thalline in origin and solid throughout. *Stereocaulon* has characteristic knobby side branches which contain photobiont cells and are called **phyllocladia**.

A unique group, which often has stalked apothecia, are the **calicioid** lichens. They are characterized by a crustose primary thallus, their fruiting bodies are often covered by a powdery mass of spores referred to as **mazaedium** and their fruiting bodies are frequently supported by a very thin and hair-like stalk. Calicioid lichens with distinctly stalked fruiting bodies are also referred to as **pin-head** lichens.

Lichens that are not attached to their substrate

Wandering lichens are globose balls that move with the wind like tumbleweed, because they are not attached to their substrate. They often assume more or less fruticose growth form although they are mostly derived from originally crustose, umbilicate, or foliose taxa. Some authors distinguish only recently detached **erratic** lichens

which clearly belong to the same species as their attached forms from **vagrant** species which are permanently separated from their ancestral taxa and are generally treated as distinct species (e.g., *Xanthoparmelia chlorochroa*). Erratic wandering lichens are mostly fertile whereas vagrant lichens are usually sterile.

Vegetative Propagules

Vegetative propagules are common among all growth forms of lichens and the various structures usually integrate both mycobiont and photobiont cells[1]. This is clearly of advantage because both partners of the lichen symbiosis can immediately establish a new lichen whereas sexual reproduction with spores requires the mycobiont to find suitable photobionts to establish a new lichen symbiosis. Vegetative reproduction, however, is asexual and the resulting populations are therefore clones. Mutation of the haploid mycelium, which may increase genetic variation, is probably quite rare (Fahselt 1996).

Vegetative reproduction (Fig. 14) in lichens usually involves some sort of fragmentation of the thallus or of thallus parts. **Fragmentation** of the entire thallus can be regarded as the simplest way but sometimes special **fragmentation regions** occur as narrow sections where branches easily break off. In *Bryoria* species some of the side branches break off when the wind moves the twigs from which the lichen thalli hang down. In *Usnea* lateral **spinules** probably have a similar function. They easily break from the thallus at their constricted base.

Soredia (adj. sorediate) are microscopic dispersal units of photobiont cells aggregated with loosely interwoven hyphae (Fig. 14). Soredia are *c.* 25-100 µm in diameter and always lack a cortex or pseudocortex. They usually form a powdery mass which easily separate from the thallus as a fine dust. Morphologically they can vary from a fine, **farinose** to a coarse, grain-like or **granular** powder. They occasionally aggregate in larger clusters called **consoredia**. Although soredia are usually white, they can also be greenish or pigmented. Soredia usually originate from the algal layer of a lichen and erupt from cracks or pores, or they develop from the disintegration of the cortex. **Diffuse** soredia cover large areas of the thallus without a definite pattern. The entire thallus of **leprose** lichens, such as *Lepraria*, is essentially a continuous layer of diffuse soredia. More often soredia are produced in clearly delimited structures called **soralia**.

Many different types of soralia may be distinguished. **Fissural** soredia occur along cracks on the thallus surface. **Capitate** soralia occur as a head-shaped, globose mass at the tip of lobes or rarely on the upper surface of lichen thalli. **Pustulate** soralia form as swellings beneath the cortex and eventually erupt into a soralium. They are also referred to as **erumpent**. **Labriform** soralia are lip-shaped along the apex or margin of thallus lobes. They usually form on the lower side of recurving lobe tips as in *Hypogymnia physodes*. Soralia may be **laminal** on the surface of the thallus, **marginal** along the thallus periphery or **terminal** on the tips of lobes or branches.

Goniocysts resemble soredia but are derived from a single photobiont cell closely surrounded by a paraplectenchymatous hyphal envelope (see thallus anatomy). Goniocysts are either formed in a distinctly delimited, often rounded **goniocystamgium** or they may form the vegetative thallus as in the basidiolichen *Omphalina* ("*Botrydina*").

Hormocysts are produced only by a few gelatinous lichens, such as *Lempholemma*. Like soredia they are composed of photobiont cells and fungal hyphae. Unlike soralia they do not form a powdery mass but they break into *gelatinous* clusters derived from a chain of cyanobacteria and associated fungal hyphae. Hormocysts are formed in distinctly delimited structures called **hormocystangia**.

Isidia (adj. isidiate) are minute outgrowths, which have similar internal organization as the entire lichen thallus. They are covered by cortical layers and often have an internal differentiation into photobiont layer and medulla. Rarely isidia develop from soralia and then the cortex may be poorly developed.

[1] Vegetative reproduction may be regarded as one form of asexual reproduction where both mycobiont and photobiont are distributed together. Other forms of asexual reproduction where only the mycobiont is distributed have been mentioned separately. Thallospores are part of umbilicate thalli and asexual reproduction from conidiomata is discussed as a separate chapter.

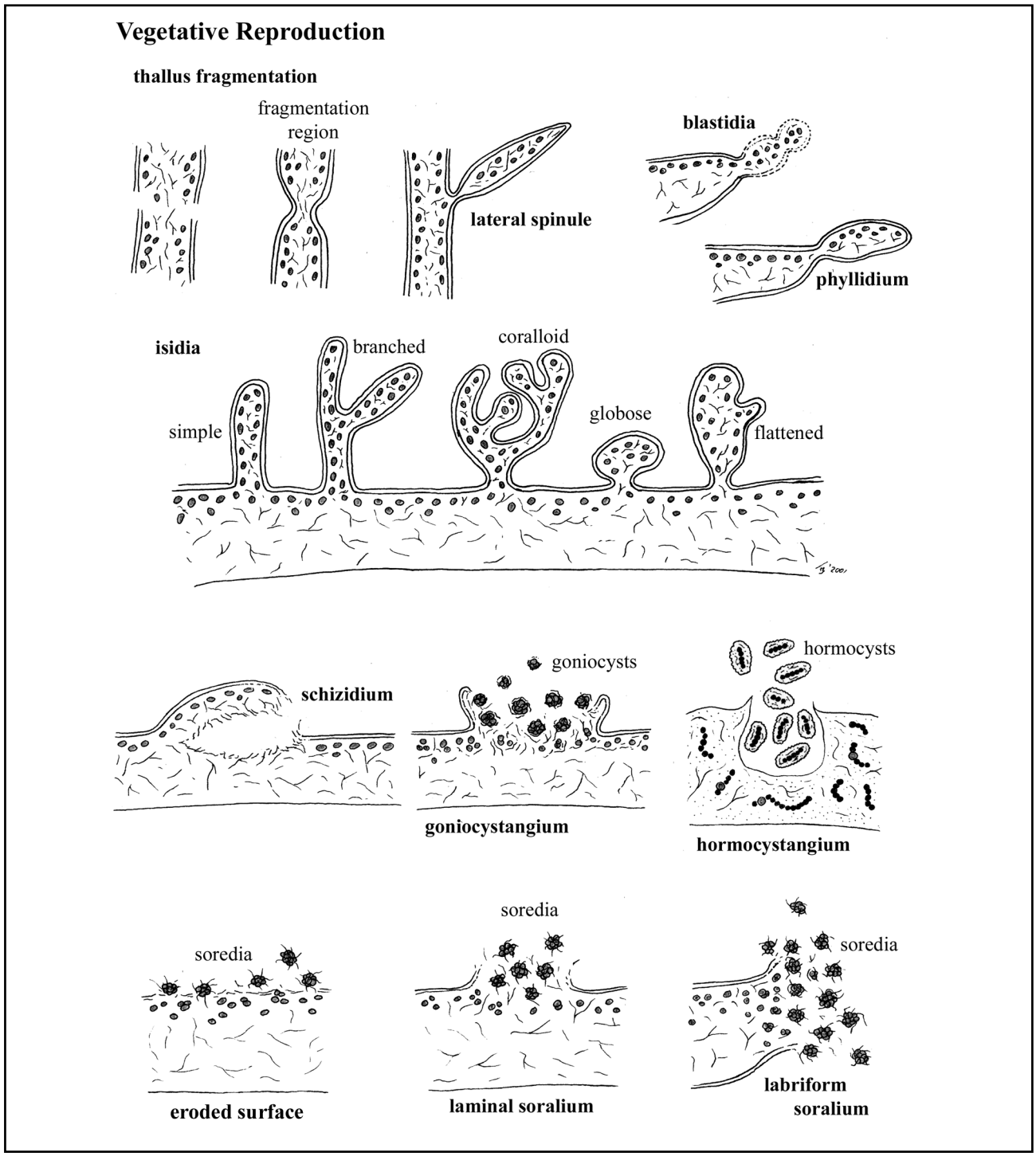

Fig. 14. Vegetative propagules, modified from Purvis et al. (1992), (not drawn to scale).

Some isidia lack a cortex at their tip and they are called **erumpent**, if they extrude thalline material from inside. Isidia are generally minute structures, mostly 0.01-0.03 mm in diameter and *c.* 0.5-1 [-3] mm long. True isidia function as vegetative dispersal units because they are only tenuously attached to the thallus surface. They are scattered over the thallus or confined to margins or ridges.

Isidia may have various shapes. They are usually **cylindrical** or **globular** and simple but may become sparsely **branched** or even **coralloid** (see Fig. 14). These elaborately branched isidia may develop from initially unbranched, simple isidia and the various stages of development are usually present on the same thallus.

Flattened isidia may develop into small scale-like lobes, which are often referred to as **phyllidia.** These lobes frequently develop along the margins or cracks. Structurally they are similar to the main thallus and sometimes the term is used interchangeably with **lobule**. Other isidia-like structures include the following (Fig. 14):

Schizidia resemble phyllidia but are formed by small parts scaling off the thallus surface. Their lower surface is therefore not covered by a thallus cortex and remains of the thallus medulla are usually attached as a residue. Schizidia are relatively rare and can be observed e.g. in *Fulgensia* or within the cups of *Cladonia pyxidata* s. str.

Dactyls (adj. dactylate) resemble swollen isidia. They are nodular, **clavate** (club-like) or broadly cylindrical structures and often open at the apex to expose the medulla. Dactyls sometimes produce soredia from their inner surface.

Blastidia are rounded, vegetative propagules containing mycobiont and photobiont cells. They are produced by a yeast-like "budding", often in series of two or more, with each new blastidium produced from the tip of the previous one. Cortical layers are usually less well developed around blastidia.

Other Surface Structures

Surface morphology of lichens may vary considerably among species or even across one individual thallus of the same species. Surface structures usually correlate closely with internal differentiation of the thallus, especially of the upper, cortical layers.

A **shiny** surface is usually the result of highly gelatinized cortical hyphae. A **dull** (= matt) thallus surface can be caused by non-gelatinized cortical hyphae, as well as dead cells or various deposits in or on the surface. Thalli that have a hoary or frosted appearance can be described as **pruinose** and granular white deposits on the thallus surface are referred to as **pruina**, which may be crystallized calcium oxalate, crystallized lichen substances or the remains of dead partially disintegrated surface cells. Lichens with a powdery surface are called **pulverulent**. Rough surfaces that have minute scales or other tiny projections are called **scabrous**. The term **scurfy** is sometimes applied for both scabrous or pulverulent lichens. **Pubescent** lichens have very fine **hairs** (much finer than cilia or isidia) on their thallus surface. Lichens without hair can be described as **glabrous**. A thick, crumbling surface is called **tartareous**.

A mottled appearance of the thallus surface may result from the presence of **maculae** (Fig. 15). They are small, rounded to irregularly elongated, pale spots. Maculae are caused by uneven thickening of the cortex and irregular distribution of photobiont cells below. Maculae are distinct from local discolorations, which are the result of pigments missing from the cortical hyphae. The thallus surface of maculae and surface discoloration remains intact although small cracks may develop in the cortex due to abrasion. Larger breaks in the thallus cortex are called **cyphelloids** (Fig. 15). Like maculae they are usually paler or more brightly colored than the surrounding thallus and probably facilitate gas exchange. Two types of cyphelloids can generally be distinguished. **Cyphellae** only occur on the lower surface in the lichen genus *Sticta* (and *Oropogon*), and are often imbedded in a tomentum. They are distinct recesses, sharply delimited, rounded or ovate, lined with a pseudocortex and surrounded by a pale ring. **Pseudocyphellae** are more widely distributed and characteristic for several different genera. They are plane to slightly convex structures where medullary hyphae break through the thallus cortex. They are less distinctly developed than true cyphellae but like cyphellae may be surrounded by a pale, less pigmented rim as in the genus *Pseudocyphellaria*. Pseudocyphellae occur in various shapes and can be found on either the upper surface (e.g. *Parmelia s. str*. or *Punctelia*) or the lower surface (e.g. *Pseudocyphellaria*) and on the thallus surface of fruticose lichens (e.g. *Bryoria* or *Cetraria*)

Raised surface features vary from rounded **papillae** (< 0.3 mm in diameter) to elongated ridges or **striae**. **Pustules** are larger (up several mm wide) than papillae. They

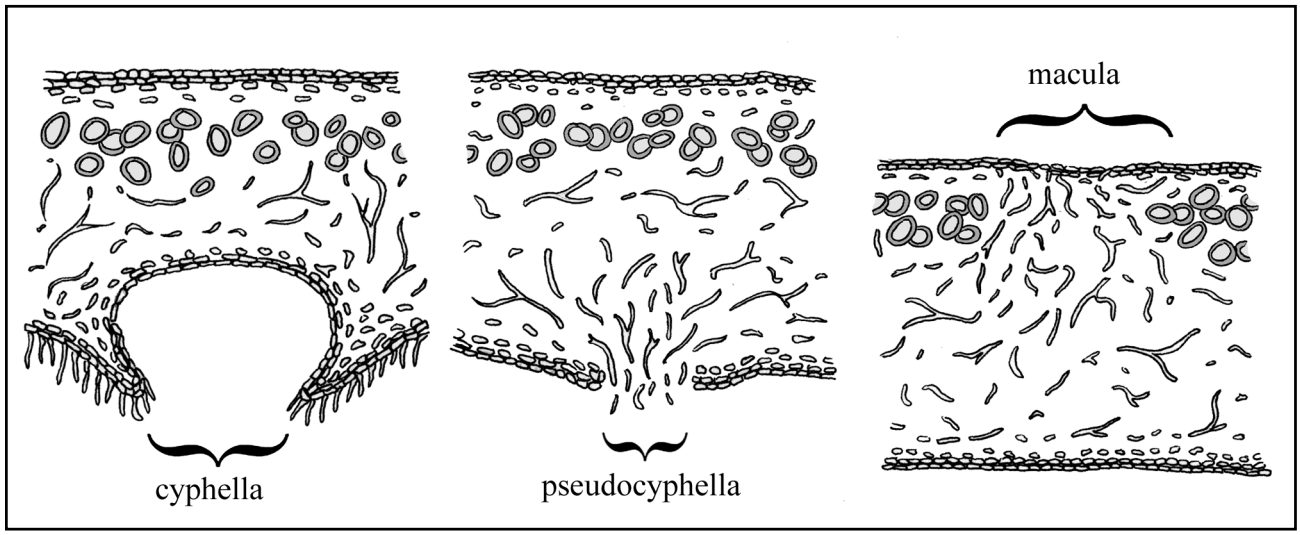

Fig. 15. The cyphelloids (cyphella and pseudocyphella), and maculae (not drawn to scale: cyphellae are usually in the range of several mm whereas pseudocyphellae and maculae are usually fractions of mm wide).

are convex, blister-like bulges on the upper side of foliose lichens, each with a corresponding to a depression in the lower surface. A **verrucose** thallus surface is characterized by **tubercules** or **verrucae**, which are relatively large (± 1 mm) and conspicuous, rounded, wart-like outgrowths.

The thallus surface can be **plane** (± flattened) or **undulate** (wavy). A **rugose** thallus has rounded wrinkles called **rugae**. They are usually evenly thickened unlike the irregular, net-like pattern of **veins** which are typical for the lower surface of foliose lichen species belonging to the genus *Peltigera.* Veins may branch and fuse, and may be pigmented. Some foliose and fruticose lichens develop a **tomentum**, a thick mat of hair-like hyphae particularly on the lower surface.

Unlike the deep irregular cracks of rimose and areolate lichen thalli, pits, depressions, channels and furrows may develop without causing a breaking of the thallus surface. A **foveate** (diminutive foveolate) surface is characterized by a honeycomb pattern of deep **lacunae**, separated by ± strong interconnecting ridges. A shallower and coarser pattern is called **scrobiculate.** Shallowly grooved or channeled depressions are called **sulcae**, as in *Parmelia sulcata*.

Unique surface structures occur in tripartite lichen symbioses where the lichen fungus associates both with green algae and cyanobacteria. **Cephalodia** are small, gall-like structures (0.5-1 mm wide) of cyanobacteria in a thallus predominantly inhabited by green algal photobionts. Sometimes they are externally formed as warty, squamulose or shrubby outgrowths of the thallus surface. However, in other lichens they form internally and can only be noticed as a discoloration or when viewed in thallus cross sections. Cephalodia are characteristic for a variety of lichen genera (e.g. *Peltigera*, *Lobaria*, and *Stereocaulon.*

Anatomy of the Lichen Thallus

Thallus anatomy of lichens varies extensively from highly differentiated thalli with several distinct layers of hyphae to ones with virtually no internal differentiation. Thalli can be classified as **homoiomerous** if the photobiont and the mycobiont are loosely interwoven and the photobiont cells are uniformly dispersed throughout the thallus (e.g. *Collema*). These thalli are usually unstratified, but in the genus *Leptogium* a thin single celled cortical layer occurs. Homoiomerous thalli are most commonly formed with cyanobacteria, and some of these lichens swell enormously if wetted with liquid water (due to its **gelatinous** structure). More frequently lichen thalli are

heteromerous, i.e. they are stratified into ± distinct layers, especially an **algal layer** which may be distinguished from one or more **cortical layers** and a **medulla**.

Thallus **consistency** can be described as **cretaceous**, if thalli are chalky due to abundance of calcareous particles (e.g. the medulla of *Schizopelte*). **Friable** thalli are fragile and brittle; **cartilaginous** thalli, somewhat stiff, firm and tough but are readily bent. Cartilaginous thalli may be translucent, and then are often referred to as **chondroid** (Fig. 16). **Flaccid** lichens are limp or flabby and **membranaceous** thalli are very thin and often **pliable**, i.e. capable of being bent without breaking. **Gelatinous** lichens are jelly-like, rubbery, sometimes slimy and often translucent. Thallus consistency reflects anatomical properties such as relative thickness and fragility or the degree of gelatinization, but these terms are relatively subjective. A more accurate description distinguishes how fungal hyphae aggregate inside the lichen thalli.

Plectenchyma of lichenized fungi

Fungi, unlike vascular plants, do not form true tissues or parenchyma. Their hyphae are arranged in "false tissues" called **plectenchyma**. Generally two types of plectenchyma have been described (Hale 1983). In **paraplectenchyma** (= pseudoparenchyma) separate hyphae cannot be distinguished and hyphal cells look ± isodiametric. This false tissue has an overall similar appearance to the parenchymatous tissue of vascular plants.

In **prosoplectenchyma** (= prosenchyma) separate hyphae can be distinguished but it may sometimes be difficult to entirely resolve the orientation of single hyphae within these false tissues.

The variation in fungal plectenchyma can be immense and various attempts have been made to describe this variety but the results are confusing because authors have not always distinguished clearly between plectenchyma texture and cell structure. Plectenchyma texture refers to the shape and orientation of hyphae within the plectenchyma. Cell structure refers to the cell lumina, cell wall and extracellular matrix. **Leptodermatous** hyphae have a thin inconspicuous cell wall with comparatively strong lumina. **Mesodermatous** cells are relatively thick-walled and usually have thinner lumina and **pachydermatous** cells are extremely thick-walled (Fig. 16). Especially in

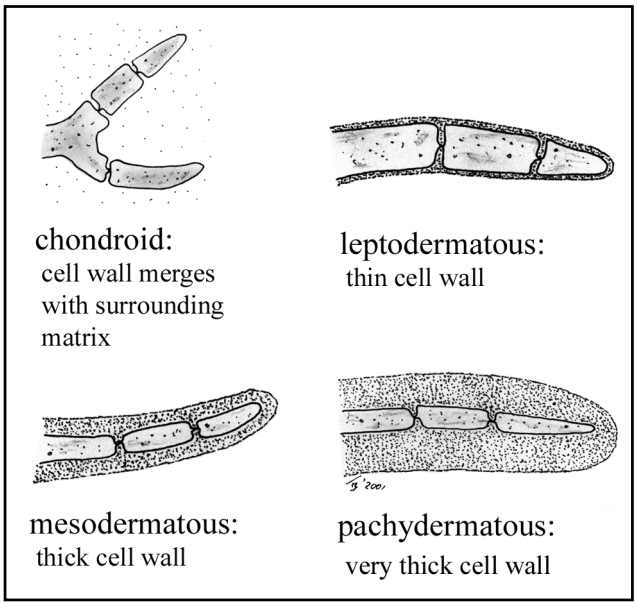

Fig. 16. Cell structure of hyphae.

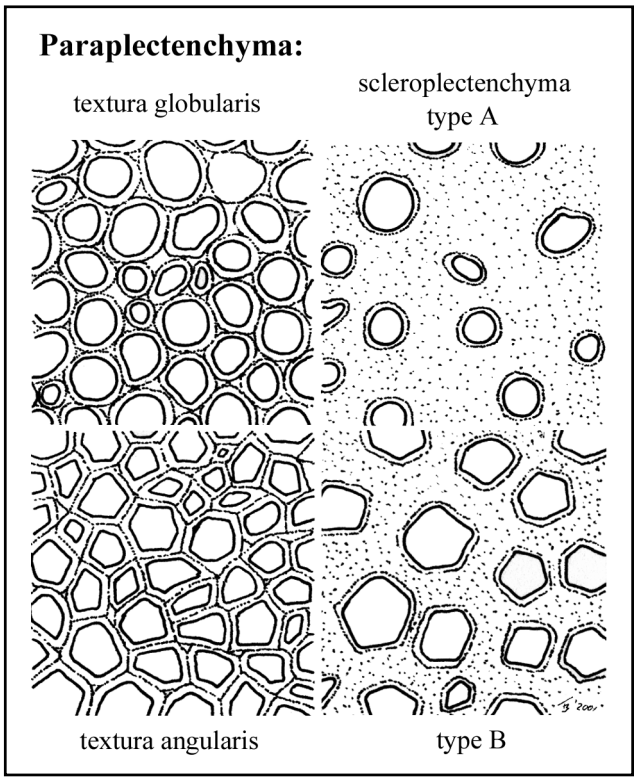

Fig. 17. Types of paraplectenchyma.

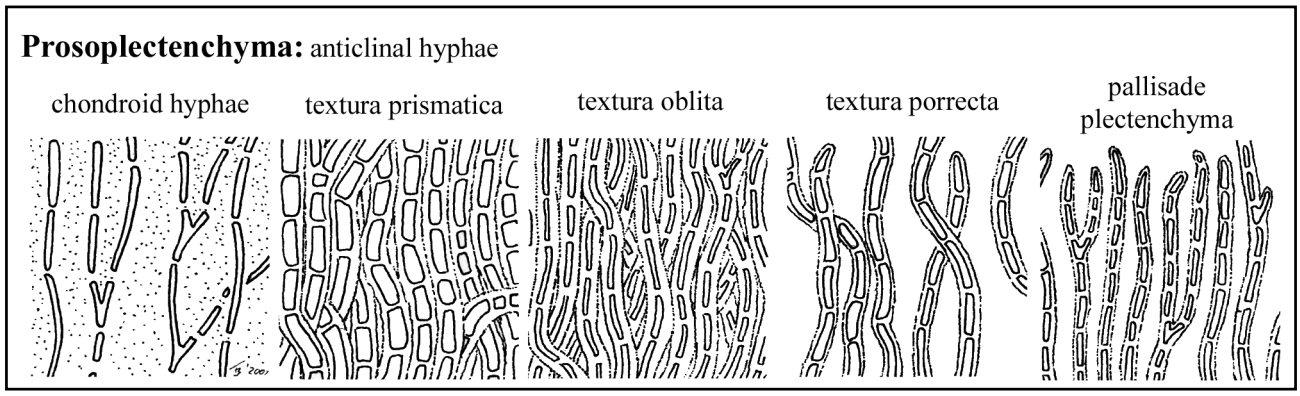

Fig. 18. Anticlinally arranged prosoplectenchyma.

gelatinous lichens it may frequently be difficult to differentiate a gelatinous or cartilaginous extracellular matrix from outer layers of the cell wall.

Several terms have been used to describe the huge variation in plectenchyma textures (Korf 1973). Paraplectenchyma in a strict sense (Fig. 17) are characterized by closely packed hyphae with little extracellular matrix. In **textura globularis** the ± isodiametric hyphal cells appear round. They are angular in **textura angularis** (Korf 1973). Yoshimura and Shimada (1980) introduced the term **scleroplectenchyma** (Fig. 17) for plectenchyma with ± isodiametric hyphal cells but frequently thick cell walls and hyphae which are widely dispersed in a gelatinous or cartilaginous extracellular matrix.

In prosoplectenchyma two general groups of hyphal textures can be distinguished: (1) **tightly packed** hyphae with little or no extracellular matrix and (2) **loosely interwoven** hyphae surrounded by large extracellular air spaces. Tightly packed prosoplectenchyma usually form distinct, dense layers (e.g. cortical layers). Loosely interwoven hyphae commonly form less distinct medullary plectenchyma. In gelatinous lichens a medulla cannot be observed but the widely interspersed hyphae are embedded in a thick gelatinous matrix (prosoplectenchyma *sensu* Henssen and Jahns 1974).

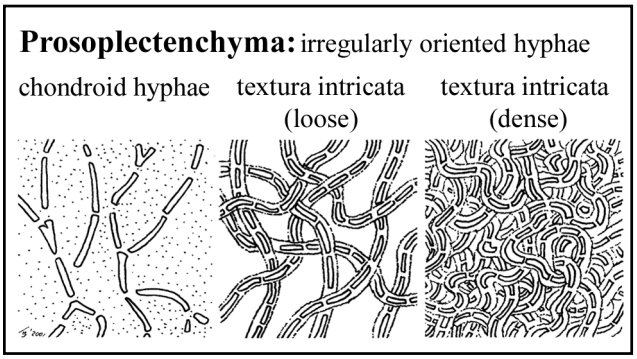

Fig. 19. Irregular arranged prosoplectenchyma.

Hyphal orientation and cell shape determines the texture of different prosoplectenchyma. In a wider sense prosoplectenchyma refers to textures of branched as well as ± unbranched hyphae. This includes irregularly interwoven hyphae as well as hyphae which run either horizontally (= **periclinally**) or vertical (= **anticlinally**) to the thallus surface.

In textura **oblita**, **prismatica** and **porrecta** (Fig. 18) hyphae are anticlinally interwoven. In textura oblita and prismatica the hyphae are tightly interwoven with little or no extracellular space. Textura oblita is characterized by mesodermatous and textura prismatica by leptodermatous cells. Hyphae of textura porrecta are loosely interwoven.

In textura **intricata** (Fig. 19), hyphae branch in an entirely disoriented pattern (Korf 1973). In a strict sense this term only applies to loosely interwoven hyphae with distinct interhyphal spaces. However, in the fruiting bodies of some lichens hyphae of irregular orientation frequently become tightly interwoven and interhyphal spaces less distinct. Yoshimura and Shimada (1980) only refer to these densely interwoven and irregularly oriented hyphae as **prosoplectenchyma**. They call loosely interwoven hyphae with a ± regular reticulate branching pattern **chalaroplectenchyma** and tightly adpressed parallel running

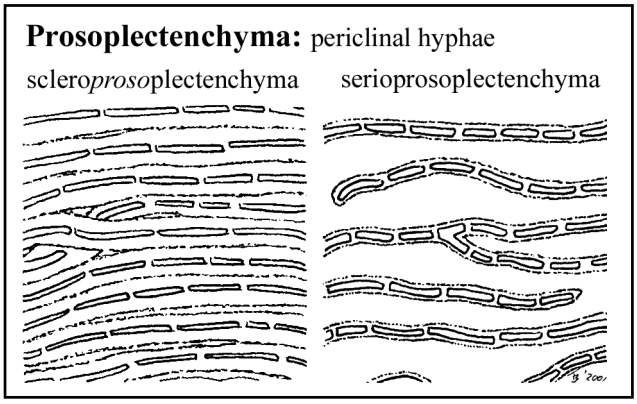

Fig. 20. Periclinally arranged prosoplectenchyma.

hyphae **sclero*proso*plectenchyma** (Fig. 20). Because of the "serial" orientation of single hyphae Yoshimura and Shimada (1980) suggest using the term **serioplectenchyma** (Fig. 20) for prosoplectenchyma with predominantly periclinal hyphae. Because of a cell arrangement similar to palisade parenchyma of vascular plant leaves they suggest the term **palisade plectenchyma** for textures formed predominantly from anticlinal hyphae. Palisade plectenchyma are commonly found in the sterile hyphae of the lichen fruiting bodies. They may branch apically in a fountain-like manner. This fountain branching is frequently also found in the false tissues of the thallus in the Lichinaceae.

Cortical layers

The surface of lichen thalli is usually delimited by hyphae which closely aggregate to form distinct **cortical layers**, that generally consist of compacted hyphae which may appear fibrous or cellular and are sometimes gelatinized. Because these layers are relatively hard, they provide mechanical protection and with their pigments or crystallized lichen substances provide sun-screen for the algae below. In a broad sense cortical layers refer to both a **true cortex** as well as other **corticoid** (= cortex-like) structures.

The term **pseudocortex** has been used for corticoid layers in various, often confusing ways[2]. Generally it applies to any poorly differentiated thalline boundary in which hyphae can be distinguished but do not aggregate into distinct fibrous or cellular fungal plectenchyma. A clear segregation from an ecorticate thallus is not always possible.

A **phenocortex** is a corticoid layer characterized by **necrotic hyphae** and residue of dead algal cells which faintly stain violet in **chlor-zinc iodine**. This emphasizes the development of the phenocortex from the algal layer below. The cortex-like structure is formed when cells of both fungus and alga die off and accumulate on the thallus surface. The resulting layer of dead organic material and dying cells may be quite thin but more commonly becomes thickened, horny and strongly gelatinized.

Unlike pseudo- and phenocortices, a **true cortex** or **eucortex** is formed from distinctly separate and actively growing plectenchyma. It refers to layers of living hyphae distinct from the algal layer below and therefore without algal cells or the remains of those. Especially in placodioid lichens (e.g. *Squamarina*) various distinct types of eucortices have been described (Poelt 1958).

In some lichens, especially members of the Parmeliaceae, a ± thin, homogeneous polysaccharide layer can be found on the surface of the cellular cortex. This amorphous layer is referred to as **epicortex**. It may be **pored** when viewed with the scanning electron microscopy, or **non-pored**.

An **epinecral layer** generally refers to any amorphous surface layer of dead organic residue. It may be present both on top of a phenocortex and a eucortex. Because of its amorphous structure is usually distinct from the necrotic cells of a phenocortex as well as the living plectenchyma of a eucortex. Frequently the epinecral layer is **hyaline** (i.e. clear) and is little differentiated. A thick epinecral layer may give the thallus a smooth, shiny or waxy appearance. It may become shallowly cracked and then appear dull white or strongly eroded and **pruinose**, especially when the calcium oxalate or crystallized lichen substances become exposed.

Not all lichen thalli are delimited by corticoid hyphae. Thalli that never form distinct layers of corticoid hyphae are **ecorticate**. In **decorticate** thalli cortical hyphae have been removed, eroded away, fallen off or decomposed.

[2] Degelius (1954) originally introduced pseudocortex for poorly differentiated cortical layers in *Collema* and *Leptogium.* Poelt (1958) coined the term "Scheinrinde" for poorly differentiated cortical layers in lobate *Lecanora* species. Weber (1975) initially translated "Scheinrinde" as pseudocortex but Poelt and Grube (1993) emphasized differences from a pseudocortex sensu Degelius (1954) suggesting the term phenocortex instead.

Morphology and Anatomy of the Fertile Structures

by F. Bungartz

As a result of fertilization ascomycetes produce meiospores (= **ascospores**) by free cell formation within a sac like structure called the **ascus** (pl. **asci**). Asci may be aggregated to various degrees in an **ascoma** (pl. **ascomata**). An ascoma may be a loose aggregation of asci or have a more complex structure and then is referred to as an **ascocarp**. More generally the ascocarp is also referred to as the so-called **fruiting body** of the lichen. However, not all lichens produce fruiting bodies. Some species appear to reproduce only asexually. Thallus structures, that aid in the vegetative dispersal of a lichen mycobiont and its photobiont, are described in the previous section and the formation of asexual spores (conidia) will be discussed in the following section. The current section focuses on the diagnostic characters of the fertile structures.

The terminology used to describe ascocarps is in disarray. Similar and almost identical structures were initially described with the same terms, but when their ontogeny was resolved it became evident that these structures often derived from different origins requiring the introduction of new terminology. The most influential concepts were Nannfeldt's (1932) classification according to the ontogeny of ascus structure and Luttrell's (1951 & 1955) classification based on ascocarp ontogeny. Much confusion stems from the attempt to integrate both concepts. The following discussion may clarify some terms without enforcing specific definitions. However, by no means can this account be exhaustive.

The Ascus

Distinct variation of ascus apical structures is an important diagnostic character for distinguishing lichen orders and families. Based on light microscopic observations of the ascus wall, two ascus types were initially proposed: the unitunicate and the bitunicate ascus. Ascus structure is closely related to the mode of ascospore release, and there is a wide variety of types of ascus dehiscence[3]:

(1) In **prototunicate** asci no ascus wall differentiation and no apical structures can be observed. The prototunicate ascus releases ascospores by a simple rupture of the ascus wall. Examples of lichen genera with prototunicate asci from the Sonoran Desert region are the common species of cyanolichens like *Lichinella, Lempholemma* and *Heppia* or less common lichens with stalked ascocarps like *Calicium* or *Chaenotheca*. It has been suggested that the more complex ascus types have evolved from the prototunicate ascus (Tehler 1990 & 1996a). However, recent studies indicate that in some groups prototunicate asci derived by reduction from more complex ascus types (Wedin and Tibell 1997, Schulz et al. 2001).

(2) In **bitunicate** asci two different wall layers have a distinctly different function (Fig. 21). Pressure ruptures the outer wall, the **exoascus** (or exotunica). When the exoascus breaks ascospores are ejected by expansion of

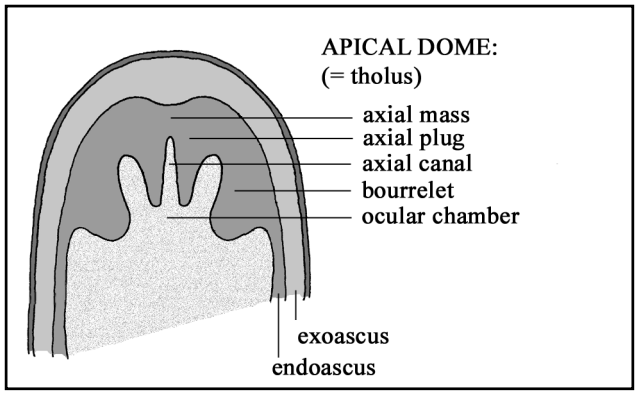

Fig. 21. The ascus apical dome (modified from Bellemère 1994).

[3] A different terminology was introduced by French mycologists following Chadefaud (Parguey-Leduc et al. 1994). From light microscopy observations of the ascus apical region the **"anneau"**, a complex ring-structure and the **"nasse axiale",** a basket-like structure have been used to describe the following ascus types: The "praearcheascus" without any differentiated apical structures, the "archaeascus" with both an apical "nasse" and ring structures the "nassascus" with only a nasse, and the "annellascus" with only an "anneau". This terminology has not been adapted by most other lichenologists. It came under scrutiny when transmission electron microscopy was first applied to study the lecanoralean ascus. Honegger (1978a) emphasized the necessity to use fresh specimens. She argued that the "nasse axiale" as well as the lamellae of the "anneau" appeared to be folds in the ascus apical region of dried herbarium material.

the inner wall called the **endoascus** (or endotunica). The explosive ejection of the endoascus is frequently referred to as "jack in the box". The asci are also referred to as **fissitunicate** because the two layers split apart to release ascospores. Many lichenized fungi have fissitunicate asci. Examples of Sonoran desert lichens can be found among *Arthonia, Opegrapha, Pyrenula* and *Verrucaria*[4].

(3) In **unitunicate** asci two wall layers can also be observed (Fig. 22. However, both layers function as a single wall and do not separate to release ascospores. Thus the term **non-fissitunicate** has also been suggested.[5] Non-fissitunicate dehiscence in a strict sense is more abundant among non-lichenized fungi. *Baeomyces* is an example of a lichen genus found in the Sonoran Desert region with non-fissitunicate dehiscence.

(4) The **lecanoralean** ascus type is the most abundant type in lichenized ascomycetes (Fig. 22). It is the characteristic ascus of the Lecanorales, which make up the vast majority of lichenized fungi. Initially the lecanoralean ascus was interpreted as functionally unitunicate, i.e. non-fissitunicate. However, a short **"arrested-bitunicate"** extension of the endoascus can be observed (Sherwood 1981, Honegger 1978a & b, 1982 Henssen 1981, Hafellner 1988). The exoascus wall ruptures and the endoascus expands into a short projection called **rostrum**. The endoascus only partially separates from the exoascus. This mode of dehiscence has therefore been called **semi-fissitunicat**e.

The lecanoralean ascus is characterized by a complex **apical dome**, which is a central apical thickening of the endoascus also referred to as the **tholus**. The internal structure of the tholus has been studied extensively with light and electron microscopy. It may be a rather simple

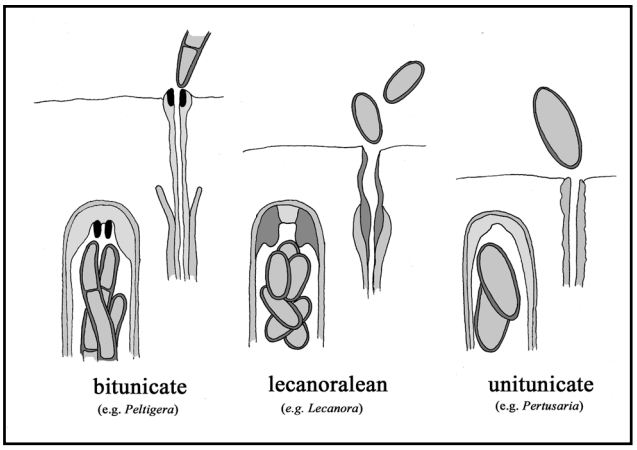

Fig. 22. Types of ascus dehiscence types (redrawn and modified from Honegger 1982, for more detailed information see also Büdel and Scheidegger 1996).

structure but more frequently becomes highly differentiated during ascal ontogeny. A central **ocular chamber** may extend from the ascoplasm into the center of the tholus. If the ocular chamber extends far into the apical dome it may become blocked by an **axial plug**. However, a thin **axial canal** may penetrate into this axial plug. The uppermost part of the plug is also referred to as the **axial body** or **axial mas**s. In cross section an apical dome with a well developed ocular chamber looks like a saddle, and the flanks on either side have therefore been called **bourrelet** (French: saddle)[6]. According to the reaction with **Lugol's iodine** (see chemistry recipes) various structures can be distinguished either by a positive, blue amyloid reaction, by a hemiamyloid red turning blue reaction or by the absence of any amyloid reaction. The structures thus distinguished provide important characters for the distinction of lichen families and genera (Hafellner 1984). The relative size of the tholus varies greatly during ascus ontogeny and according to Rambold (1989) and Rambold and Triebel (1992) the following general groups may be distinguished (Fig. 23):

[4] Grube (1999) observed that in *Verrucaria* ascus dehiscence does not follow the typical fissitunicate mechanism. The exoascus does not rupture but gelatinizes: "Gliding of ascus wall layers apparently occurs not along a distinct layer between exo- and endotunica but in an undifferentiated way in the gelatinized endotunica matrix." (Grube 1999, p. 245-246).

[5] Ascus wall structure is far more complex than the term "unitunicate" suggests and several additional types have been recognized by mycologists (Sherwood 1981). The **annular** ascus opens with a small central pore surrounded by a complex ring structure (the **annulus**). In **hypodermataceous** asci this annulus cannot be observed with light microscopy because the asci are extremely thin-walled. The **operculate** ascus has a much wider annulus covered by a hinged cap, the **operculum**. At maturity this operculum flips open to release the ascospores. **Ostropalean** asci are thin walled with a thick, non-refractive cap. Spores are released through a slender central pore, which penetrates the cap. In **pseudooperculate** asci the whole, thick apical cap breaks off from a thin lateral ascus wall.

[6] The lecanoralean ascus has been studied intensively by French lichenologists, who argued that it represents an evolutionary ancient type, therefore called **"archaeascus"**. This evolutionary concept has not been followed by most lichenologists. Honegger (1978a) argued, that the lecanoralean ascus is too complex to represent the most ancient ascus type but like the unitunicate ascus may have evolved from bitunicate asci. The terms lecanoralean or semi-fissitunicate are less ambiguous and are therefore be used herein instead of "archaeascus".

- The asci of the ***Lecanora-, Bacidia***- and ***Lecidella*-type** are characterized by a tholus, which is more or less amyloid throughout with a well defined non-amyloid axial mass. The ***Catillaria***-type, however, has no axial structures.
- The asci of ***Fuscidea***, ***Teloschistes*** and ***Umbilicaria*** react strongly amyloid on the outside and the tholus is more or less amyloid throughout. These asci have no axial structures but a well developed ocular chamber.
- Asci with a strongly amyloid central tube can be found in various genera. In ***Porpidia*** only the central tube is amyloid whereas the lateral tholus is not amyloid. The central tube of ***Lecidea***-type asci is reduced to an apical cap; otherwise the tholus is not amyloid. The ***Cladonia***-type is characterized by weakly amyloid flanks and a strongly amyloid central tube. In the ***Rimularia***-type the central amyloid tube is much reduced and separated from the strongly amyloid tholus by a non-amyloid part. In the ***Trapelia***-type the amyloid reaction of the cap as well as the lateral tholus is much less obvious.
- ***Peltigera***, ***Coccocarpia***, ***Collema*** and other cyanolichens with lecanoralean asci are also characterized by asci with conspicuous amyloid tubes.
- *The* ***Lobaria*-**type has more or less diffuse amyloid caps.
- Not necessarily related genera have a distinct tholus without amyloid structures, e.g. ***Nephroma***, ***Acarospora***, ***Tremolecia***.

These groups are by no means exhaustive and in some groups the tholus appears to be strongly reduced (e.g. ***Schaereria***-type). Many more types have been recognized (Hafellner 1984), but they are beyond the scope of this flora. Malcolm and Galloway (1997) also illustrate a variety of ascus types. Less schematic illustrations are given by Purvis et al. (1992). The dehiscence of various types has been illustrated by Büdel and Scheidegger (1996).

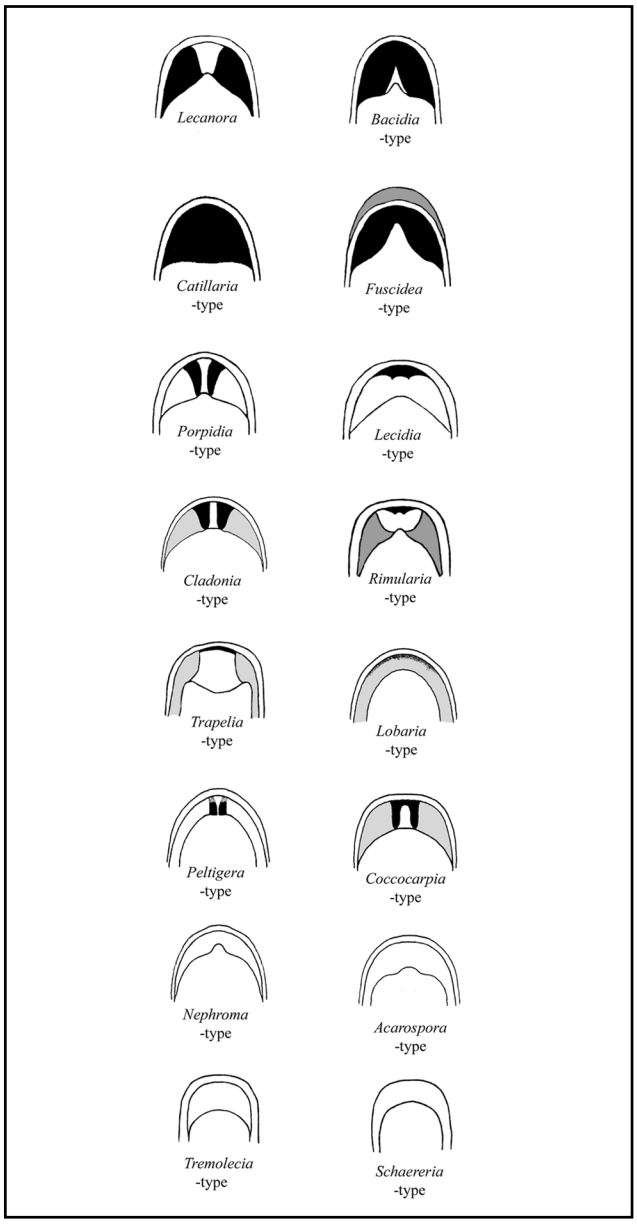

Fig. 23. Variation in ascus apical structure (black – strong reaction, gray – weak reaction with Lugol's iodine; redrawn from Rambold 1989 and Rambold and Triebel 1992).

The Ascospore

Typically eight ascospores are formed within an ascus. However, multiples of eight (16, 32 etc.) may occur. Some genera (e. g. *Acarospora* or *Polysporina*) even produce a hundred or more ascospores. Their spores are commonly rather small (some *Acarospor*a species have spores shorter than 2 µm). Lichen genera, which frequently produce less than eight spores, can also be found and their spores are usually very large (some *Pertusaria* species have spores more than 300 µm in length).

Ascospores are produced within the ascus by free-cell formation. The ascus membrane cleaves the **ascoplasm** and forms an **enveloping membrane system** (EMS) segregating **spore cytoplasm** from the surrounding **epiplasm**. Each spore is thus surrounded by two cell membranes. Between the membranes cell wall material is deposited. Three to four layers can usually be distinguished at high magnification of the light microscope (oil immersion, 1000x). Even more detail can be distinguished in the transmission electron microscope (Fig. 24). The outermost layer is the **perispore**. It is differentiated into an outer, amorphous mucilage and a dense, inner part. The mucilage can become very thick and then appears to surround the spore like a **halo**. During spore ontogeny the inner layer may develop conspicuous **ornamentation**. Between the perispore and the **proper spore wall** (or **epispore**) a narrow intermediate layer ca n be observed. This **intermediate layer** is usually visible only in strongly pigmented ascospores. In most spores the innermost layer is not the proper wall but a separate **endospore**.

Simple spores lack septa. Many lichenized ascomycetes, however, form distinct spore septa and the ontogeny of septum formation as well as the septum arrangement has been used to distinguish a variety of spore types (Fig. 25).

A **pseudoseptum** is a thin, protoplasmatic or vacuolar membrane similar to a septum but not formed from any parts of the cell wall. If only the endospore layer participates in septum formation, the septum has been referred to as **distoseptum**. Some authors interpret distosepta as originated without the formation of a septal spore plate (Nordin 1997). **True septa** (or **eusepta**) are formed by invagination along a layer referred to as the septal spore plate.

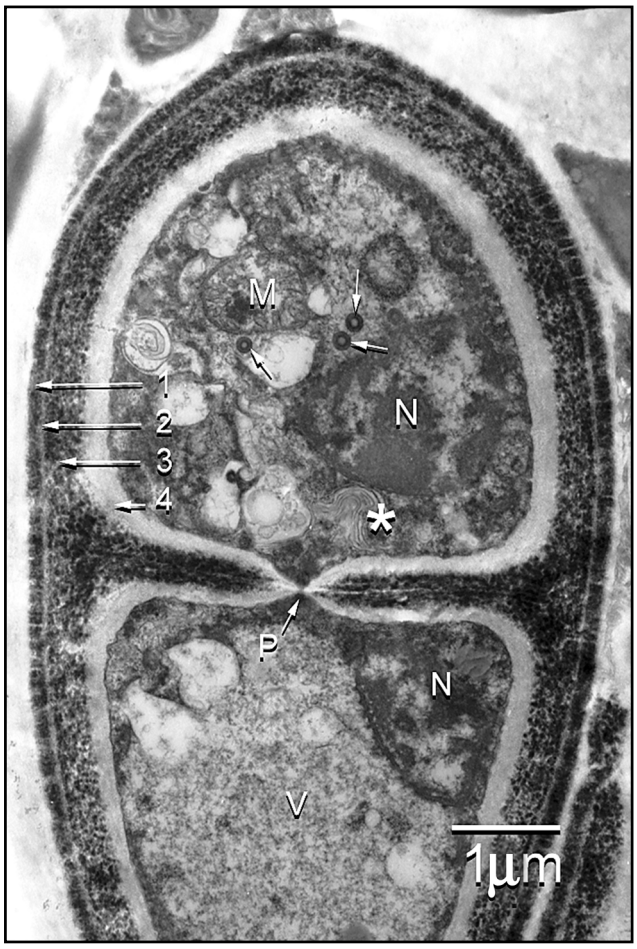

Fig. 24. Transmission electron micrograph of a one-septate ascospore of *Buellia dispersa.* Several spore wall layers can be distinguished: (1) perispore, (2) intermediate layer, (3) proper wall, (4) endospore. Cell organelles in the two ascospore cells are: M – mitochondria, N – nuclei, P – septal pore plug, V – vacuole. The arrows indicate concentric bodies a structure with unknown function, frequently observed in lichenized fungi.

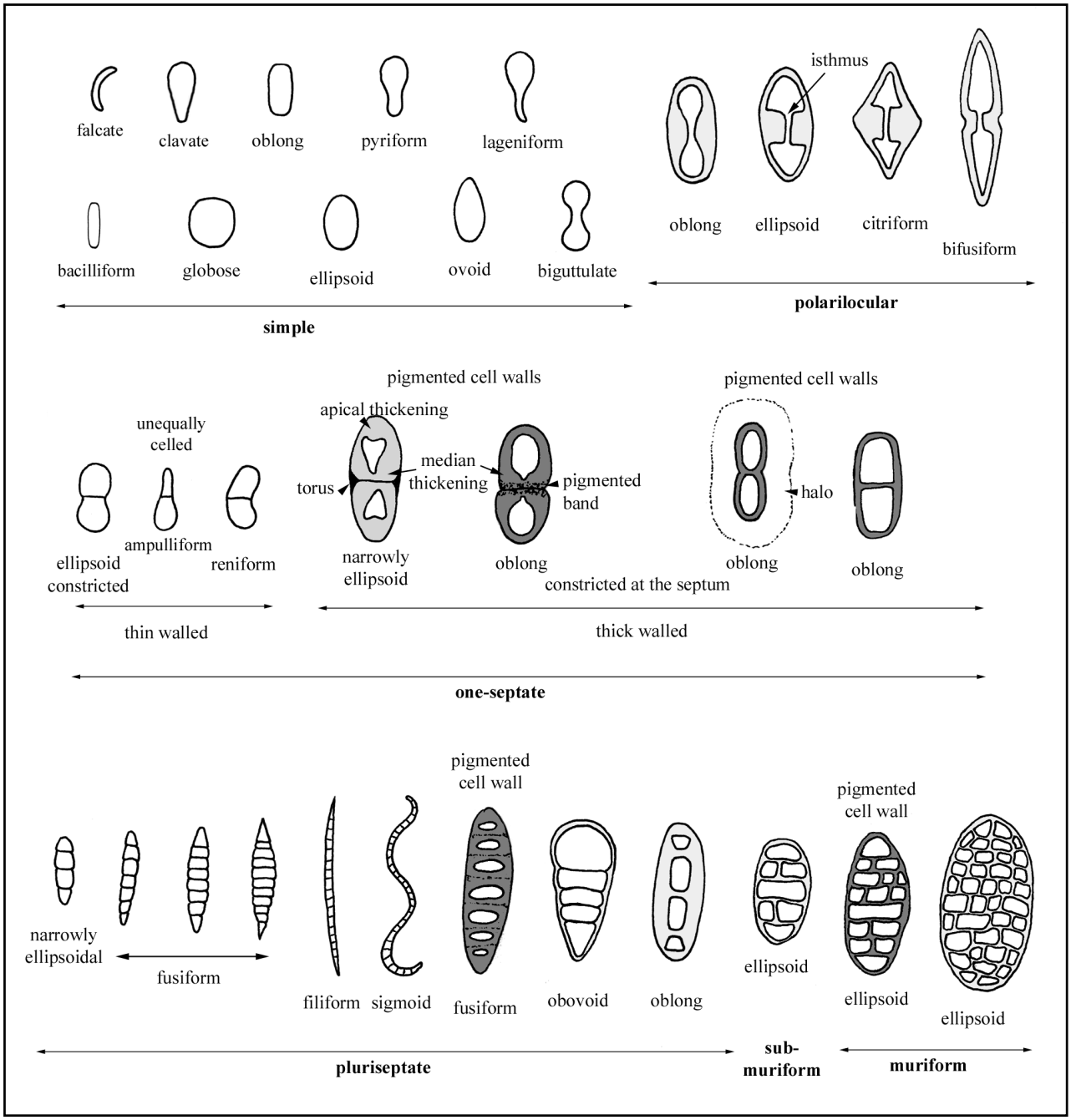

Fig. 25. Variation in ascospore structure, modified from Clauzade and Roux (1985).

Like the septa of ascomycetous hyphae, spore septa are characterized by a central **pore**, which can only be observed in transmission electron microscopy (Fig. 24). However, in *Physciaceae* an *Teloschistaceae* a thick **central canal** may be distinguished even with light microscopy. In *Teloschistaceae* the **central canal** usually remains visible during the entire spore ontogeny. The cells of the spore appear connected and are thus often referred to as **spore locules**. Only the endospore wall forms the septum of these **polarilocular** spores.

In *Physciaceae* the central canal often becomes very narrow and almost disappears. The spore septum is formed both by the endospore as well as the proper wall layer. It therefore must be interpreted as a true septum. Spores of *Physciaceae* are frequently characterized by the presence of a **torus**, a ring like, dark structure around the septum of the ascospore. However, this torus cannot be observed in the transmission electron microscope and the structure may be a light microscopy artifact.

Spores may be **one-septate** with only a single **transverse** (= **median**) septum. **Pluriseptate** spores have several transverse septa. Spores become **submuriform** if **longitudinal** septa are occasionally formed between the transverse septa. Truly **muriform** spores always have several transverse as well as longitudinal septa. Septa, that arise at an **oblique** angle, are called **angular** septa.

The Hymenium

Asci differentiate within a layer of fungal plectenchyma generally referred to as the **hymenium**[7]. In a **hemiangiocarpous** development the hymenium is initially covered by layers of hyphae, which disintegrate during the ontogeny of the ascocarp. It is not covered during all stages of a **gymnocarpous** development.

Only in very few cases are photobiont cells associated with the hymenium. These photobionts may either be **hymenial**, i.e. incorporated within the hymenium (e.g. *Staurothele* and *Endocarpon*), or **epihymenial**, i.e. on the surface of the hymenium (e.g. *Lichinella*). In both cases the photobiont cells are much reduced in size, closely associated with the mycobiont, and ejected together with the ascospores. The germinating ascospore will thus be provided with a suitable photobiont.

Within the hymenium, asci are usually surrounded by sterile hyphae generally referred to as **interascal filaments** or **hamathecium**. According to the ontogeny of the ascocarp, hyphae of the hamathecium may have a very different origin: (1) in the **ascolocular** development sterile hyphae differentiate prior to or during the formation of asci into **paraphysoids** or rarely into an **interascal pseudoparenchyma**; (2) in the **ascohymenial** ontogeny sterile hyphae arise secondarily as **true paraphyses** from below the asci, while **pseudoparaphyses** originate from above the asci. Above the hymenium pseudoparaphyses may later break apart and secondarily fuse with the hyphae below. In mature fruiting bodies pseudoparaphyses may thus not easily be distinguished from true paraphyses. The two ontogenies will be discussed in more detail in the following section on the ascocarp.[8]

In most lichen fungi the hymenium forms a distinctly defined layer. However the hymenium may form a **mazaedium**, if both the hamathecium and the asci break down into a powdery mass of spores and fragments of hyphae. Sonoran lichen genera with a mazaedium, (e.g. *Calicium*, *Chaenotheca*, or *Chaenothecopsis*), have minute stalked ascocarps; however, *Cyphelium* has a sessile fruiting body.

The Ascocarp

The dominant generation of filamentous ascomycetes is haploid. In fungi these hyphae are generally referred to as **somatic** rather than vegetative, a term preferably used in vascular plants. The lichen thallus is therefore largely made up from haploid hyphae. Fertilization of the female gametangium called **ascogonium** results in the formation of **ascogenous hyphae**. These generative hyphae are dicaryotic, i.e. they share two haploid nuclei, one female and one male nucleus. Ascal formation is the result of the fusion of the two nuclei and subsequent formation of ascospores. Ascogenous hyphae do not establish an inde-

[7] Traditionally hymenium used to be restricted to basidiomycetes. In ascomycetes **thecium** was originally used instead of hymenium. Modern literature, however, uses hymenium for both asco- and basidiomycetes.

[8] The distinction between paraphysoids and interascal pseudoparenchyma versus true paraphyses and pseudoparaphyses has rarely been followed meticulously and the hyphae are often loosely referred to as paraphyses. Unless the origin of the hamathecium is emphasized in a taxonomic treatment, sterile hyphae within the hymenium would be best referred to as interascal filaments.

pendent mycelium, but they are usually enveloped by layers of somatic hyphae. Both somatic and generative hyphae thus form the ascocarp and two different ontogenies can generally be distinguished:

(1) In the **ascolocular** ontogeny fruiting bodies arise from an **ascostroma**[9] formed by somatic undifferentiated hyphae. These hyphae differentiate into the a **primordium** by the formation of **locules**. As a result of fertilization of the ascogonium, generative, ascogenous hyphae grow into these pre-formed locules. The ascolocular ontogeny therefore begins essentially with the development of the somatic hyphae.
(2) In the **ascohymenial** ontogeny ascocarp formation initiates from the fertilized ascogonium. The primordium differentiates from the generative, ascogenous hyphae and somatic hyphae form secondary layers around this primordium.

The primordium of both ascolocular and ascohymenial fungi differentiates into the **centrum** (or carpocenter) of the fruiting body. In general, primary structures derived directly from the primordium can be distinguished from secondary structures which later envelop the fruiting body: (1) The inner envelope or **parathecium** differentiates directly from the primordium and (2) the outer envelope or **amphithecium** derives from the surrounding thallus hyphae. To which extent these two envelopes participate in the formation of the ascocarp may vary greatly and will be discussed in more detail below.

In non-lichenized fungi the entire ascocarp is usually seasonal. In contrast, most fruiting bodies of lichenized ascomycetes persist for years and new asci regularly arise within the ascocarp with each new season.

Structural Aspects of the Ascocarp: Apothecium vs. Perithecium

Two main types of ascocarps have generally been distinguished: (1) in an **apothecium** (pl. apothecia) the hymenium is exposed in an open disc at least at maturity[10], (2) in a **perithecium** the hymenium is not exposed during any stage of the ontogeny, but it remains enclosed in a round or flask-like structure which opens with a small, darkened pore, called the **ostiole**.

Both apothecium and perithecium strictly refer to fruiting bodies with an **ascohymenial** ontogeny and ascolocular fruiting bodies would thus have to be called **pseudothecia** (e.g. the ascocarp of *Roccella*). However, mature fruiting bodies of both origins can look very similar and especially in lichenized fungi intermediate ontogenies have also been described (Henssen and Jahns, 1974, and Henssen and Thor 1994: *Arthoniales*). In this flora we use the terms, apothecia and perithecia, in a broad sense including both ontogenies, although quotation marks are used when they are ascolocular.

Variations in Ascocarp Formation

The fruiting bodies of some *Lichinaceae* do not develop from a primordium. Generative hyphae arise directly within the somatic plectenchyma to form a fertile gall-like structure, the **thallinocarp** or the generative hyphae first develop into a pycnidium which secondarily differentiates into the mature ascocarp. This ascocarp is superficially very similar to an apothecium, but due to its origin it is called a **pycnoascocarp**. Within the Sonoran flora the thallinocarp is represented by the genus *Lichinella*. The pycnoascocarp is characteristic for the genera *Paulia* and *Thyrea*.

Fruiting bodies with the hymenium arranged in an elongated slit are referred to as **lirellae** (sl. lirella). **Lirellate** fruiting bodies may be derived from apothecia or from perithecia. They can be simple or branched in outline. Examples of lichens with lirellate ascocarps are represented in the Sonoran Desert region by the Graphidaceae and the genus *Opegrapha*. Also, some species of *Arthonia* have lirellate apothecia.[11]

The Apothecium (Fig. 26)

The most important diagnostic characters of apothecia are shape, color, texture, position on or in the thallus and internal structure. The internal structure may be derived

[9] A **stroma** is a compact somatic plectenchyma on which or in which fruiting bodies are formed. In lichens the thallus can essentially be interpreted as a lichenized stroma.
[10] However, in **poriform** (= **perithecioid**) apothecia the disc is almost entirely obscured by the margin of the fruiting bodies.
[11] Some lichenologists have used the term **hysterothecium** to refer to lirellate fruiting bodies. This term, however, was initially coined for the strongly carbonized lirellae of the non-lichenized ascomycete *Hysterium* and in a strict sense it only applies to this genus.

from various ontogenies and plectenchyma arrangement within the apothecium can be very complex. However, the ontogeny of the internal structure of the apothecium is frequently used to define diagnostic characters and therefore needs to be discussed in detail. In general an apothecial disc can be distinguished from the apothecial margin and hyphae surrounding the hymenium can be distinguished from hyphae below the hymenium. The distinction, however, is not always clear. Parts of the margin may be derived from the hymenium and thus the apothecial disc. Also, some hyphae below the hymenium may extend into the margin.

The Disc

The hymenium in apothecia frequently forms a more or less circular open **disc**. Lichen apothecia thus have also been called **discocarps** and lichens with apothecia are frequently referred to as **discolichens**. More generally they have been classified among fungi called discomycetes. Although initially suggested as a taxonomic group, it is now realized that the discomycetes are of polyphyletic origin.

The apothecial disc may be exposed, flat, convex or concave and then frequently deeply immersed in the surrounding thallus (e.g. *Aspicilia*) or even covered by membrane like structures (*Thelotrema*).[12]

The fertile part of the hymenium can either be continuous across the entire disc or it may be separated by hyphal layers of sterile, interascal filaments. In **gyrose** apothecia threse layers of sterile and fertile hyphae are circularly folded and the apothecium therefore has a brain-like appearance. In the Sonoran Desert gyrose apothecia can be found in the genus *Umbilicaria.*

A **columella** is an column-like aggregation of interascal filaments. Apothecia are called **umbonate** if the upper part of the columnella forms a distinct button-like **umbo** on the surface of the hymenium. Both structures occur in a variety of different genera.

In most discolichens the uppermost part of the hymenium is distinctively colored. This colored region is often called **epihymenium** even though it is not a separate, distinct layer of hyphae. The coloration may be caused by pigments within the hyphae or by extracellular caps or both. Frequently crystals can be **interspersed** as **episamma** between the paraphysal tips of the hymenium. These crystals can be of different size and they are often responsible for the **pruinose** appearance of the epihymenium. The term interspersed should not be confused with **inspers**, i.e. a hymenium where cellular detail is obscured by oil droplets or mucilage.

In a strict sense only very rarely a separate layer of hyphae will be differentiated above the hymenium of lichenized fungi. This separate plectenchyma on top of the hymenium should be called an **epithecium**. It must clearly be distinguished from the coloration referred to as **epihymenium**. It is unfortunate that few authors have followed this terminology in the strict sense and that some have even used both terms interchangeably.

The Margin

The **margin** surrounding the apothecial disc is not always obvious and may be almost entirely absent in some species. Frequently it is **excluded** during apothecium ontogeny, i.e. in **poriform** (= **perithecioid**) apothecia (e.g. *Pertusaria*) the disc is almost entirely obscured by the margin of the fruiting bodies. Like a perithecium, poriform apothecia open only with a minute pore. However, this pore is not homologous to the ostiole of the perithecium. It is pale and the pore opening is not darkened like the ostiole of a perithecium.

The margin of an apothecium can be concolorous with the thallus or the disc. This color is often consistent with internal differentiation of the hyphae but it may also obscure the structure of the apothecium. If the internal plectenchyma structure is continuous with the surrounding thallus this margin can be interpreted as evolved from thallus differentiation. Accordingly these apothecia have a **thalline margin** (Fig. 26). On the other hand it can be postulated that a structure, which is continuous with sterile hyphae of the hymenium originated from the differentiation of the fruiting body itself. This structure is therefore generally called the **proper margin** (Fig. 26)**.**

Another approach emphasizes ascocarp ontogeny. Two different layers differentiate around the centrum of the ascocarp, an inner envelope or **parathecium** and an outer envelope or **amphithecium**. Both layers are not necessarily represented in all fruiting bodies. Following different ontogenies the inner envelope can differentiate into the proper margin, or it remains poorly differentiated, or even becomes almost entirely reduced. The develop-

[12] For comparison refer to the discussion on the apothecial margin.

ment of the amphithecium also varies considerably. Frequently it may develop into the thalline margin, but it can also be much reduced even becoming devoid of algae.

Another term often applied to the apothecial margin is **exciple** (lat. excipulum). The term is often used as synonym for apothecial margin. Accordingly a **proper** (or

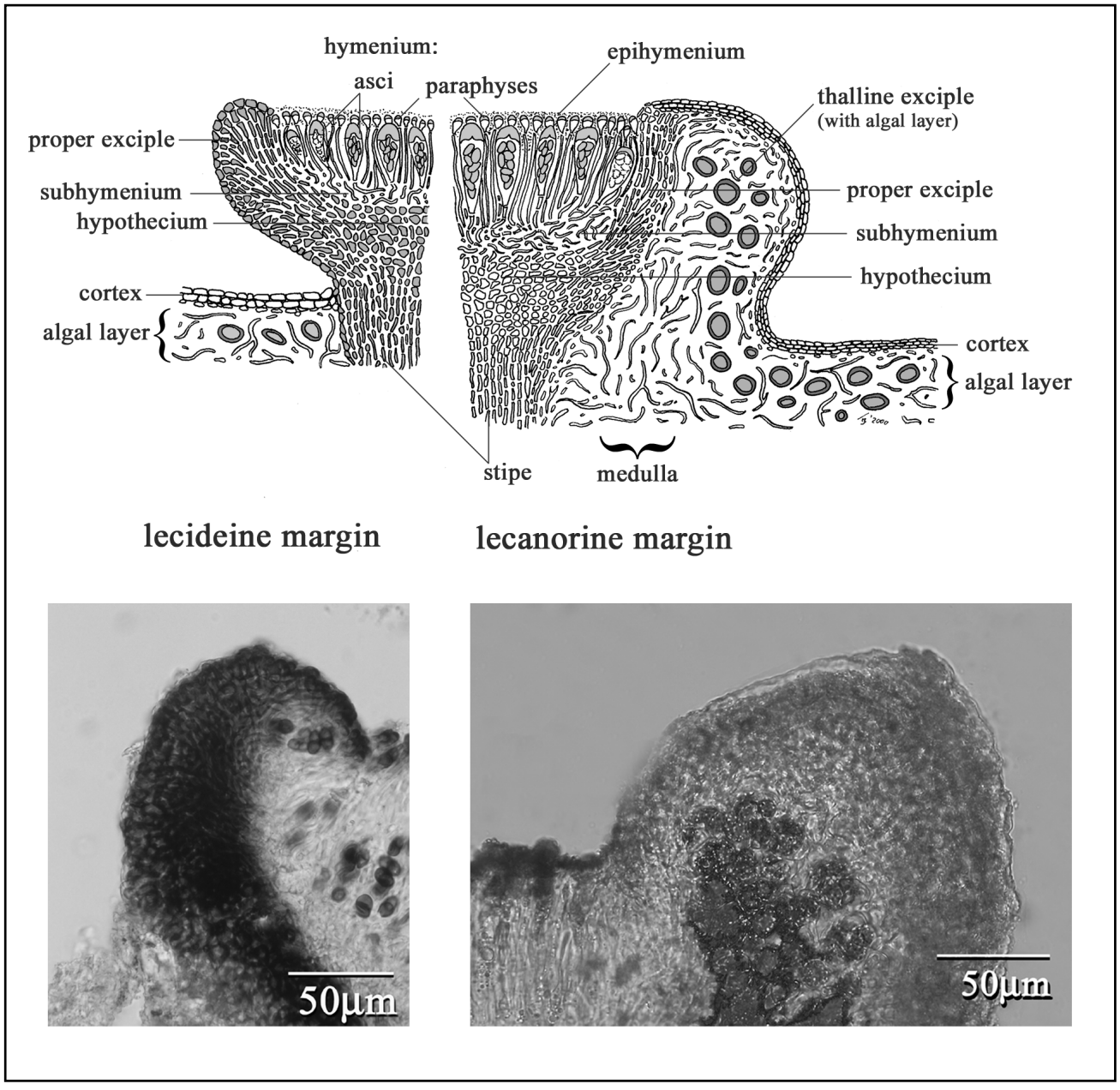

Fig 26. Apothecial anatomy; left – the lecideine, right – the lecanorine apothecium.

true) **excipl**e can be distinguished from a **thalline exciple**. The proper margin of an **annular** exciple does not extend below the hymenium but embraces it like a ring. A **cupular** exciple, however, extends below the entire disc and embraces the hymenium like a cup. In this case the term exciple not only refers to the margin but it is also applied to hyphae below the apothecial disc. The hyphae of a cupular exciple can be strongly black pigmented ("carbonized" like the exciple of *Porpidia*) or they may just be part of the same plectenchyma (hyaline cupular exciple of many genera in the Parmeliaceae).

Apothecia with a thalline margin (or thalline exciple) have been called **lecanorine** because they typically occur in *Lecanora*. Like the thallus a lecanorine margin will have algae incorporated within, and it will often be delimited by a cortex[13]. Apothecia with only a proper margin are referred to as **lecideine** or **biatorine** respectively, named after the lichen genera *Lecidea* and *Biatora*. Many species of *Lecidea* have a margin which is strongly pigmented throughout. In "carbonized" apothecia the proper margin is deeply stained by a dark blackish pigment. *Biatora* generally lacks dark pigmentation and a biatorine margin is thus not referred to as "carbonized". Biatorine apothecia have also been called **pseudolecanorine** (Dughi 1952). The distinction of lecanorine versus lecideine/ biatorine is not as clear as the terminology may suggest. Plectenchymata of different origin develop a mature apothecium and several terms have been employed to explain this diversity. Apothecia surrounded both by a proper as well as a thalline margin have be called **zeorine**. To specify that only the thallus cortex but not the thallus itself extends around the proper margin, the term **superlecideine**[14] has been proposed. **Eulecanorine** apothecia have a much reduced proper margin which is surrounded not only by a thalline cortex but also contains algae in the central part (Sheard 1967, Dughi 1952). In a **mycolecanorine** apothecium the reduced proper margin is surrounded by layers of thalline hyphae, which form a distinct cortex, but the algal layer only extends below the apothecium and does not enter the thalline margin.

Hyphal layers below the disc

The development of distinctly separate layers of hyphae below the apothecial disc may vary considerably. The asci arise into the hymenium from ascogenous hyphae, that form the **subhymenium**. Thus, the subhymenium is the initial layer immediately located below the hymenium. The ascogenous hyphae of the subhymenium are frequently not very pronounced, usually unpigmented and sometimes difficult to distinguish from a more distinct layer below called **hypothecium**.

The hypothecium may extend into the apothecial margin becoming part of the **cupular exciple**, or it may extend far down into the thallus, and thus form a **stipe**[15]. In several lichens the stipe elongates and lifts the apothecium from its substrate. This structure, which truly originates from the fruiting body is called **podetium** (pl. podetia). In the genus *Cladonia*, algae are subsequently incorporated into the podetium. They are absent from the podetia of *Baeomyces*. Minute, stalked fruiting bodies also occur in *Chaenotheca* and *Calicium*. In these genera the apothecium can be divided into the stalk itself and the globose or lens-shaped top, the **capitulum**. In both genera the stalk is part of the apothecium and thus a true podetium.

A **pseudopodetium** is a very similar structure but of thalline origin. Pseudopodetia occur for example in the genus *Stereocaulon*.

Sessile apothecia are initially immersed but very early in their ontogeny become free from the surrounding thallus. They are either **distinct** on the thallus surface or **adnate**, i.e. closely appressed to the thallus. In sessile apothecia the margin will usually be **persistent** if the disc remains more or less flattened. If the disc rises and becomes strongly convex with age the margin is usually pushed below the fruiting body and thus becomes **excluded**.

Other apothecia only partially emerge from the thallus or even remain deeply immersed during their whole ontogeny. **Immixt** apothecia are separate from the surrounding thallus, but they do not rise above the thallus surface. Concave apothecia with a deeply immersed disc have been called **cryptolecanorine** or **aspicilioid**, (named after the genus *Aspicilia*). Both proper and thalline mar-

[13] For the distinction of a pseudocortex and a eucortex see the chapter on Morphology and Anatomy of the Thallus.

[14] The margin of a superlecideine apothecium has also been referred to as **pseudoexciple**.

[15] Henssen and Jahns (1974) and Henssen (1995b) clearly interpret the hypothecium as part of the cupular exciple while Roux et al. (1993) and Letrouit-Gallinou (1968) differentiate the hypothecium as a distinct layer above the cupular exciple.

gins may be greatly reduced and the hyphae are often not clearly differentiated from the surrounding thallus. However, immersed apothecia frequently display a well developed margin along the edge of the thallus areoles. Towards the center of the thallus no margin may be distinguished and the apothecium then displays an **incomplete margin**.

The internal differentiation of the various plectenchyma types may be obscured by crystals. The size, position and structure of these crystals can be best observed with polarized light. These characters have especially been emphasized in the taxonomy of the large genus *Lecanora*.

The Perithecium

In a perithecium (Fig. 27) the hymenium is enclosed in a flask-like structure, which is also called a **pyrenocarp**. **Pyrenocarpous** lichens are thus frequently referred to as **pyrenolichens**, or more general as pyrenomycetes. Like the discomycetes pyrenocarpous ascomycetes do not represent a taxonomic group; they are polyphyletic. Ascospores are always released from a perithecium through a darkened apical pore, the **ostiole.**

The initial ontogeny of perithecia and apothecia is very similar. The primordium may be derived either from an ascolocular ascostroma or in the ascohymenial ontogeny directly from the ascogenous hyphae. In lichenized fungi both ontogenies are not clearly differentiated and further studies may be necessary.

The primordium of a perithecium differentiates into a centrum (or carpocenter) usually surrounded by a **perithecial envelope**. The inner envelope is homologous with the **parathecium** and it is thus also called the **proper exciple**. In lichenized ascomycetes perithecia develop within the surrounding thallus, which may form a second, outer envelope homologous to the amphithecium (or thalline exciple) of an apothecium.

The degree to which perithecia emerge from the thallus and the development of the two envelopes varies greatly. The thalline envelope can develop into a distinct outer layer around the perithecium or be confined to the

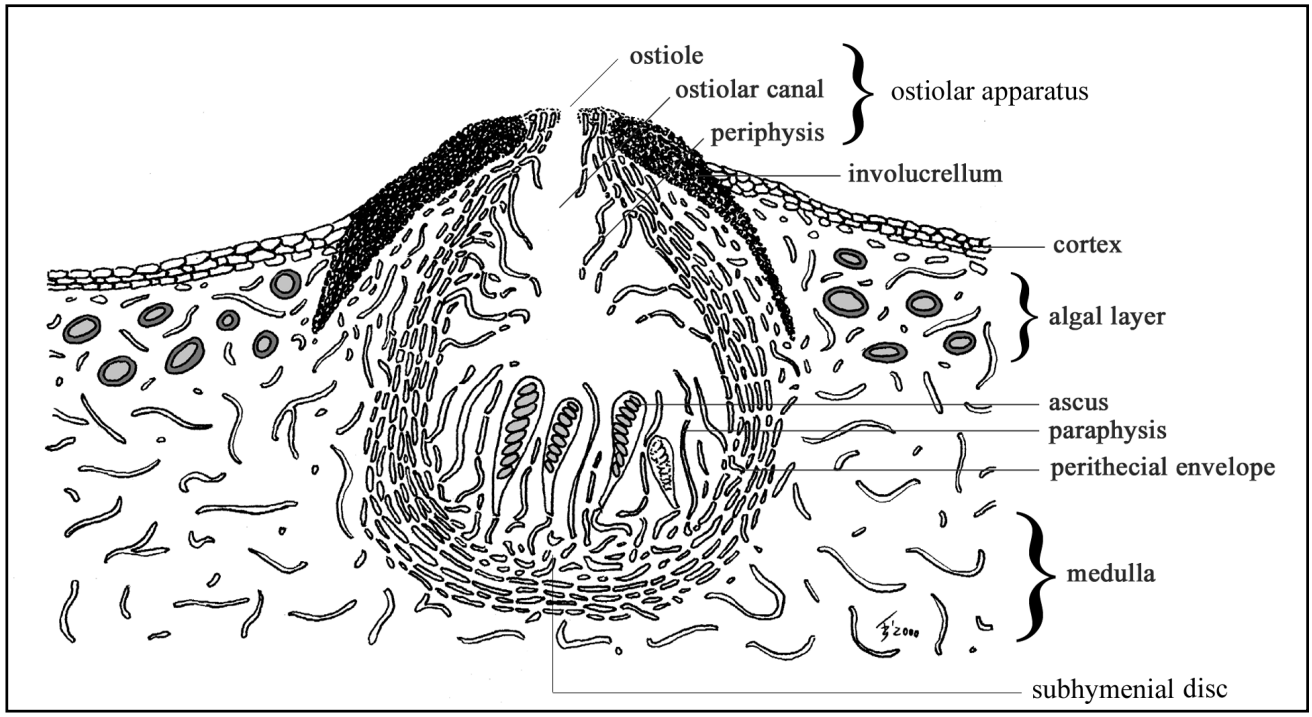

Fig. 27. Anatomy of the perithecium.

upper parts of the perithecium, where it may become confluent with the surrounding thallus. Like the cupular exciple of an apothecium the inner envelope of a perithecium always surrounds the whole centrum. It can either be hyaline (= colorless) or carbonized like the lecideine exciple of an apothecium. This **carbonaceous** pigmentation may extend all around the perithecium, or only down the sides, or just be confined to a ring around the ostiole.

The asci of a perithecium arise from the lower half of the inner envelope, called the **subhymenial disc**. Accordingly the upper half of the inner envelope is often referred to as **subhymenial bell**. It may differentiate into a simple ostiole or a complex **ostiolar apparatus**. An **ostiolar canal** penetrates the ostiolar apparatus from the central cavity of the perithecium. This canal may be lined with sterile hyphae called **periphyses**.

The surface of perithecia is frequently covered by a shield-like stromatic[9] layer called the **clypeus**. This shield may cover a single perithecium or it extends across several apothecia. Although clypeus is a general term for any shield-like structure which covers a perithecium (or even pycnidium) the term is frequently applied specifically to a structure which incorporates tissue of the phorophyte, i.e. the plant on which the lichen grows. In lichens a clypeus is thus found only in endophloeic crustose pyrenolichens, which inhabit the outer layers of the bark of a tree.

More familiar to most lichenologists is the term **involucrellum**. Like a clypeus it is a collar-like structure around the ostiole of a perithecium. However, neither the substrate nor the tissue of the phorophyte is incorporated, and the involucrellum always surrounds only the ostiole of a single perithecium[16]. The involucrellum is frequently carbonized like the proper envelope. Both plectenchymata merge around the ostiole. However, the proper exciple of the perithecium envelops the entire fruiting body whereas the involucrellum usually spreads out like a shield or collar and does not extend far beyond the lower half of the fruiting body.

[16] The involucrellum differentiates from an **epicentral cone**, a plectenchyma which can be observed during perithecium ontogeny above the proper envelope of the perithecium.

Morphology and Anatomy of Conidia-Producing Structures

by F. Bungartz

A **conidium** (pl. conidia) is a specialized, non-motile fungal spore, which is not developed inside a sporangium by cytoplasmatic cleavage[17] but externally from specialized **conidiogenous cells**. Conidia may be subglobose, bacilliform, ellipsoid, falcate, sigmoid, or filiform to thread-like. They are usually simple, non-septate and colorless but can rarely be branched, septate or even be pigmented.

The role of conidia has been the subject of much debate. Most conidia probably germinate in a suitable environment, and thus reestablish a lichen symbiosis with an appropriate photobiont. These conidia function as **diaspores**, i.e. for the asexual dispersal of the lichen fungus. However, some may function both as asexual spores and as the male gametes. If these sex cells are no longer able to germinate they are referred to as **spermatia** and it is now generally assumed that fungal spermatia are evolutionary reduced from conidia (Alexopoulos et al. 1996). In several lichen genera spermatia have been observed to attach to specialized female hyphae (Honegger 1984). In this mode of sexual reproduction the female structure is the **ascogonium** which receives the male gamete via an elongated fungal hypha called **trichogyne**. Fertilization of an ascogonium from a specialized conidium may be the most common form of sexual reproduction. However, because of their polyphyletic origin, some other modes, which are common in non-lichenized ascomycetes may also be represented in lichen-forming fungi[18].

The asexual morphotype of a fungus is called the **anamorph**. Imperfect fungi only reproduce asexually. For most imperfect fungi it is a challenging task to establish its sexual counterpart, the **teleomorph**. In some cases the teleomorph may have become extinct, and for non-lichen-

[17] Unlike ascospores or sporangiospores several conidia are thus not enclosed by a separate wall but they form chains of cells which easily break apart.

[18] In general four different processes of sexual reproduction have been observed in ascomycetes: (1) two unspecialized somatic hyphae fuse (somatogamy), (2) two morphological similar gametangia fuse (gamiotangiogamy), (3) the gametangia are differentiated in a male antheridium and a female ascogonium, or (4) the **antheridium** releases a male spermatium which fertilizes the female ascogonium via a long hyphal structure called the trichogyne.

ized fungi the Botanical Code (Greuter et al. 1993) therefore accepts separate names for the sexual and asexual morphotypes. But this is not allowed in the lichenized fungi. Lichens very rarely reproduce only from conidia. Even then their thallus morphology and chemistry are very similar to that of its teleomorph counterpart. In most cases conidia-producing structures can be found on the same thallus as lichen apothecia or perithecia. Lichen anamorphs thus cannot be named separately. Furthermore, in several lichen genera such as *Lepraria* or *Leproloma* neither fruiting bodies nor conidia have been found and these genera are thus imperfect lichens.

The size and shape of conidia varies considerably, and in some lichen species more than one type of conidia may be observed. **Microconidia** may be less then 1 x 0.5 µm. They are usually thin-walled, subglobose to bacilliform and have scarcely any protoplasm. It is thus likely that they have lost their ability to germinate and serve solely as spermatia. **Macroconidia** reach sizes up to 100 x 2 µm. If macroconidia can be found with microconidia on the same thallus, then it can be assumed that macroconidia are more likely to function as germinating diaspores. Occasionally three distinct sizes of conidia may be found on the same lichen species, with the intermediate conidia thus referred to as **mesoconidia**.

Conidiogenesis

Conidia are formed from conidiogenous cells by a process called **conidiogenesis**. Following a **blastic** development the conidium develops a distinct swelling before a septum segregates it from the conidiogenous cell[19]. In **hologenous** ontogeny both outer and inner wall layers of the conidiogenous cell form the wall of the conidium. The first conidium always develops from this ontogeny. However, most lichen conidia subsequently are derived from an **enterogenous** development, where the conidium wall is newly synthesized along the internal wall of the conidiogenous cell[20]. In this enterogenous development two modes of conidia formation may be distinguished: (1) proliferation of the inner wall layer prior to conidium formation leads to ring-like scars called **annelations** around the neck of the conidiogenous cell [The conidiogenous may thus be called an **anellide**], (2) in the **phialidic** mode no scars can be observed since conidia development is not preceded by proliferation. The conidiogenous cell is often referred to as a **phialide** (Fig. 28). Most lichen conidia seem to follow a phialidic development (Büdel and Scheidegger 1996), however, mixtures of proliferating and non-proliferating phialides have been reported (Vobis 1980, Vobis and Hawksworth 1981).

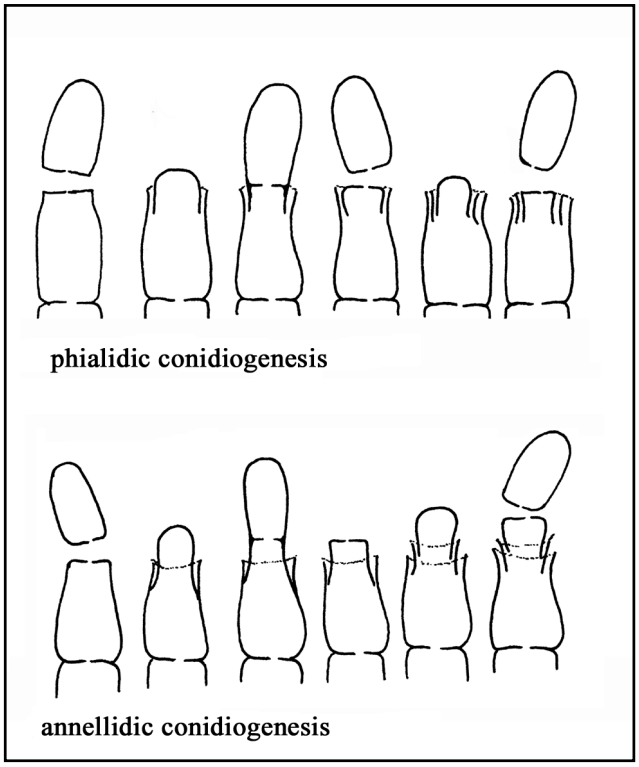

Fig. 28. Conidiogenesis, redrawn from Hawksworth (1988).

Conidiomata and Conidiophores

Conidiogenous cells are most commonly borne on specialized fungal hyphae called **conidiophores**[21]. In li-

[19] **Thallic** conidiogenesis where a septum segregates the conidium before a swelling occurs has not yet been observed in lichens (Hawksworth 1988).

[20] Also, the terms holoblastic for a blastic hologenous development or enteroblastic for an blastic enterogenous development are quite frequently used.

[21] Conidiophores have also been called basidia, spermatiophores or fulcra. The term basidium should, however, be restricted to the specialized spore-bearing structure of basidiomycetes. The term spermatiophore is inappropriate unless it has clearly been established that the conidium is as a spermatium. The term fulcrum as a specialized structure of lichenized fungi

chen-forming fungi conidiophores will most often be closely aggregated in a specialized structure called a **conidioma** (pl. conidiomata). Very few lichens have conidiophores which are not aggregated but arise as distinctly separate hyphae. In the Sonoran Desert region *Chaenotheca furfuracea* is an example of a lichen with conidiophores not aggregated in conidiomata.

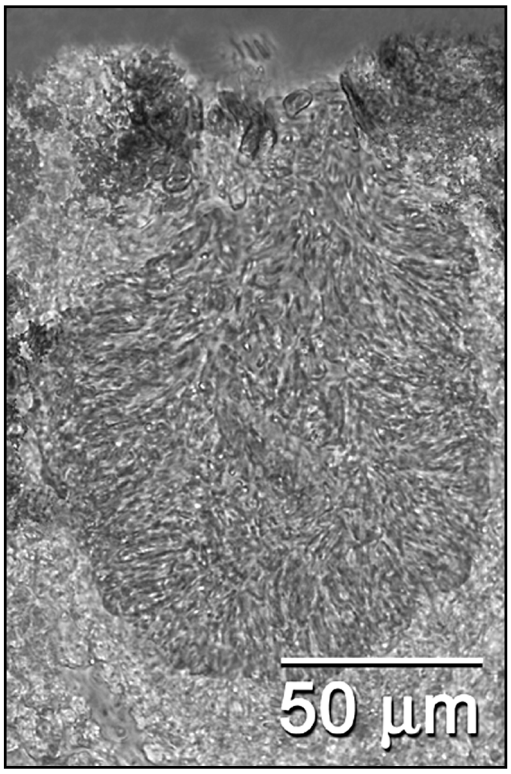

Fig. 30. Light micrograph of a typical lichen pycnidium.

The following **types of conidiomata** can be distinguished among lichens from the Sonoran Desert region:

(1) A **synnema** is a stalked structure of closely aggregated conidiophores bearing chains of conidia at the apex. Peltate synnemata are called **hyphophores**. They produce chains of conidia hanging from a somewhat rounded apex (Fig. 29). In the Sonoran Desert region hyphophores have only be observed in the rare genus *Gyalideopsis.*

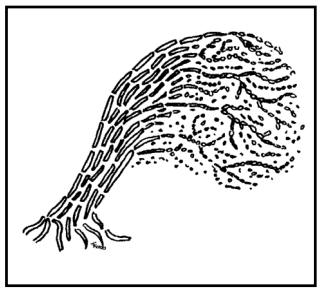

Fig. 29. Hyphophore of *Gyalideopsis.*

(2) A **sporodochium** is a dense, cushion-like tuft of aggregated conidiophores. So far sporodochia have only been found in *Micraea adnata*, an inconspicuous lichen not yet recorded from the Sonoran Desert region.

(3) **Thalloconidia** (German: "Brutkörper") have been described from the genus *Umbilicaria*. These button-like structures on the underside of some umbilicate thalli are, however, better described as vegetative propagules rather then conidia.

(4) The most abundant conidioma of lichen fungi is the **pycnidium** (Fig. 30). It is a flask-like structure opening with a small pore called **ostiole**. Pycnidia are thus very similar to perithecia, from which they may be distinguished only by microscopic sections. Mature perithecia always bear asci whereas pycnidia are internally lined with conidiophores. Pycnidia may be deeply immersed in the thallus and then only be recognized by their opening, or they may emerge and even become stalked. In lichen genera such as *Paulia* and *Thyrea,* the pycnidium is merely a stage in the ontogeny of fruiting bodies.

Important characters to distinguish a variety of pycnidia are the types of conidiophores found within a pycnidium as well as the structure and ontogeny of the pycnidium itself. Unfortunately pycnidia from only a rather limited amount of lichen species have yet been studied, and it is more than likely that future studies may discover several other types conidiophores or pycnidia.

Types of Conidiophores from Lichen Pycnidia

The distinction as to whether conidia arise lateral along the sides of intercalary conidiogenous cells or terminal from apical cells is an important diagnostic

is obsolete. Conidiophores of lichenized fungi are not fundamentally different from those of any other fungi.

character[22]. It is, however, not the only character to distinguish conidiophores.

Conidiophore types of lichenized fungi have first been described in detail by Glück (1899), who named them after the lichen genera in which he found them. More recent accounts rearranged these types, and to avoid confusion with previous names or with pycnidial types, a system of Roman numbers is now most widely accepted (Vobis 1980, Vobis and Hawksworth 1981, Hawksworth 1988, Fig. 31):

Type I – The conidiogenous cells are flask-shaped (doliform to ampulliform). Therefore they are difficult to distinguish from the surrounding tissue. No separate conidiophores can be observed and the conidiogenous cells are borne directly from the paraplectenchymatous tissue of the pycnidial wall. In lichen-forming fungi this type is rather rare.

Type II – The conidiogenous cells are distinctly elongated and may therefore clearly be distinguished from the surrounding tissue. The conidiophore cells are, however, poorly differentiated from the pycnidial wall. Type II conidiophores are known from *Peltigera*, *Psora* and *Lecanactis* species.

Type III – Both conidiogenous and conidiophore cells are clearly differentiated from the surrounding cells of the pycnidial wall. The uppermost cell of the short conidiophore is non-septate and branched and thus supports several elongated conidiogenous cells. Type III conidiophores occur in genera such as *Dirina* and *Roccella*.

Type IV – The conidiophore is a regularly branched, septate hypha with one main axis and several lateral branches. All conidiogenous cells are located terminally on the tip of the branches and conidia are thus borne apically. This type is common in genera such as *Cladonia* or *Ramalina*.

Type V – Like in the previous type the conidiophore is a septate hypha. It is, however, less regularly branched. Most conidiogenous cells are located terminally and only have a few intercalary cells, from which lateral conidia may arise. Type V has been observed in *Alectoria* and *Cetraria.*

[22] Older literature refers to conidiophores with terminal conidiogenous cells as "exobasidial" versus intercalary located cells as "endobasidial". Both terms suggest a close relation to "basidium", which should be restricted to the spore producing structure of Basidiomycetes. To avoid confusion the terms "exobasidial" an "endobasidial" should therefore no longer be used.

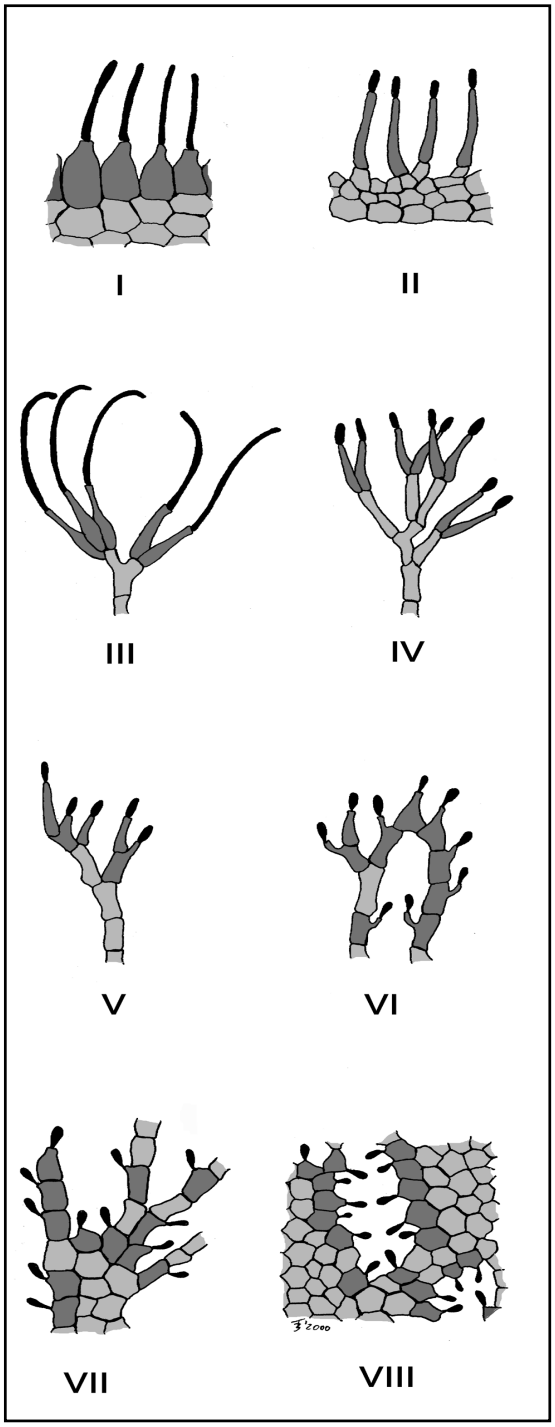

Fig. 31. Conidiophore types from lichen pycnidia (redrawn after Vobis 1980).

Type VI – The branched, septate conidiophores of this type frequently anastomose at their apices. From the tip of the anastomosing cells terminal conidia may arise. However, most conidiogenous cells are located intercalarily where conidia are borne on bayonet-like protrusions along the side of the conidiophores. Type VI conidiophores have been found in a wide range of genera such as *Hypogymnia, Phaeophyscia, Physconia* and *Umbilicaria*.

Type VII – The conidiophores form a densely branched network of hyphae composing rows of intercalary conidiogenous cells. Almost all conidia thus develop laterally and only a very few terminal conidiogenous cells with apical conidia can be observed. Species of *Anaptychia, Lobaria, Nephroma* and *Psoroma* have conidiophores of this type.

Type VIII – Separate hyphae can no longer be distinguished in this tissue of pseudoparenchymatous conidiophores. Inside the tissue, which fills the entire cavity of the pycnidium, several small locules develop. These are lined with conidiogenous cells. A distinction of intercalary and terminal conidiogenous cells is thus not possible. *Dermatocarpon* and *Xanthoria* are examples of genera with this type of conidiophores from the Sonoran Desert region.

Types of Lichen Pycnidia (Fig. 32)

All types of conidiophores (I to VIII) may be observed in a variety of different **pycnidia**. While some conidiophores appear to be more closely related to a specific type of pycnidial conidioma, there are others which can be found in very different lichen pycnidia. The types of pycnidia first described by Vobis (1980) therefore not only take into account the types of conidiophores but also the internal anatomy and ontogeny of the pycnidium. Due to the relatively few species and genera studied so far, these types may not be the only ones to be found among lichenized fungi.

***Lecanactis*-type** – The *Lecanactis*-type is the only one, which does not open with a well defined pore but rather a wide open disc. It is therefore not a true pycnidium, but a cup-shaped conidioma which has also been called acervular (Hawksworth 1988)[23]. The mature conidioma is primarily unilocular and cup-shaped (cupuliform). It is usually ± immersed in the lichen thallus. The wall is lined with elongated conidiogenous cells, and the conidiophore cells are poorly differentiated from the surrounding tissue (type II). The conidia may have various shapes. In the Sonoran Desert region this type is represented by *Lecanactis* and *Arthonia*.

***Roccella*-type** – Like all of the following types the *Roccella*-type is a true pycnidium opening with a well defined ostiole. The central cavity of this primarily unilocular pycnidium is lined with short-branched, non-septate conidiophore cells (type III). These conidiophores bear elongated conidiogenous cells with long filiform conidia. The central cavity of the *Roccella*-type is mainly filled with long filiform conidia and conidiophore cells only line the wall of the pycnidium. In the Sonoran Desert region this type is represented by the two genera *Roccella* and *Roccellina.*

***Lobaria*-type** – A mature pycnidium of this type is globose and unilocular in cross section. Unlike the previous type, the central cavity of a *Lobaria*-type pycnidium is almost entirely occupied with densely branched hyphae composing rows of intercalary conidiogenous cells. (type VII). *Lobaria*-type pycnidia have been described from *Lobaria* but most likely also occur in *Nephroma* species.

***Umbilicaria*-type** – At maturity cross sections of this type are typically pear-shaped (pyriform) to ovoid. The pycnidia are either unilocular with a single central cavity or they may become multilocular, i.e. secondarily segregated by the conidiophore tissue. Conidia are borne on branched, septate hyphae either apically on terminal conidiogenous cells (conidiophore type V), or both laterally from intercalary and apically from terminal conidiogenous cells (type VI). The *Umbilicaria*-type can be found in *Cetraria, Hypogymnia* and several parmelioid genera.

***Xanthoria*-type** – Unlike pycnidia of the *Umbilicaria*-type, *Xanthoria*-type pycnidia are primarily multilocular. Several cavities originate from tissue rupturing early during pycnidium ontogeny. The pycnidium is thus filled with multilocular pseudoparenchymatous tissue (conidiophore type VIII). The locules lined with conidiogenous cells are not necessarily connected and liberation of conidia is probably a result of further disintegration of the pycnidium (Glück 1899). The type is not only represented in *Xanthoria* and closely related genera of orange (K+ violet) lichens but has also been found in

[23] However, a true acervulus is a saucer shaped conidioma of phytopathogenic fungi which develops below an integument of host tissue.

Dermatocarpon and *Endocarpon*, both abundant genera in the Sonoran Desert region.

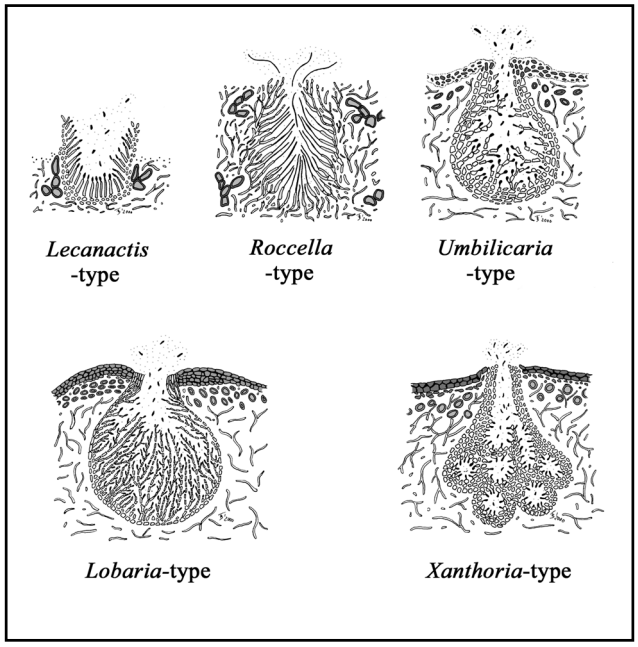

Fig. 32. Pycnidia-types from lichen-forming fungi (redrawn after Vobis 1980).

Lichen Photobionts

by Frank Bungartz

A lichen is a **symbiotic association**, a very tight relationship between at least two very different organisms. The nature of this relationship was not recognized until Schwendener (1869) suggested that so-called lichen "**gonidia**" within a lichen thallus were not outgrowth of the fungus but separate organisms. These organisms living within the structure provided by the fungus are referred to as **photobionts** (Friedl and Büdel 1996). Their photosynthetic activity provides the basis for the lichen symbiosis.

Photobionts are populations of **procaryotic** and **eucaryotic algae**. Within the lichen symbiosis eucaryotic algae are referred to as the **phycobiont** and the procaryotic algae or cynobacteria as **cyanobiont**. In nature both groups assume very similar ecological roles as "**algae**". They are predominantly aquatic, photosynthetic organisms of marine and fresh-water habitats, although some algae also grow in **terrestrial** habitats: They inhabit soil (**psammophytic**) or live on stone (**lithophytic**). **Epiphytic** algae live on other plants, e.g. on bark, leaves or bryophytes. Terrestrial algae also occur as photobionts in lichen symbioses.

Lichen taxonomy is largely the taxonomy of the lichen fungus and far fewer photobiont taxa are involved in lichen symbioses than are mycobiont taxa. However, the lichen symbiosis possesses several characteristics, which either of the partners would not display by itself. In culture the isolated fungus will not form a differentiated thallus and under natural conditions it will not survive outside the symbiosis. Lichen fungi are thus **obligate symbionts**.

The morphology of the photobiont is often strongly modified by the fungus. Sexual and asexual reproduction is usually suppressed. In the lichen symbiosis photobiont cell walls become leaky and photobiont metabolism is modified to facilitate the uptake of carbon assimilates by the fungus. Most lichen photobionts have also been found free-living and although some photobionts may be highly adapted to perform within a lichen symbiosis, they are usually regarded as **facultative symbionts**.

It is not clear to what extent mycobionts are dependent on a specific photobiont. It has been argued that the lichen symbiosis should favor co-evolution of both partners. Tschermak-Woess (1988) gives examples where mycobiont genera only associate with a single photobiont genus as well as genera which associate with a variety of different photobiont genera.

Most lichen thalli are characterized by a single photobiont. However, there are species which regularly form thalli with several different photobionts. Some lichens are characterized by a green algal primary photobiont present all across the thallus and a secondary blue-green photobiont confined to specialized structures called **cephalodia**. Examples can be found among green *Peltigera* species or the lichen genus *Stereocaulon*. Cephalodia of *Lobaria amplissima* may become detached from the main thallus and establish independent fruticulose lichen thalli. The relationship has long been overlooked and the thalli were even described under the separate name *Dendriscocaulon umhausense*, a name now obsolete. The phenomenon has been referred to as **photosymbiodemes** or

morphotype-pairs (Honegger 1996). Photosymbiodemes can establish as distinctly different, **heteromorphic** thalli or as **isomorphic** thalli which essentially look identical apart from their color caused by different photobionts.

Some lichens with primarily green algal photobionts form loose associations with cyanobacteria (**cyanotrophy,** see Poelt and Mayrhofer 1988). Lichen symbioses may become even more complex with **lichenicolous lichens** (parasitic lichens growing on lichens, see Rambold and Triebel 1992; also refer to Vol. II of this Flora).

The Cyanobiont

Procaryotic blue-green algae are true **bacteria** (**Eubacteria**) although they may reach considerable size with some species even displaying characteristics of truly **multicellular** organisms (cell differentiation and specialization, branching pattern, cell communication, etc.; Garcia-Pichel 2000, Castenholz and Waterbury 1989). Cyanobacteria form a distinct phylogenetic[24] entity within **gram-negative**[25] Eubacteria. They are characterized by a form of photosynthesis very similar to that of green algae or plants. Cyanobacteria essentially use the same photosynthetic pigments (chlorophyll *a*, and rarely also b[26]) but some of the accessory pigments are different (phycobilins). Unlike other phototrophic bacteria their photosynthesis is oxygenic (i.e. like photosynthesis of algae and plants, it generates oxygen). Traditionally the ecological role of cyanobacteria as blue-green algae has been much emphasized. Their taxonomy was treated under the **botanical code** reflected by naming conventions like Cyanophyta, Cyanophyceae *etc*.[27] With the advance in microbiology their procaryotic nature was recognized and the bacterial code applied. This led to two different valid naming conventions and much taxonomic turmoil (see Garcia-Pichel 2000, Castenholz and Waterbury 1989). A process of reconciliation is reflected by the attempt to augment both taxonomic codes to avoid further taxonomic confusion[28].

Like their eucaryotic counterparts lichen cyanobionts are strongly modified within lichen symbioses. The characteristic filaments of multicellular cyanobacteria often break apart, motile stages are lost, the reproduction by specialized spore-like cells (**baeocytes**) is suppressed and cells and thalli often become strongly deformed. Mycobiont hyphae either penetrate only the gelatinous sheath (**intragelatinous haustoria**), they may form **wall-to-wall appositions** or penetrate the cyanobiont cell wall and grow as **intracellular haustoria**.

In nitrogen deficient habitats the lichen symbiosis benefits greatly from the ability of some cyanobacteria to fix atmospheric nitrogen. This process depends on the oxygen sensitive enzyme nitrogenase. Nitrogen fixation is therefore restricted to specialized cells called **heterocysts**[29]. These cells are slightly larger then vegetative cells, have thick cell walls impermeable to oxygen, lack photosynthetic pigments and their photosynthetic membranes (**thylakoids**) are reduced.

Although the name implies a blue-green pigmentation blue-green algae come in a variety of colors. Free-living terrestrial or aerophytic colonies commonly appear black to dark brown. Cyanolichens are often dark gray, deep brown, reddish black or pure black. Cephalodia may have a bluish tinge. Under the microscope most cyanobionts are somewhat brownish. This pigmentation is usually the result of accessory pigments (**phycobilins**) from specialized membrane bound enzyme complexes called **phycobilisomes**. Other accessory pigments like carotenoids (yellow-orange) and anthocyanins (reddish violet) may also be present in various amounts. Many cyanobacteria

[24] Modern taxonomy demands that only groups of related organisms be recognized as taxonomic entities. Phylogenetic related groups share a common ancestor.

[25] Gram-negative bacteria have cell wall composed of an outer membrane and an inner peptidoglycan layer. This inner layer is usually thicker than that of other Gram-negative bacteria.

[26] Cyanobacteria s.str. with only chlorophyll a and phycobilins are sometimes distinguished from "*Prochlorophytes*" with both chlorophyll a and b but lacking accessory phycobilins. According to molecular studies some of this distinction is questionable (Garcia-Pichel 2000).

[27] In the botanical code (Greuter et. al 1993) all taxonomic groups have defined endings which indicate their taxonomic rank as well as implicate that the taxon belongs to the plant kingdom. Divisions end with –phyta, classes end with –phycae etc. Fungal taxa are traditionally treated under the botanical code but endings like –mycota or –mycetes indicate that fungi are not plants. The use of classical botanic terms for blue-green algae implies their role as plants and therefore somewhat negates their role as bacteria.

[28] Both codes now recommend that for newly described taxa a preserved type specimen should be stored in a herbarium and a permanent type culture should be maintained in a culture collection. Both codes accept a description as valid if it applies to either one of the two codes (Castenholz and Waterbury 1989).

[29] Less often used but more accurate is the spelling "heterocytes". Strictly speaking the term heterocysts is incorrect because these cells are not dormant cysts. Very few cyanobacteria can fix atmospheric nitrogen without these specialized cells but the mechanism is only poorly understood

are characterized by large gelatinous sheaths, which may be hyaline or distinctly colored.

Two general groups of cyanobionts can be distinguished. **Chroococcoid** cyanobacteria are single-celled and often aggregate in small packages or large colonies. Rarely chroococcoid cyanobacteria form **pseudofilaments**. Pseudofilaments are loose associations of cells assuming a somewhat filamentous structure.

Truly **filamentous** cyanobacteria show closely aggregated cells which repeatedly divide to form distinct rows of cells (**trichomes**). In *Scytonema* filaments are **uniseriate**, i.e. composed of a single cell rows (Fig. 33). The

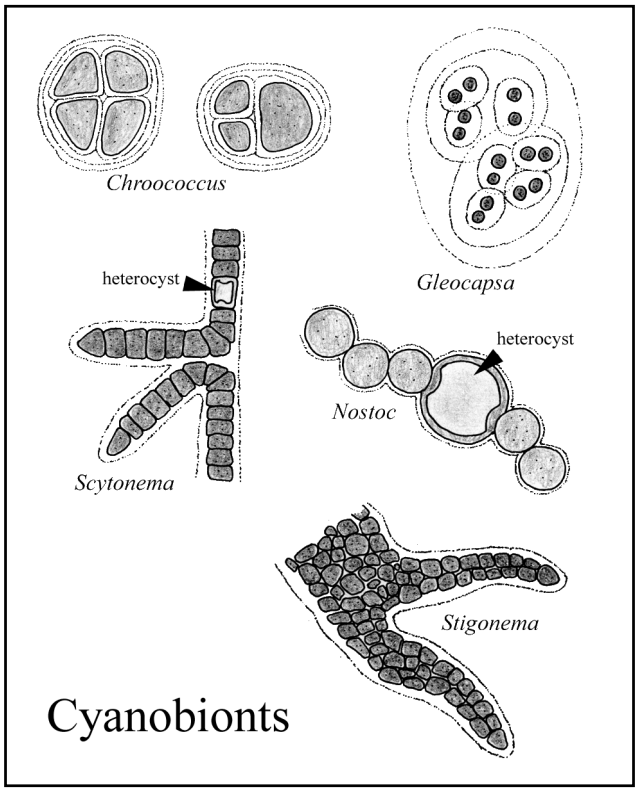

Fig. 33. Common cyanobacteria in lichen symbioses (redrawn from Purvis et al. 1992).

single cells appear like coins stacked upon each other. Occasionally thicker heterocyst cells are interspersed. **False branching** occurs, when the filaments break but the sheath remains intact. Both branches continue their growth by cells dividing in one plane. *Stigonema* is composed of several (**multiseriate**) rows of cells, and cell division occurs in several planes giving rise to **true branches** (Fig. 33).

In the lichen symbiosis the filamentous structure of cyanobacteria is often broken apart. However, in a few filamentous lichen genera (e.g. *Polychidium, Ephebe, Synalissa* etc.) the cyanobiont remains intact and determines the growth form of the filamentous lichen thallus.

The most common cyanobiont is *Nostoc* (Fig. 34). *Nostoc* filaments show no branching. They resemble a "necklace of pearls". Most of the beads are dark brown vegetative cells, interspersed with slightly larger, colorless heterocysts. Even within non-filamentous lichen thalli *Nostoc* often maintains this characteristic structure. In some lichens the chains are tangled into ± compact coils. Very common in desert lichens is the cyanobiont *Chroococsidiopsis.* It forms densely packed regular cubical aggregates within a thin gelatinous sheath.

The Phycobiont

Eucaryotic algae comprise a very wide range of organisms. In lichens most phycobionts belong to the green algae or **Chlorophyta** (Ahmadjian 1967, Tschermak-Woess 1988). The most obvious characteristic of the Chlorophyta is their vivid-green color.

Heterococcus (Fig. 34), so far only isolated from the lichen genus *Verrucaria*, is the only phycobiont genus which belongs to the yellow-green algae or **Xanthophyceae** (**Heterokontophyta**)[30].

The most common lichen photobiont is *Trebouxia* (Fig. 34). It has relatively large (*c*. 9-18(-20) µm in diameter), single cells, which may be somewhat associated in loose groups. *Trebouxia*, however, does not form distinct colonies. Most characteristic is the large central chloroplast with radiating lobes. The nucleus lies off center in a distinct depression of the chloroplast. *Trochiscia* has a similar chloroplast but it can clearly be distinguished from *Trebouxia* by its strongly ornamented cell wall.

[30]Wynne (1969) also reports the brown alga *Petroderma maculiforme* (Phaeophyta) isolated from a maritime *Verrucaria.*
Some fungi also form symbiotic relationships with marine algae but these associations are usually not referred to as lichens but called **mycophycobioses**. (Feldman 1938, Kohlmeyer and Kohlmeyer 1979)

The chloroplast of *Trebouxia* and many other green algae may have one to several **pyrenoids**, proteinaceous areas, which usually can be observed as a distinctly pale area within the otherwise green chloroplast. Some pyrenoids are "naked" but most are characterized by a coat of starch granules which react strongly blue with iodine.

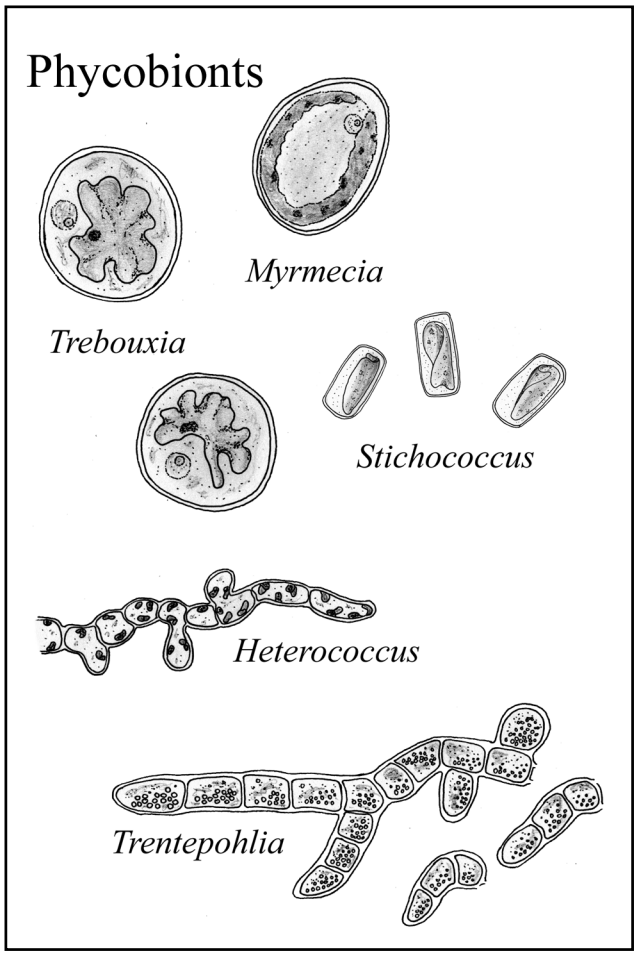

Fig. 34. Common eukaryotic algae in lichen symbioses. (redrawn from Purvis et al. 1992).

Apart from *Trebouxia* several other single-celled green algae may be observed as phycobionts. They are generally referred to as **coccoid** green algae.

Micareoid algae are small coccoid green algae (< 7 µm in diameter), distinctly grouped in pairs. Their cell walls are penetrated by fungal hyphae. The term does not have any taxonomic implication but micareoid algae can be observed in the lichen genus *Micarea*. They may belong to the genus *Chlorella*.

Trentepohlia is the second most common phycobiont (Fig. 34). Like other algae of the order Trentepohliales it is truly multicellular and the chloroplast lack pyrenoids and true starch. **Trentepohlioid** algae have rather thick cell walls, which strongly react violet with chlor-zinc iodine (Poelt 1969). Their cells are generally characterized by huge amounts of carotenoids which give the algae their characteristic orange, yellow to reddish-yellow color. In herbarium material this characteristic color fades and cultured algae often become more greenish. In very humid habitats extended tufts of free-living *Trentepohlia* species are common. Within the lichen symbiosis their filamentous growth is often strongly modified. The thalli break down into short fragments or even single cells and may appear ± grouped rather than multicellular. However, in *Cystocoleus ebeneus* and *Racodium rupestre* the filamentous structure of *Trentepohlia* determines the growth form of the lichen. Their thalli are essentially *Trentepohlia* filaments closely entangle by lichen hyphae.

In general growth morphology of the phycobiont within the lichen symbioses is strongly affected by the mycobiont. The lichen fungus often breaks apart cell aggregates or multicellular thalli. Cell shape may be modified by **haustoria**: Fungal hyphae may surround algal cells in close contact (**wall-to-wall apposition**). **Appressoria** deform the cell structure of the phycobiont but do not penetrate its cell wall. **Intracellular** (or **transparietal**) haustoria penetrate both cell wall and plasma membrane of the phycobiont. **Intraparietal** haustoria only penetrate the cell wall, not the plasma membrane.

Under suitable culture conditions phycobiont cells usually resume their original shape and growth habit and characteristic spore formation can be observed. Some genera form motile, flagellate spores (**zoospores**) as well as non-motile resting spores (**autospores**). Other genera only form autospores. These stages of the algal life-cycle as well as the study of regular growth are often essential for genus or species identification.

Key to the lichen Photobionts

As previously emphasized confident identifications of lichen photobionts can only be made from cultures and this is also reflected in several choices of this key (for detailed information refer to Ahmadjian 1967, 1973, 1982, Friedl 1989, Ettl and Gärtner 1995, Büdel and Henssen 1983 and Büdel 1985). For extensive reviews of photobionts isolated from lichen thalli refer to Ahmadjian (1967) and Tschermak-Woess (1988). It is likely that additional genera not mentioned in this key will eventually be isolated from lichen symbioses. The key to the lichen phycobionts is adapted from Ettl and Gärtner (1995), Gärtner (1992), Wirth (1995) and Poelt (1969), the key to the cyanobionts is largely based on information given by Büdel (1992).

1. Cell content ± blue-green to dark brown throughout (diffuse); without distinct cell organelles or cellular compartmentalization; no chloroplast or pyrenoid [**Cyanobionts: Cyanobacteria; procaryotic blue-green algae**] 2
1. Cell content green to vivid green, rarely screened by a bright orange pigment (carotenoids) and then yellow to brownish orange or vivid orange; with a distinct chloroplast, often with one or several pyrenoids [**Phycobionts: eukaryotic algae**] 11

2. Cells single or in colonies; all cells uniform, globose to ellipsoid; colonies usually forming packages of 2-8 cells, rarely forming pseudofilaments (but single cells distant from each other) [**chroococcoid cyanobacteria**] 3
2. Cells always growing in rows (trichomes)[31], forming true filaments, vegetative cells uniform or of various shape [**filamentous cyanobacteria**] 7

3. Cells forming pseudofilaments (in culture) ..... ***Pleurocapsa***-group[32]
3. Cells not forming pseudofilaments, but often in packages of 2-8 (to many) cells 4

4. Cells with an inconspicuously thin, colorless, ± uniform or tightly layered gelatinous sheath 5
4. Cells with a thick, conspicuously layered sheath 6

5. Predominantly grouped in aggregates of 2-4 (-6) cells; cells 8-32 µm in diameter ..... ***Chroococcus***
5. Grouped in densely packed colonies of many cells; cells 2-12 µm in diameter ..... ***Chroococcidiopsis*** or ***Myxosarcina***[33]

6. Gelatinous sheath distinctly colored, yellow to brown or reddish; cells 2-7 µm in diameter; usually 2-8 cells in one colony ..... ***Gloeocapsa*** s.l.[34]
6. Gelatinous sheath colorless; cells 1 (-2)-15 µm in diameter; many cells forming a colony ..... ***Synechocystis*** s.l.[35]

7. Filaments composed of several rows of cells (trichomes) of cells (multiseriate), filaments up to 1mm wide; with true branching forming from cell divisions in different planes, cells mostly blue-green in color, oblong to ellipsoid, 9-15 x 3-11 µm [in fruticulose to filamentous lichens of seepage tracks on siliceous rocks, e.g. *Ephebe*, *Spilonema*] ..... ***Stigonema***[36]

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[31] In the lichen thallus trichomes may break apart into short fragments.

[32] Büdel (1992) distinguishes *Hyella* from *Hormathonema*. *Hyella* is included under *Pleurocapsa* in Bergey's Manual of Systematic Bacteriology by Castenholz and Waterbury (1989); *Hormathonema* is not mentioned.

[33] *Chroocopsidiopsis* is very polymorphic with developmental stages that resemble *Gloeocapsa* or *Entophysalis* (Büdel and Henssen 1983). According to Büdel (1992) and Waterbury and Stanier (1978) *Myxosarcina* can be distinguished by motile baeocytes. Büdel (1992) also mentions *Cyanosarcina*, a similar genus without baeocytes. This genus, however, is not recognized in Bergey's Manual of Systematic Bacteriology by Castenholz and Waterbury (1989)

[34] Older literature distinguishes between yellow to brown "*Xanthocapsa*" and reddish to violet "*Gloeocapsa* s.str." but the color of the sheath varies according to the pH of the environment. *Gloeocapsa* appears to be the most common cyanobiont besides *Nostoc.* Büdel (1992) also mentions *Entophysalis* with a yellowish to brown sheath and a polar orientation of the colony.

[35] Büdel (1992) mentions *Aphanocapsa* and *Microcystis* as lichen cyanobionts. These two genera are includes by Bergey's Manual of Systematic Bacteriology under *Synechocystis* (Castenholz and Waterbury 1989). *Synechocystis* s.str., however, does not form colonies. The two genera *Aphanocapsa* and *Microcystis* are difficult to distinguished by the way their colonies grow from cell division in different planes.

7. Filaments always formed by a single row of cells (uniseriate trichomes, but several filaments often crowded and appearing closely aggregated); not branching or rarely with false branching 8

8. Filaments distinct 9
8. Filaments indistinct; cells ± deformed ..... various undifferentiated filamentous cyanobionts [requires culturing]

9. Filaments forming chains of uniformly globose to barrel-shaped cells (3-7 µm in diameter) interspersed with larger colorless cells (heterocysts); filaments looking like a chain of beads ("pearl necklace"); chains not branched, widely dispersed in a thick gelatinous matrix (e.g. *Collema*) or tangled in compact gelatinous coils (non-gelatinous cyanolichens, e.g. *Sticta*, *Nephroma*, *Pannaria* and *Parmeliella*) ..... ***Nostoc***
9. Filaments with cells not uniformly globose; cells broader than 5 µm; filaments often appearing as a stack of ± flattened cells, like a string of coins; rarely with false branches (difficult to observe within the lichen) 10

10. Filaments blunt, not tapered; cells oval to oblong-cylindrical, *c.* 5-25 µm wide, interspersed with few larger colorless cells (intercalary heterocysts); frequently with false branching ..... ***Scytonema***[37]
10. Filaments gradually tapered at the apex (often difficult to see without culture); cells at the base of the filaments 2.5-20 µm; with basal heterocysts [**rivularioid cyanobacteria**] ..... ***Calothrix*** s.l.[38]

11. Cells orange, greenish-orange, yellow-orange or reddish-brown (i.e. always with orange pigments [carotenoids] - best observed in fresh material as the color of herbarium specimens fades with time - often visible if freshly collected lichens are scratched); cells always conspicuously thick-walled but not ornamented (always strongly reacting ZnIK+ violet); true starch absent (non-amyloid) [**trentepohlioid algae**] 12
11. Cells vivid green to yellowish green; cells usually thin-walled (at most weakly ZnIK+ violet), rarely thick walled and ornamented (*Trochisia*) or with localized lateral thickening (*Myrmecia*); true starch present or absent 14

12. Thallus in the free-living stage or in culture usually forming ± long filaments, not radially oriented but irregularly branched; in the lichenized stage often breaking down into short irregular rows of cells or even single cells; cells cylindrical to oblong; rarely ± globose; orange to yellow-red within the lichen thallus (often becoming greenish in culture) ..... ***Trentepohlia*** s.str.
12. Thallus forming radially oriented filaments or cell plates (predominantly in tropical lichen genera, doubtful if in the Sonoran region) 13

13. Thallus forming radially oriented filaments or multi-layered cell plates (predominantly subcuticular in folicolous lichen genera; e.g. *Strigula*) ..... ***Cephaleuros***
13. Thallus forming single-layered cell plates or dense nets (predominantly in epiphytic, non-subcuticular tropical lichens) ..... ***Phycopeltis***

14. Plastids yellow-green and always without starch (non-amyloid), phycobiont of single ellipsoid cells or forming short filaments of nearly globose to oblong cells; (so far only found in the lichen genus *Verrucaria*) [**Heterokontophyta*: Xanthophyceae***] ..... ***Heterococcus***
14. Plastids bright green (fresh specimens) to vivid grass-green and always with starch granules (I+ deep blue, amyloid); phycobiont of single cells, in short cell filaments, irregular cell clusters or regular cubic aggregates; in various lichen thalli [**Chlorophyta: coccoid green algae**] 15

15. Cells single (rarely in small groups but not forming consistent aggregates), or (in culture) rarely forming short filaments which easily break into groups of few cells 16

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[36] Büdel (1992) also mentions *Hyphomorpha* as a very similar genus found in the lichen genus *Spilonema*.
[37] Büdel (1992) also recognizes *Tolypothrix* distinguished from *Scytonema* s.str. by false single branching which is generally associated with a heterocyst. *Scytonema* s.str. always branches in two and the branches are often but not always associated with a heterocyst cell.
[38] Büdel (1992) also mentions *Dichothrix* which may be distinguished in culture from *Calothrix* s.str. by filaments with a subdichotomous branching pattern and rarely develops several filaments unified in a single gelationous sheath.

15. Cells forming distinct aggregates, colonies or filaments 24

16. Cells short-cylindrical, often slightly curved, with rounded to slightly tapered ends, rarely ellipsoid to irregularly globose; in culture forming short filaments which easily break ..... ***Stichococcus***
16. Cells not cylindrical; not forming filaments which easily break 17

17. Cell wall with a thick, warty to rugulate ornamentation; cells globose, up to 30 µm in diameter [chloroplast often central and distinctly lobed, reminiscent of the chloroplast in *Trebouxia*] ..... ***Trochiscia***
17. Cell walls without ornamentation; cells various 18

18. Chloroplast without pyrenoids 19
18. Chloroplast with one (or several) pyrenoid (s) 22

19. Cells globose; chloroplast distinctly net-like, irregularly reticulate or hollow; asexual reproduction (in culture) from auto- and zoospores[39] ..... ***Dictyochloropsis***
19. Cell shape various; chloroplast not net-like or hollow; asexual reproduction (in culture) only from autospores or both from auto- and zoospores 20

20. Cells ellipsoid to pyriform (pear-shaped), only the young cells almost globose; chloroplast parietal, two-lobed to deeply incised, almost filling the entire cell lumen; cell wall often with lateral thickening; asexual reproduction (in culture) from auto- and zoospores ..... ***Myrmecia***
20. Cells globose, ellipsoid, ovoid or even ± fusiform but not pyriform; chloroplast parietal, incised or not, not filling the entire cell lumen; cell wall uniform; asexual reproduction (in culture) only from autospores (i.e. cells without flagella) 21

21. Chloroplast parietal, not incised; cells ellipsoid to ± fusiform, also ovoid or almost globose; with or without a conspicuous gelatinous sheath ..... ***Coccomyxa*** s.l.[40]
21. Chloroplast parietal, deeply incised and thus two-lobed or bowl-shaped; cells ellipsoid to globose; never with a gelatinous sheath ..... ***Elliptochloris***

22. Chloroplast parietal, bowl-shaped, often also irregularly lobed; cells globose, ellipsoid to ovoid, small, <16 µm in diameter ..... ***Chlorella*** s.l. [41]
22. Chloroplast ± central, lobed or not lobed, cell shape various 23

23. Chloroplast massive and ± central with irregularly lobed margin; nucleus central or ± off-center, not in a distinct depression of the chloroplast; cells globose and rather small (2.5 – 12 µm in diameter), in culture often forming large, mulberry-shaped clusters (isolated from *Lecidea* species) ..... ***Pseudochlorella***
23. Chloroplast central, sometimes massive, always with large and distinct marginal lobes; nucleus always off-center, in a distinct depression of the chloroplast; cells globose to ellipsoid or ± irregular; rarely aggregated but not forming mulberry-shaped clusters (the most common lichen photobiont) ..... ***Trebouxia*** s.l.[42]

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[39] To distinguish the following genera it is necessary to study well developed algal cells. In the lichen thallus cells are often deformed and the formation of zoospores and autospores is usually suppressed. Correct identification will often be misleading without culturing specimens isolated from lichen thalli.

[40] *Coccomyxa* s.str. forms ± loosely aggregated colonies within a gelatinous mucilage. The mucilage derives from the gelationous sheaths which surround each cell and may be initially distinctly layered but later becomes confluent. Species without a gelatinous sheath and not associating in colonies may have to be transferred to *Choricystis* (Gärtner 1992).

[41] The taxonomy of the genus *Chlorella* is not well resolved. The name has commonly been applied to group of coccoid green algae which is not necessarily closely related. So-called "micareoid" green algae which are typical for many *Micarea* species probably belong to *Chlorella* s.l. Micareoid algae are always rather small cells (4-7 µm), grouped in distinct pairs and separated by a thin to ± normally thickened cell wall. They are characterized by haustoria where the cell hyphae penetrate the algal cell wall.

[42] The taxonomy is not clearly established (Ahmadjian 1993). The genus *Pseudotrebouxia* has been distinguished from *Trebouxia* according to a different mode of cell division during asexual spore formation. Gärtner (1985), however, re-examined specimens and suggested that spore formation is not distinctly different. Friedl (1989) also argued that *Pseudotrebouxia* should be included in *Trebouxia.* König and Peveling (1984) and Peveling and König (1985) found cell-wall

24. Cells forming colonies with a distinct gelatinous sheath (best observed in India Ink) 25
24. Cell forming colonies without a distinct gelatinous sheath 27

25. Gelatinous sheath distinctly layered and not confluent; cells forming irregular colonies ..... ***Gloeocystis***
25. Gelatinous sheath not distinctly layered and soon becoming confluent 26

26. Cells ellipsoid to ± fusiform, ovoid or almost globose; single cells usually ± loosely aggregated and dispersed within a gelatinous mucilage (compare with choice 21) ..... ***Coccomyxa*** s.l.
26. Cells globose to ± flattened, forming closely grouped packages within a confluent gelatinous sheath [isolated from *Lecidea* species] ..... ***Chlorosarciniopsis***

27. Chloroplast without a pyrenoid [isolated from *Verrucaria nigrescens*] ..... ***Coccobotrys***
27. Chloroplast with a pyrenoid (difficult to distinguish in the light microscope) 28

28. Phycobiont (in culture) always forming branched filaments 29
28. Phycobiont (in culture) mostly aggregating in small packages (very rarely forming short filaments) 30

29. Zoospores with 4 flagella ..... ***Dilabifilum***
29. Zoospores with 2 flagella ..... ***Leptosira***

30. Cells mostly aggregating in pairs or small, cubic packages, zoospores unknown ..... ***Diplosphaera***[43]
30. Cells in groups of (2-) 4, usually forming cubic packages, in culture also forming short filaments; asexual reproduction by cell-division and the formation of auto- or zoospores ..... "***Protococcus***"[44]

differences between *Pseudotrebouxia* and *Trebouxia* (for a more detailed discussion see Tschermak-Woess 1988). *Asterochloris*, another very similar genus, is sometimes recognized because of the formation of a large number (64-128) of zoospores during asexual reproduction.

[43] The very closely related species *Nannochloris normandinae* has been isolated from the lichen *Normandina pulchella*.

[44] "*Protococcus*" refers to a group of very closely related genera such as *Apatococcus*, *Desmococcus* etc. (see Ettl & Gärtner 1995 for details).

Colors and Chemistry

by T. H. Nash III and J. A. Elix

One of the exciting aspects about lichens is the myriad of colors that one finds among the species (Wirth 1995, McCune and Geiser 1997, Brodo et al. 2001, etc.). Various shades of white, gray, orange, yellow, green, brown and black are the most common, but one also finds occasional reds and even bluish tinged lichens. There is a chemical basis for the different colors, frequently due to the accumulation of secondary metabolites[45] in the upper cortex of the lichens. For example, gray colors frequently reflect the accumulation of atranorin; yellow-green, the accumulation of usnic acid, bright yellows, the accumulation of vulpinic acid derivatives or rhizocarpic acid; and orange, the accumulation of anthraquinones. Browns usually reflect the occurrence of pigments, that have not been fully characterized. In the Sonoran region most black lichens have a cyanobacterium as the photobiont and the pigments within the cyanobacterium account for

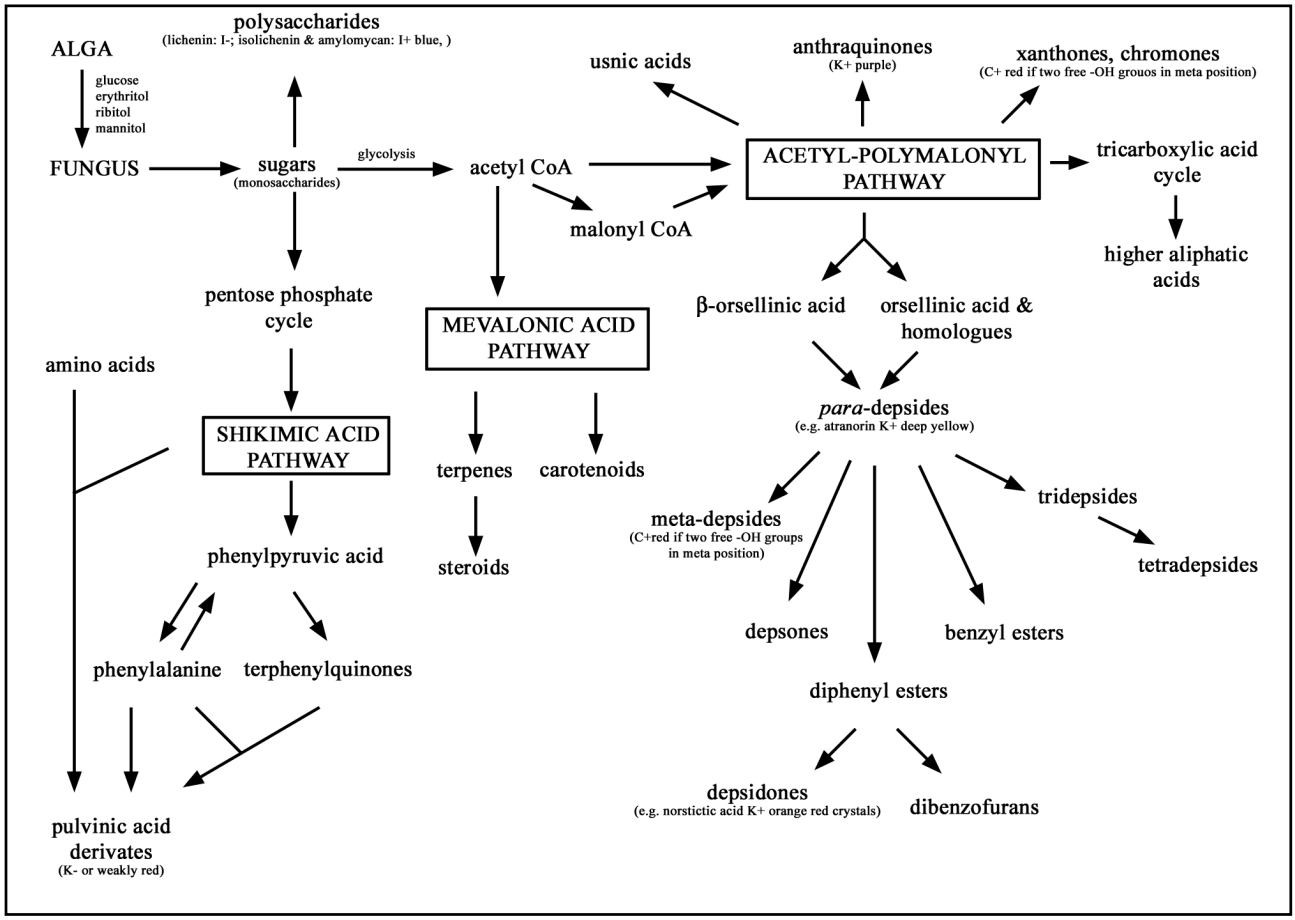


Fig. 35. Metabolic pathways of lichen secondary metabolites.

[45] Secondary metabolites occur extracellularly whereas primary products occur intracellularly. Intracellular products include the proteins, amino acids, carotenoids, polysaccarides, sugars and vitamins found in all organisms.

the black color. In general a particular color is characteristic of a species or a genus, and in some cases even a family. Consequently, these colors are given in our descriptions. However, one needs to be cautious because colors may vary due to different environmental conditions (e.g. degree of illumination, hydration status of the lichen, length of time of storage in a herbarium, etc.).

In addition to the pigments found in the external cortices, some pigments (e.g. anthraquinones, secalonic acids, etc.) may also contribute to colors within the thallus (e.g. in the medulla), but usually the hyphae are white. On the exterior surface of interior hyphae in green algal-containing lichens, colorless crystals frequently accumulate. These represent a wide range of secondary metabolites (Fig. 35 for the major classes), many of which are unique to the lichen symbiosis. The depsides, depsidones, depsones and dibenzofurans are perhaps the most diverse and well known and are products of the acetyl-polymalonyl pathway (Fig. 35). In general a species is characterized by a particular constellation of secondary metabolites (see recipes the species descriptions) that are biosynthetically related. In fact secondary metabolite chemistry provide important characters at many levels of classification (Culberson and Culberson 1970, Elix 1996).

The detective work involved in determining the secondary metabolites occurring in a particular lichen is both a challenge and enjoyable aspect of dealing with lichens. Fortunately, the use of simple spot tests (see recipes) is frequently sufficient to identify a species. In addition, the use of a black light (long wave UV lamp – do not look at it!) provides a rapid means to identify the occurrence of xanthones and a few other secondary metabolites. However, the multitude of secondary metabolites known (over 700 currently) requires additional investigative procedures, if precision in determining secondary metabolites present is required. Accurate analyses can be achieved using standard thin layer chromatographic (TLC) procedures (see Culberson 1972, Culberson and Amman 1979, Culberson et al. 1981, White and James 1985, Elix 1996 and Culberson and Elix 1989 for details), for which a fume hood should be used. The TLC procedure involves extraction (with acetone), spotting extracts on chromatographic plates, running duplicate plates in 2-5 different organic solutions, and checking the plates under ultraviolet light (UV) before and after spraying (or brushing) with a 10% H_2SO_4 solution and charring in an oven (100°C for *c.* 10-15 minutes). The colors obtained (visual or under UV) and the distance migrated in the different solutions (relative to standards) generally provide a unique combination of observations for determining a particular secondary metabolites. Fortunately, computer programs are available to aide the process (Elix et al. 1988, Mietzsch et al. 1993 & 1994). Many lichen systematists have mastered these techniques but for the most intractable determinations high performance liquid chromatography (HPLC, Feige et. al 1993), mass spectrometry or other advanced, chemical techniques may be necessary.

Recipes and other techniques

by F. Bungartz

The presence or absence of many common lichen substances can often be detected with relatively simple spot tests. Only minor amounts of test solutions should be applied to thallus fragments with micropipettes or dissecting needles. Discard the fragments afterwards. Care must be taken to differentiate color reactions of the thallus surface from the medulla. Lichen metabolites, which are present only in minor concentrations, frequently show only faint reactions. These reactions can often be observed only under a compound microscope. A brief overview of typical spot test and UV reactions for common lichen substances can be found in Wirth (1995).

P: This abbreviation (also as PD or Pd) stands for a saturated solution of *p*-phenylenediamine in 95% ethyl alcohol. The solution is highly unstable and should be made immediately prior to testing by dissolving a few *p*-phenylenediamine crystals in a few drops of 95 % ethyl alcohol. Steiner's solution is a more stable P-reagent which will last a few month but must be tested regularly for consistent results (dissolve 1g of *p*-phenylenediamine with 10 g sodium sulfite in a solution of 5 ml liquid dishwashing detergent in 100 ml distilled water, and store in a brown bottle). P characteristically gives yellow to orange or red color reactions with depsides and depsidones containing aldehyde groups. The reaction usually is rapid but sometimes develops slowly.
WARNING: The substance is easily absorbed through the skin, is known to cause dermatitis and is cited as carcino-

genic (Dobson 2001). Also *P*-phenylenediamine is a highly aggressive stain, that will slowly disintegrate any paper or cotton it contacts.

K: This is a 10 % aqueous solution of potassium hydroxide (10g of KOH pellets in 100 ml distilled water). K is a useful reagent to differentiate between anthraquinones and pulvinic acid derivates. The orange or red anthraquinones (e.g. in *Caloplaca*) turn deep purple with K. Pulvinic acid derivates (e.g. in *Candelariella*) react K- or rarely have a very weak reddish reaction. The gray cortical pigment atranorin (a depside) turns deep yellow with K and the depsidone norstictic acid forms strongly orange-red crystals in K. Also K is used as a clearing agent for sections of fruiting bodies and thalli. It often dissolves crystalline lichen substances and removes some of the mucilage which may obscure detail in sections. A 5% solution is usually sufficient.
WARNING: The solution is caustic and should be handled with care.

C: It is a saturated solution of aqueous calcium hypochlorite [$Ca(OCl)_2$]. The solution is highly unstable and can be substituted with common household bleach that may last several months if stored in a light-proof container. However, the reagent must be tested regularly for consistent results. It commonly gives a reddish pink color reaction with depsides and xanthones containing two free hydroxyl groups (-OH) in the meta position. The reaction usually fades quickly. If K is applied first immediately followed by C the reaction can be more pronounced.
WARNING: The solution is an aggressive bleaching agent and should be handled with care.

I: Iodine solutions do not react with lichen secondary metabolites, but rather with starch-like polysaccharides in the thallus or fruiting body. The most common polysaccharides isolated from lichen thalli are lichenan and isolichenan. It appears that blue iodine reactions of the thallus are due to the presence of isolichenan whereas lichenin reacts red-brown. Blue color reactions in lichen asci has also been ascribed to isolichenan, but Common (1991) argues that staining characteristics of the ascus are different and the substance should better be referred to as amylomycan.

Lichenologists have routinely used Lugol's iodine to study the ascus tip. The reactions must be observed under the compound microscope. A droplet of solution is placed at one edge of the cover slip and sucked under the cover slip with a strip of filter paper. The color change can thus be observed during the application.

Color reactions not only vary according to concentration but also depend on the nature of the polysaccharides present. Euamyloid reactions are characterized by a strong blue color reaction. Hemiamyloid reactions are characterized by a reddish reaction which changes towards blue especially after the application of 5 to 10% KOH ("induced bluing"). Mycologists have traditionally studied ascal structure with Meltzer's reagent as a clearing agent (i.e. iodine solution in 50% aqueous chloral hydrate). Lichenologists prefer Lugol's iodine and usually recommend a pre-treatment with potassium hydroxide. Results of these tests may be different (Common 1991, Baral 1987). As a routine test sections should first be observed in iodine solution without pre-treatment, then be treated with chloral hydrate followed by iodine application and finally be treated with potassium hydroxide (5%) followed by Lugol's iodine.

Thallus reactions with iodine can also be consistent taxonomic characters. The presence of a starch-like polysaccharide in the thallus may reflect the ability of the lichen to store polysaccharides and this storage product may thus not be present in lichen thalli at consistently high concentrations. The application of a routine iodine thallus test does not differ from other spot test reactions, but the use of a more strongly concentrated iodine solution than being used for asci is recommended.

Active iodine content of the test solutions changes because of the high volatility of iodine. Dilute concentrations lose iodine more rapidly than high concentrated solutions. Dilute solutions should therefore regularly be mixed from high concentrated stock solutions.
Iodine Stock Solution (3 % IKI): dissolve 1 g iodine crystals and 2 g potassium iodide (KI) in 30 ml distilled water.
Lugol's Iodine (0.3 % IKI): dissolve 2 ml stock solution in 20 ml distilled water.
Strongly concentrated iodine (1.5 % IKI)**:** dissolve 3 ml stock solution in 6 ml distilled water.
Chlor-Zinc Iodine (ZnIKI): Stock solution – dilute 100g zinc chloride and 35 g potassium iodide in 60 ml distilled water. Working solution – combine stock solution with 1.5% IKI in the proportion 9:1. ZnIKI is a useful reagent

to distinguish dead algal cells in the phenocortex of some lichens.

N: This stands for concentrated nitric acid (HNO_3), that gives purple or red color reactions with aeruginose (blue-green) pigments in the exciple and epihymenium of many lecideine fruiting bodies. In some lichen species the bluish black hyphae of the hypothallus react N+ red and in the genus *Neofuscelia* the upper cortical hyphae react N+ blue-green. Nitric acid dissolves most crystalline lichen metabolites and many mineral crystals in thallus sections.
WARNING: It is a very strong acid and can easily damage microscopic gear. Store in a clear glass bottle with a tightly sealed glass stopper.

S: This is a 10% aqueous solution of sulphuric acid (add 10 ml of conc. H_2SO_4 to 90 ml distilled water). It forms colorless, needle-shaped crystals with calcium or magnesium oxalates, that are easily observed in polarizing light. A more accurate method to analyze mineral crystals in lichen thalli is X-ray diffractometry. Also 10% H_2SO_4 is used in standardized thin layer chromatography to develop characteristic color reactions of lichen substances after heating.
WARNING: Sulfuric acid is a strong acid.

Polarized Light – Most compound microscopes can easily be modified for polarizing light microscopy to observe crystals of various origin in sections of lichen thalli and fruiting bodies. Orientation and size of these crystals may have taxonomic importance (e.g. in the *Lecanora subfusca* group). Two polarizing filters are used: one (the polarizer) is inserted below the specimen between light source and microscope stage, the other one (the analyzer) is inserted above the specimen, usually between the objective lens and the eyepiece. Both filters eliminate all light waves except from one plane. Rotating the polarizer relatively to the analyzer eventually eliminates all light. Crystals in a specimen section, however, change the plane of light waves coming from the polarizer. Some of this light will pass through the analyzer and the crystals thus become visible against a dark background.

Ultraviolet Light – A number of lichen secondary metabolites exhibit a characteristic fluorescence under UV-light. These reactions are commonly used to analyze lichen secondary metabolites in thin layer chromatography. The reactions can also be observed if the entire lichen is placed under a UV lamp. Reasonably priced UV lamps can be obtained from stamp collection supplies but the lamps should be tested before purchase. The amount of UV fluorescence differs according to wavelength and not all lamps are equally suited.
WARNING: Ultraviolet light is harmful to the eye. Do not look straight into the light!

Microscopic stains – Various microscopic stains may be used to enhance low contrast of hyaline plectenchyma.
Lactophenol Cotton Blue (LCB) – To make it, add 20 g phenol crystals and 20 g lactic acid to 20 ml distilled water. The solution is then applied to microscope sections (adding drop-by drop until the desired intensity is reached). Staining can usually be enhanced if the sections are heated (*c.* 90° C, avoid boiling of the solution). For semi-permanent slide mounts 40 g glycerin may be added to the original recipe. Slide mounts in glycerin will dry out less rapidly and may be sealed with nail polish for prolonged storage. Other stains sometimes used in mycology and lichenology are **toluidine blue O** and **methylene blue**.
WARNING: Phenol is carcinogenic.

India Ink – Although it is not a microscopic stain because it does not react with microscopic sections, it is commonly used to render spore halos visible because the ink particles do not penetrate the mucilaginous outer layer of the spore wall. The thick mucilage coat will thus become visible against the gray background of the ink solution.

TLC: (Thin Layer Chromatography) The following solvents are commonly used (the relation is given in parentheses):
A - toluene/dioxane/acetic acid (180: 45: 5). Dioxane in solvent A is hygroscopic and absorbs water over time. The solvent thus rapidly deteriorates and accurate R_f-values can only be recorded with relatively fresh solvent.
B' - hexane /methyl tert-butlyl ether /formic acid (140: 72: 18). It usually lasts several days.
C - toluene/acetic acid (170: 30). For many lichen metabolites C provides the best discrimination. It is also very stable (several weeks) and therefore the most common solvent routinely used.

Solvents E and G are mostly used only to discriminate substances which will otherwise not be resolved very well:

E - cyclohexane/ethyl acetate (75: 25). It discriminates among non-polar derivates of lichen compounds and metabolites that have very high R_f-values in A, B' and C. It needs to be prepared fresh daily.

G - toluene/ethyl acetate/formic acid (139: 83: 8). It is very stable and discriminates well between metabolites with very low R_f-values in A, B' and C.

WARNING: All solvents are highly volatile and flamable. Do not inhale! Always use under a fume hood!

Collecting, Curating, and Conservation

by B. D. Ryan and F. Bungartz

Collecting lichens requires good observation skills in the field. Some species are very small and detail should be observed with the aid of a good (10x) hand lens. Specimens should be collected in paper bags. In moist climates specimens must soon be air dried to prevent infestation by imperfect fungi (molds). Some herbaria freeze specimens to kill pests. However, lichens are usually not infested by pests which may easily destroy large collections of vascular plants.

It is important to record locality information meticulously in the field. Collection data should include a collection number, the collector, detailed description of the collecting site (longitude, latitude, elevation, Country, State, County, area), collecting date and detailed habitat information (especially the of the substrate). This information will later be recorded on the specimen label together with the species name and the identifier. Modern herbaria store label data in computer databases.

Specimens on bark or wood can be removed with a stout knife, care being taken not to cut into the living tissue of the tree. Pruning shears or a small hacksaw are useful for twig-inhabiting species. The collection of specimens on rocks and other hard materials often necessitates the use of a geological hammer and a masonry cold chisel.

Specimens on soil or sand easily become powdered, so should be collected in small jars or boxes and wrapped with soft tissue paper (this also applies to fragile lichens on other substrates, e.g., species with stalked ascocarps). Excessive soil (or bryophytes) should be removed in the field, and in foliose genera further cleaning, including washing in water, is often necessary to facilitate observation of rhizines or other features of the lower side. After collection soil-inhabiting lichens can be stabilized by a soil-binding agent such as white glue (e.g., "Elmer's") diluted approximately 1 part glue in 3 parts water. The glue is applied as a stabilizer to the underside of the specimens, leaving them to dry overnight soil-side up.

Curation methods vary according to preferences of collectors and their herbaria. In general lichens are stored in herbarium packets folded from acid-free paper (Fig. 36). Crustose lichens are often glued with their substrate on cards. This prevents the lichen from movement and supports small and brittle specimens. Most macrolichens,

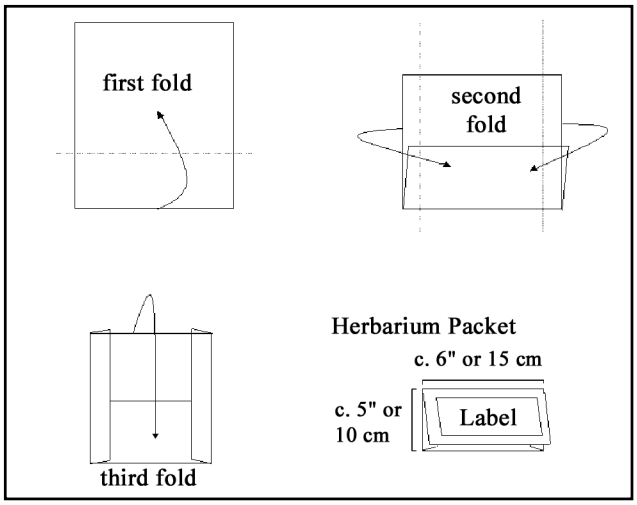


Fig. 36. Folding specimen packets. The second fold is reversed if the packet is mounted on a herbarium sheet.

and specimens on twigs should not be glued on cards.

Brittle or delicate lichens can be protected by layers of cotton or stored in small paper boxes rather than herbarium packets. Most large macrolichens can be moistened, pressed flat and dried to fit into packets. This substantially reduces the potential for fragmentation. When rewetted specimens will reassume their original three-dimensional structure, which may be critical for identification. Specimen packets can be stored either upright in filing cabinets or glued to large herbarium sheets and stack-

ed horizontally. Specimens in filing cabinets are more accessible but fragile specimens need extra protection.

Most lichens grow extremely slowly, often less than a few millimeters each year. Lichens are notably sensitive to subtle environmental changes and frequently impacted more strongly than vascular plants. Within the geographic region treated in this flora especially California and to a somewhat lesser extent Baja California have many specialized and endangered habitats with species known to be rare or threatened. Once lost from a habitat, reestablishment may at worst never occur and at best take several generations.

To collect on private land permission from land-owners must be obtained. Special permits are necessary to collect material in National or State Parks, Indian Reservations or otherwise protected areas.

It is advisable to avoid collecting along trails, campgrounds or other public places. Special care must be taken not to damage walls, churchyard memorials and other man-made structures. It may be possible to identify specimens from these sensitive sites by careful observation in the field and collecting fragments of lichen thalli for chemical or microscopic analysis in the laboratory.

KEYS TO THE GENERA OF LICHENS AND SIMILAR FUNGI

Introduction and Outline

by B. D. Ryan

[**Caution:** All keys are designed primarily for taxa occurring in the Sonoran region, and thus may not work well for other areas or as-yet-unknown taxa.]

1. Fungal fruiting bodies a basidiocarp (producing basidiospores on the tips of microscopic club-shaped structures called basidia); basidiocarps in Sonoran region a lichenized, rounded, shelf- or bracket-like structure (**BASIDIOMYCOTA**) ..... ***Dictyonema***

1. Fungal fruiting bodies, if present, an ascomata (producing ascospores inside microscopic sac-shaped structures called asci); ascomata rounded to elongated, immersed to sessile or stalked [**Note:** superficially similar conidiomata produce conidia on the surfaces of ± specialized conidiophores [Fig. 31] and are often present in addition to or instead of the ascomata] (**ASCOMYCOTA**) 2

2. Photobiont a cyanobacterium (without nucleus or chloroplasts; usually blue-green or dull blackish brown) ..... **I. CYANOLICHENS**, page 55

2. Photobiont, if present, a eukaryotic alga (with nucleus and chloroplasts; green, yellow, orange, or rarely brown) ... 3

3. Ascomata either lirellate (distinctly horizontally elongated), pyrenocarpous (perithecia, opening by a pore and usually with a darkened wall), or calicioid (on a hair-like stalk and/or with ascospores forming a mazaedium on the surface) .4

3. Ascomata not as above or absent 6

4. Ascomata distinctly horizontally elongated ..... **II. LIRELLATE LICHENS**, page 61

4. Ascomata rounded to irregular in outline 5

5. Ascomata opening by a pore ..... **III. PYRENOLICHENS**, page 63

5. Ascomata with a hair-like stalk and/or mazaedium (a powdery mass of dark ascospores)..... **IV. CALICIOID LICHENS** (Vol. II)

6. Photobiont trentepohlioid (orangish to yellowish when fresh, usually with cells somewhat elongated and forming at least occasional short filaments or plates, algal cell walls strongly ZnIK+ violet; true starch absent) .... **V. LICHENS WITH TRENTEPOHLIOD PHOTOBIONTS** see page 66
6. Photobiont otherwise, usually chlorococcoid (greenish when fresh, usually with round cells not forming filaments or plates; algal cell walls at most weakly ZnIK+ violet; frequently with true starch in the chloroplasts and then I+ blue) 7

7. Thallus surface (and often ascomata) ± orange to yellow, reddish, or somewhat whitish, but always K+ purple (containing anthraquinones) ..... **VI. ORANGE LICHENS** (Vol. II)
7. Thallus surface not as above (but medulla, soredia, or apothecia may be yellow, orange or red, and sometimes K+ weakly reddish (without anthraquinones) 8

8. Thallus relatively large (mostly > 1 cm across) and conspicuous ("macrolichens"), often loosely attached to the substrate, appearing irregularly leaf-like, lobed, or stalked to shrub-like or beard-like 9
8. Thallus, if evident, small (< 1 cm across) or if larger then diffuse and often inconspicuous ("microlichens"), usually closely attached to the substratum and appearing crust-like (to scaly, lobed, or minutely shrubby). [**Note:** squamulose, lobate, and dwarf-fruticose genera are sometimes treated as macrolichens] 11

9. Thallus fruticose (or cladoniiform), with erect or hanging (less often prostrate) stalks or lobes, which are either rounded to angular in cross-section, or flattened to channeled but then distinctly elongated and often similar in appearance and structure on both sides, and growing loosely or attached at only one or few places, without specialized attachment organs ..... **VII. FRUTICOSE LICHENS**, page 69
9. Thallus foliose or umbilicate and frequently with specialized attachment organs 10

10. Thallus divided into ± distinct lobes, which are often elongated and radiating towards the margins; tightly to loosely attached over a broad area ..... **VIII. FOLIOSE LICHENS**, page 73
10. Thallus usually without distinct marginal lobes; each thallus (or subunit) attached only by a single, short, discrete, ± central stalk (umbilicus) ..... **IX. UMBILICATE LICHENS**, page 83

11. Thallus squamulose (with ± horizontal or somewhat ascending leaf-like or scale-like structures, which are usually flattened to somewhat concave, convex or swollen and generally different on the two sides), **or** lobate (to dwarf-fruticose) ..... **X. SQUAMULOSE AND LOBATE LICHENS**, page 84
11. Thallus, if present, crustose, effuse 12

12. Ascomata absent (or apparently so) ..... **XI. STERILE CRUSTOSE LICHENS** (Vol. II)
12. Ascomata present 13

13. Not growing on lichens or allied fungi (or if so, then distinct thallus present and containing photosynthetic cells) .... **XII. CRUSTOSE DISCOLICHENS** (Vol. II) ..... [but *Diploschistes* and *Pertusaria* in Vol. I and keyed here under III. Pyrenolichens (page 63)]
13. Growing on lichens or allied fungi; separate thallus and photobiont usually absent .... **XIII. LICHENICOLOUS FUNGI** (Vol. II)

I. CYANOLICHENS

by M. Schultz

1. Ascomata true perithecia, with ± dark wall; ascospores 1-septate; thallus immersed or superficial, on rock or barnacles, in the intertidal zone ..... ***Collemopsidium***
1. Ascomata apothecia (sometimes perithecioid, but then with pale wall), or thallus sterile; thallus growing entirely above the substrate 2

2. Thallus squamulose, granulose to coralloid, spongiose (dark gray to brownish, composed of cephalodia containing cyanobacteria; "true thallus" containing green algae but reduced to a thin, grayish ring surrounding large apothecia) ..... ***Solorina* (*spongiosa*)** (Vol. II)
2. Thallus otherwise 3

3. Thallus sorediate, soralia laminal or marginal, limited or confluent; thallus few mm or few cm in size 4
3. Thallus not sorediate but often granular, isidiate or with lobules; size various 7

4. Thallus lower surface veined and with long rhizines, lobes ear-shaped, rounded, *c.* 1 cm wide ..... ***Peltigera* (*didactyla*, juvenile)**
4. Thallus lower surface not veined and with long rhizines 5

5. Thallus lower surface tomentose and with pseudocyphellae ..... ***Pseudocyphellaria* (*anomala*)**
5. Thallus lower surface not tomentose, without pseudocyphellae 6

6. Thallus large, foliose, a few cm to some cm across, lobes *c.* 1 cm wide or wider, with bluish-gray, granulose soredia at ascending lobe margins ..... ***Nephroma* (*parile*)**
6. Thallus smaller, peltate to squamulose or crustose, lobes if present < 1 cm 7

7. Squamules strongly concave, light gray; anatomy of thick, perpendicularly oriented hyphae ..... ***Heppia* (*conchiloba*)**
7. Squamules or areoles plane or slightly convex, olive or bluish brown but gray in one species; anatomy different 8

8. Thallus olive-brown or rarely grayish, shape various (peltate or crustose); always with a thick lower cortex; photobiont is a single-celled cyanobacterium ..... ***Peltula***
8. Thallus bluish brown, squamulose; lower cortex absent, photobiont *Nostoc* (in chains of globose cells) ..... ***Fuscopannaria***

9. Thallus large, several cm across, lobate, lobes often > 1cm wide, often dorsiventrally stratified or at least corticate **[Large Cyanolichens**, page 55**]** 10
9. Thallus smaller, few mm to few cm across, lobes usually < 1 cm wide, dorsiventrally stratified or not, corticate or not corticate **[Medium-sized Cyanolichens**, page 56 **or Small Cyanolichens**, page 57**]** 16

[Non-sorediate Large Cyanolichens]

10. Lower surface not tomentose (except on the veins of some species of *Peltigera*), without numerous short hairs; rhizines present and distinct or lacking; lower cortex present or absent 11
10. Lower surface tomentose (to glabrous in some species of *Nephroma*), with numerous short hairs; without veins; rhizines absent or few, small, and indistinct; lower cortex present 12

11. Lower surface without cortex, pale or brownish but not concolorous with the upper surface; with veins forming a distinct network around pale areas; if not distinctly veined, then at least with distinct, 2-10 mm long rhizines ..... ***Peltigera*** (Vol. II)
11. Lower surface corticate, glabrous or somewhat wrinkled but not veined and without distinct long rhizines ..... ***Leptogium*** (large species, excluding sect. ***Mallotium***) (Vol. II)

12. Lower surface tomentose and with cyphellae (distinct circular holes through the tomentum); thallus color brownish to olive ..... ***Sticta*** (Vol. II)
12. Lower surface tomentose and without cyphellae (but sometimes with rounded pseudocyphellae); thallus color various 13

13. Lower surface tomentum interrupted by pale spots or pseudocyphellae 14
13. Lower surface tomentum continuous; photobiont *Nostoc* (in chains of globose cells) ..... ***Leptogium*** **(**sect. ***Mallotium*****)** (Vol. II)

14. Lower surface tomentum with small, roundish (but not crater-like) spots (pseudocyphellae); apothecia on upper side ..... ***Pseudocyphellaria*** **(*anthraspis*)**
14. Lower surface without pseudocyphellae, tomentum sometimes with broader, irregular spots without hairs, or with pale raised papillae; apothecia on upper or lower side 15

15. Apothecia on lower side, if lacking then thallus usually sorediate (see 3) ..... ***Nephroma***
15. Apothecia on upper side; if lacking then thallus not sorediate ..... ***Lobaria*** (Vol. II)

[Non-sorediate Medium-sized Cyanolichens]

16. Thallus medium sized and foliose with lobes usually 2-10 mm wide (± *Parmelia*-like; stratified or not) 17
16. Thallus smaller and usually squamulose, peltate, dwarf fruticose or crustose but including very narrow lobed (0.1-0.5 mm wide) foliose species **[Small Cyanolichens**, page 57**]** 26

17. Thallus P+ orange (pannarin present) ..... ***Pannaria***
17. Thallus P- (pannarin absent) 18

18. Thallus light to medium gray, rarely brownish gray 19
18. Thallus dark gray to black, dark olive or light to dark brown 20

19. Hypothallus present; photobiont *Scytonema* (in chains of short cylindrical cells stacked like "coins") ..... ***Coccocarpia***
19. Hypothallus absent; photobiont *Nostoc* (in chains of globose cells) ..... ***Leptogium*** (Vol. II)

20. Thallus light to medium brown 21
20. Thallus dark olive or dark bluish to brownish black 22

21. Thallus light brown; lacking white tomentum on the lower side ..... ***Massalongia*** **(*carnosa*)**
21. Thallus medium brown; with tomentum on the lower side ..... ***Leptogium*** sect. ***Mallotium*** (Vol. II)

22. Thallus with white hairs on the upper surface or with a white tomentum on the lower surface 23
22. Thallus without white hairs or white tomentum 24

23. Thallus with white hairs (use hand lens) on the upper surface ..... ***Leptochidium*** **(*albociliatum*)**
23. Thallus with white tomentum on the lower surface ..... ***Leptogium*** **(*saturninum*)**

24. Thallus often resting on a blue-black hypothallus and often squamulose in the center; apothecia (if present) with a proper margin only ..... ***Parmeliella***
24 Thallus not on a hypothallus and not squamulose in the center; apothecia (if present) with a thalline margin 25

25. Thallus with a single-celled cortex ..... ***Leptogium*** (Vol. II)
25. Thallus without a cortex ..... ***Collema*** (Vol. II)

[Non-sorediate Small Cyanolichens]

26. Thallus small foliose or centrally crustose and with slender (up to 0.5 mm), elongated, often stellate-radiating lobules 27
26. Thallus squamulose, peltate or small fruticose (fruticulose), or if crustose then without distinctly stellate-radiating lobes 31

27. Lower surface blackish, upper surface olive or grayish or brownish, without isidia, upper and lower surface never concolorous 28
27. Lower surface pale or of the same color as upper surface 29

28. Upper surface grayish, longitudinally striate (marked with fine lines), often with whitish rhizines ..... ***Coccocarpia* (*stellata*)**
28. Upper surface olive to brownish, not striate, not with whitish rhizines ..... ***Placynthium***

29. Upper surface dark olive to blackish; thallus ecorticate; photobiont *Nostoc* (in chains of globose cells) ..... ***Collema*** (Vol. II)
29. Upper surface olive or olive brown, thallus at least indistinctly corticate; photobiont *Scytonema* (in chains of short cylindrical cells stacked like "coins") 30

30. Upper surface striate (marked with fine lines), thallus olive ..... ***Koerberia***
30. Upper surface not striate, thallus olive-brownish ..... ***Placynthium* (*stenophyllum* var. *isidiatum*)**

31. Thallus small fruticose (fruticulose), lobules terete or flattened but always predominantly erect 32
31. Thallus squamulose, peltate or crustose 35

32. Thallus corticate 33
32. Thallus ecorticate 34

33. Lobes smooth, shiny, regularly dichotomously branched ..... ***Polychidium* (*muscicola*)**
33. Lobes often wrinkled when dry, shiny or not, more irregularly branched, sometimes with isidia ... ***Leptogium*** (Vol. II)

34. Lobes resting on a blackish hypothallus; lobes irregularly branched, very slender (< 0.1 mm), often with more slender side branches; photobiont *Stigonema*; ascospores septate; ascus with amyloid tip .... ***Spilonema* (*revertens*)**
34. Lobes never resting on a blackish hypothallus; lobe shape various; photobiont various; ascospores never septate; asci not with amyloid tip ..... [see *Peccania*, *Lichinella*, *Paulia* and *Synalissa* in Lichinales key]

35. Blue-black prothallus present 36
35. Blue-black prothallus absent 38

36. Thallus crustose; photobiont *Scytonema* (in chains of short cylindrical cells stacked like "coins") ..... ***Placynthium* (*nigrum*)**
36. Thallus squamulose; photobiont *Nostoc* (in chains of globose cells) 37

37. Thallus light brown to olive; terpenes or fatty acids present ..... ***Fuscopannaria***
37. Thallus dark olive to blackish; terpenes and fatty acids absent ..... ***Parmeliella***

38. Photobiont *Nostoc* (in chains of globose cells) 39
38. Photobiont a single celled cyanobacterium or *Scytonema* (in chains of short cylindrical cells stacked like "coins")... ..... **I. A. Lichinales**, page 58

39. Thallus crustose 40

39. Thallus squamulose 41

40. Thallus gelationous, black or olive-black ..... ***Lempholemma***
40. Thallus not gelationous, blue to ash-gray or olive ..... ***Moelleropsis* (*nebulosa*)**

41. Thallus without a cortex ..... ***Collema*** (Vol. II)
41. Thallus with a distinct cortex 42

42. Ascospores 1(-3)-septate; apothecia with proper margin; thallus medium brown; rare in mountains of California .... ***Massalongia* (*microphylliza*)**
42. Ascospores simple (Fig. 25); apothecia with thalline margin; thallus dark bluish brown to black; common in spruce-fir to subalpine habitats ..... ***Protopannaria* (*pezizoides*)**

I. A. Lichinales

1. Thallus fruticose, lobules terete or slightly flattened but always predominantly erect and discrete 2
1. Thallus foliose, squamulose, peltate, or crustose; if appearing fruticose-lobate, then lobes ± appressed **or** lobes distinctly flattened 6

2. Cells of the photobiont surrounded by reddish, K+ purplish sheath; thallus forming small cushions of slender, terete, branched lobes; apothecia often with tiny side branched around the margin; hymenium I- (not amyloid); ascospores 8 .... ***Synalissa* (*matogrossensis*)**
2. Cells of the photobiont surrounded by yellowish-brown sheath, K-; lobe shape various; apothecia without tiny side branches along the margin; ascospores 8 or 16-32; hymenium amyloid (I+ blue) or not 3

3. Thallus lobes hollow, terete to slightly flattened; ascospores 16-32; hymenium amyloid (I+ blue); thallus forming small irregularly branched cushions ..... undescribed species of the Lichinaceae
3. Thallus lobes not hollow, shape various; ascospores 8 or 16-32; hymenium amyloid (I+ blue) or not 4

4. Thallus forming dense cushions (caespitosely branched), lobes ± terete; ascospores 8; hymenium not amyloid (I+ blue); anatomy loosely reticulate with large photobiont cells, only basally with central hyphal strands .... ***Paulia* (*caespitosa*)**
4. Thallus not forming dense cushions (caespitosely branched), branching ± dichotomous; lobes terete or occasionally slightly flattened; ascospores 8 or 16-32; hymenium always amyloid (I+ blue); anatomy usually with a thin or thick central cord which is sometimes fountain-like 5

5. Lobes with a distinct central strand of ± parallel hyphae; apothecia dark red or black when wet; ascospores 8; hymenium with red blotches; conidia filiform (thread-like), sigmoid (curved) to falcate (sickle-shaped) ..... ***Peccania***
5. Lobes with a single or a few central strands in a fountain-like arrangement; apothecia concolorous with thallus, blackish olive when wet; ascospores 16-32; hymenium covered by thalline hyphae; conidia bacilliform (cylindrical) and small .....***Lichinella*** (Vol. II)
6. Ascospores numerous, (16-) 24-64 (-128), small, < 7.5 µm 7
6. Ascospores (4-) 8, larger, > 7.5 µm or sterile [**Note:** crustose species cannot be determined properly without ascomatal characters] 10

7. Thallus stratified, lower cortex present; ascospores (32-) 64-128; ascus with an amyloid (I+ blue) tip; thallus subgelatinous when moistened ..... ***Peltula***
7. Thallus not distinctly stratified, lower cortex absent; ascospores (8-) 16-32; ascus without an amyloid (I+ blue) tip; thallus consistency various 8

8. Thallus subgelatinous, thallus color brownish-olive or brownish-yellow when wet, **not** blackish-olive; thallus areoles with air spaces; thallus crustose to crustose-squamulose ..... ***Gloeoheppia* (*polyspora*)**
8. Thallus gelatinous, thallus color blackish-olive when wet; thallus without internal air spaces, thallus shape various 9

9. Ascomata are thallinocarps, e.g. the hymenium is covered by portions of thalline hyphae, the hymenium either continuous or separated into partial hymenia, the surface of "apothecial disc" often appearing dotted, thallus shape extremely variable: foliose-fruticose with distinctly flattened lobes, branched or unbranched, squamulose to peltate or crustose; photobiont cells of various size, sheath always yellowish-brown, K-; without a colorless gelatinous sheath surrounding the entire thallus ..... ***Lichinella***
9. Ascomata are apothecia; thallus crustose or with tiny squamulose cushions; photobiont cells large, sheath usually yellowish-brown, K- but occasionally reddish and K+ purplish, often with thick colorless sheath surrounding the entire thallus ..... ***Phloeopeccania* (*pulvinulina*)** (Vol. II)

10. Thallus stratified, with a distinct upper and/or lower cortex; hyphae thick (>5 mm), vertically oriented, rarely densely reticulate (irregularly prosoplectenchymatous); not gelatinous or subgelatinous when wet; thallus squamules ± appressed, growing on soil ..... ***Heppia***
10. Thallus never corticate, hyphae usually thinner, usually reticulate (irregularly prosoplectenchymatous) or paraplectenchymatous; thallus usually gelatinous when wet, rarely subgelatinous; thallus shape various, usually growing on rock but sometimes on soil 11

11. Thallus subgelatinous, squamulose-peltate, up to 3 mm wide, the margin often crenate or placodioid, olive-brownish; apothecia open, immersed, the disc brown; hymenium divided by bands of sterile hyphae .... ***Pseudopeltula* (*heppioides*)**
11. Thallus gelatinous, in size and form not as above; apothecia immersed to sessile, disc open or punctiform; hymenium divided by bands of sterile hyphae or not divided..... 12

12. Photobiont *Nostoc* (in chains of globose cells) ..... ***Lempholemma***
[**Note:** small *Collema* species are similar but always have septate ascospores, amyloid (I+ blue) ascus apices and a different type of pycnidia; the genus is also treated among the small non-Lichinales cyanolichens]
12. Photobiont not *Nostoc* (in chains of globose cells) 13

13. Thallus foliose-peltate, squamulose-peltate, not crustose; if appearing fruticose, then lobes distinctly flattened 14
13. Thallus (at least appearing as) crustose 18

[Thallus more or less foliose with flattened lobes to distinctly squamulose-peltate]

14. Apothecia with red patches in the upper parts of the hymenium; conidia large (>15 µm), falcate (sickle-shaped) to sigmoid (curved); subhymenium connected to the central strand forming a stipe; thallus variously shaped: ± foliose or with appressed, radiating, gyrose lobes ..... ***Peccania***
14. Apothecia without red patches in the upper parts of the hymenium; conidia less than 15 µm long; subhymenium elongated as a stipe or not; thallus variously shaped 15

15. Thallus surface warty-papillose, thallus foliose, lobes ± appressed and not distinctly ascending, sparingly branched, the lobules rotund, 2-5 mm wide ..... ***Thyrea* (*pachyphylla*)**
15. Thallus surface not warty-papillose, thallus foliose to foliose-fruticose, repeatedly and deeply branched, ascending or not 16

16. Thallus rosette-shaped; lobes lingulate (tongue-shaped), appressed to erect, narrow (*c.* 0.5 - 1 mm), with lower side furrowed; dichotomously divided, often with globose to scale-like isidia ..... ***Digitothyrea***
16. Thallus irregularly rosette-shaped; lobes not lingulate, appressed to erect, usually broader (1 - 5 mm), with or without isidia 17

17. Thallus blackish, usually not pruinose, irregularly branched, the lobes erect, often with globose isidia or lobes ± flat but conspicuously folded (plicate) ..... ***Lichinella*** **(**if sterile: ***nigritella*** and ***cribellifera*****)**
17. Thallus grayish-pruinose, irregularly branched, the lobes ± flat but with ascending, branched margins; small globose isidia may be present ..... ***Thyrea*** **(*confusa*)**

[Thallus (appearing) crustose]

18. Thallus subfruticose, composed of numerous confluent tiny cushions giving the whole thallus a crustose appearance, the cushions composed of tiny closely aggregated subfruticose lobules; anatomy paraplectenchymatous; on calcareous soil crusts over limestone ..... ***Peccania*** **(*arizonica*)**
18. Thallus truly crustose (rarely subfruticose); anatomy **not** paraplectenchymatous; usually on rocks or thin soil crust on rocks 19

19. Anatomy loosely reticulate (irregularly prosoplectenchymatous); photobiont cells large, surrounded by a thick gelatinous sheath (> 2 µm); thallus tiny squamulose 20
19. Anatomy ± paraplectenchymatous or densely reticulate; photobiont cells small, surrounded by a thin gelatinous sheath (< 1 µm); thallus crustose 22

20. Thallus roundish, up to 4 mm in diameter; surface tessellate (mosaic-like, checkered); margin effigurate ("surface areoles" enlarged along the margins); apothecia small, immersed, the disc flat ..... ***Paulia*** **(*myriocarpa*)**
20. Thallus otherwise, not distinctly tessellate and effigurate; apothecia larger, the disc depressed or urceolate (urn-shaped) 21

21. Thallus small squamulose-peltate, 0.25-2 mm; surface smooth, crenate or notched; apothecia with a prominent thalline margin; proper exciple lacking; on volcanic rock ..... ***Phloeopeccania*** ["***major***"] (Vol. II)
21. Thallus small squamulose but appearing crustose; surface rough; apothecia with a distinct but not prominent thalline margin; proper exciple thin but distinct, mostly on limestone ..... ***Anema*** **(*progidulum*)**

22. Areoles quite large, 0.5 - 2 mm, apothecia immersed to semi-immersed, discs open and expanded, well visible at least when moistened, discs sometimes umbonate or divided; thallus composed of upright growing densely packed "lobules", "lobules" up to 50 µm broad 23
22. Areoles usually smaller, 0.1 - 1 mm, apothecia immersed to sessile, discs often punctiform, rarely expanded (if expanded, then not surrounded by a crenate or nodulose margin) or disc not conspicuously blackish colored when moistened; thallus not composed of "lobules" 24

23. Surface of thallus areoles almost regularly tessellate, apothecial disc open, expanded (to 0.5 mm), sometimes umbonate but hymenium not multiply divided; margin warty to nodulose; exciple distinct; paraphyses apically distinctly moniliform; on limestone ..... ***Stromatella*** **(*bermudana*)**
23. Surface of thallus areoles rough, not finely-tessellate (mosaic-like, checkered); apothecial disc indistinct in dry state, in moist condition disc with conspicuous black dots reflecting multiply divided hymenium; margin not crenate or nodulose; exciple distinct; paraphyses apically not distinctly moniliform; on seepage surfaces .... ***Metamelanea*** **(*melambola*)** (Vol. II)

24. Ascospores large, (12.5-) 15-17.5 (-22.5) µm long; entire exciple yellowish to golden colored, distinct; on limestone (especially caliche) ..... ***Lemmopsis*** **(*arnoldiana*)**
24. Ascospores usually smaller; exciple not or faintly colored; on various rock substrates 25

25. Thallus of dispersed to aggregated areoles, the surface warty; proper exciple thick at least in mature apothecia (approximately as thick as a thalline margin or thicker); paraphyses thin, not moniliform; on mosses or eroded siliceous rock (especially volcanic rock) ..... ***Porocyphus* (*coccodes* s.l.)**
25. Thallus not as above; proper exciple, if present, much thinner than thalline margin; paraphyses moniliform or not; on calcareous or non-calcareous rocks 26

26. Sheath of the photobiont cells reddish, K+ violet; ascus usually thick-walled, lecanoralean (opens with a rostrum) with an amyloid (I+ blue) inner layer or rather thick-walled but inner amyloid (I+ blue) layer indistinct or lacking; paraphyses moniliform; on non-calcareous rock ..... ***Pyrenopsis*** (Vol. II)
26. Sheath yellowish-brown, K-; ascus always thin-walled, prototunicate, non-amyloid (K/I-) ; paraphyses not distinctly moniliform; usually on calcareous rock or soil ..... ***Psorotichia*** (Vol. II)

II. LIRELLATE LICHENS

by B. D. Ryan

[**Note:** genera such as *Arthonia*, with ascomata that are mainly irregular or stellate rather than distinctly elongated, are treated in key **XII. CRUSTOSE DISCOLICHENS** (Vol. II).]

1. Ascospores simple; ascomata mostly elongated parallel to the texture of the wooden substrate .... ***Xylographa*** (Vol. II)
1. Ascospores septate or muriform (Fig. 25); ascomata usually irregularly oriented; on various substrates 2

2. Ascospores I+ purple, septate, fusiform (spindle-shaped, Fig. 25) with several lenticular (lens-shaped) to spherical cells, the cell walls irregularly thickened; asci unitunicate, I- (but hymenial gelatin may be I+ blue) .... **Graphidaceae** (Vol. II)
2. Ascospores I-, septate and fusiform (Fig. 25) with several cubical to rectangular cells, **or** ascospores ellipsoid and simple (Fig. 25), the walls evenly thin; asci bitunicate 3

3. Ascospores 1-septate, ± distinctly brown when mature[Lecanorales: family uncertain] .... ***Melaspilea* (*constrictella*)** (Vol. II)
3. Ascospores 3- or more-septate, hyaline or brown 4

4. Thallus sorediate; California [non-Sonoran] ..... **"*Sclerophyton*" (*occidentale*)**
4. Thallus not sorediate (at least in Sonoran species) 5

5. Ascomata with hyaline or pale brown hyphae only [systematic position unknown] .... **"*Chiodecton*" (*ochroleucum*)** (Vol. II)
5. Ascomata at least with some layers of carbonaceous (strongly blackened) hyphae [Arthoniales] 6

6. Ascomata with a thalline margin ..... **II. A. Roccellaceae**, page 62
6. Ascomata without a thalline margin [Opegraphaceae s.l.] 7

7. Ascomata ± immersed in the thallus; margin and exciple scarcely developed margin; "subhymenium" hyaline 8
7. Ascomata sessile (less often immersed); margin and exciple ± well developed ("lecideine" and dark); "subhymenium" often brownish or yellowish 9

8. Ascospores distinctly dark (at least when mature), not curved, constricted at least at the transverse (median) septum, ± thick walled and rounded at the ends, with gelatinous sheath (*circumscriptum*-type); hamathecium of thick paraphysoids ..... ***Sclerophyton*** (excluding "*S. occidentale*")

8. Ascospores hyaline (at most brownish when old), often slightly curved, not constricted, thin-walled with ± narrowed ends and gelatinous sheath (*vulgata*-type) or thick-walled with rounded ends and without gelatinous sheath (*enterographa*-type); hamathecium of very slender paraphyses ..... ***Enterographa*** (Vol. II)

9. Discs covered by persistent whitish, grayish or yellowish pruina; ascomatal margin dull, pruinose; some exciple hyphae differentiated in margin; base of exciple extending towards the medulla or substrate; hamathecium with distinct strands of interascal filaments (pluricarpocentral); exciple and pseudoepithecium with granules and/or crystals; asci clavate (club-shaped), *grumulosa*-type, perispore absent ..... ***Lecanographa*** (Vol. II)
9. Discs epruinose; ascomatal margin shiny, epruinose; exciple hyphae not differentiated; base of exciple delimited in medulla or substrate; hamathecium without distinct strands of interascal filaments (monocarpocentral), without hymenial bands; exciple and pseudoepithecium without granules and crystals; asci clavate-cylindrical, *vulgata*-type, perispore thick and very reactive ..... ***Opegrapha*** (Vol. II)

II. A. Roccellaceae

by A. Tehler

1. Thallus crustose 2
1. Thallus fruticose, subfruticose or subfoliose or placodioid 7

2. Thallus C+ red 3
2. Thallus C- 4

3. Ascospores (if present) 3-septate; saxicolous or corticolous; cortex hyphae anticlinally arranged; lower medulla not brown ..... ***Dirina***
3. Ascospores pluriseptate; corticolous; cortex hyphae mixed intertwined or sometimes partly anticlinal; medulla .... **"*Schismatomma*" (*pluriloculare*)**

4. Discs tomentose; thallus K+ yellow/red (norstictic acid); ascomata up to 1.6 mm in diameter, stromatoid (assembled in a group and surrounded by a plectenchyma of sterile, darkened hyphae); thallus without a cortex .... ***Syncesia* (*depressa*)**
4. Discs pruinose; thallus without norstictic acid (but unidentified K+ yellow then red substance present in *Roccellina conformis*); ascomata not stromatoid; thallus with a cortex 5

5. Ascomata usually > 1 mm diameter [but 0.8-1.2 mm in *R. conformis*], often stromatoid; thallus cortex conspicuous, 20-50 µm thick, cortical hyphae irregularly arranged; lower medulla brown ..... ***Roccellina***
5. Ascomata rarely > 1 mm diameter, never stromatoid; thallus cortex thin or inconspicuous, up to 10 µm thick 6

6. Ascomata sessile, 0.2-1 mm diameter; thallus P+ yellow, with psoromic acid ..... ***Sigridea* (*californica*)**
6. Ascomata nearly immersed, 0.2-0.5 mm diameter; thallus P-, with roccellic acid ..... ***Schismatomma* (*rediunta*)**

7. With ascomata 8
7. Without ascomata 13

8 Ascospores brown; spore surface verrucose (warty); ascomata terminal; schizopeltic acid present .... ***Schizopelte*** **(** usually ***californica*****)**
8. Ascospores hyaline; spore surface smooth; ascomata (if present) lateral, only occasionally terminal; without schizopeltic acid 9

9. Thallus fruticose 10
9. Thallus subfruticose or foliose or placodioid 13

10. Thallus C+ red ..... ***Roccella* (*decipiens*)**
10. Thallus C- 11

11. Branches white-grayish, terete; cortex with irregularly arranged to anticlinal hyphae ..... ***Roccella* (*portentosa*)**
11. Branches brown, flattened; cortex with periclinal hyphae ..... ***Dendrographa***

12. Ascomata lirellate; foliose or placodioid ..... ***Hubbsia* (*californica*)**
12. Ascomata apothecioid (disk-like) or stromatoid (assembled in a group and surrounded by a plectenchyma of sterile, darkened hyphae); subfruticose ..... ***Roccellina* (*franciscana*)**

13. Thallus subfruticose or subfoliose or placodioid, hollow, fragile ..... ***Hubbsia* (*parishii*)**
13 Thallus fruticose, solid, firm 14

14. Thallus C+ red, sorediate; cortex with irregularly arranged to anticlinal hyphae..... ***Roccella* (*peruensis*)**
14. Thallus C-, never sorediate; cortex with periclinal hyphae ..... ***Dendrographa***

III. PYRENOLICHENS

(lichens with perithecioid ascomata and related non-lichenized genera)

by B. D. Ryan, A. Aptroot and O. Breuss

1. Ascospores many (30-300 per ascus) 2
1. Ascospores 1-8 per ascus 3

2. Ascospores (0-) 1-septate; perithecia sunken in thalline warts, exciple pale; on bark or rocks ..... ***Thelopsis* (*isiaca*)**
2. Ascospores simple; perithecia black; exciple dark; on bark ..... ***Trimmatothele* (*umbellulariae*)**

3. Ascomata apothecia a with pale wall; ascospores rather large (40-200 µm long); simple with thick outer wall (often over 10 µm thick) and double walled ..... ***Pertusaria***
3. Ascomata perithecia (or pseudothecia) with a dark wall; ascospores mostly smaller; septate or muriform (Fig. 25) with a thin-wall (*c.* 1 µm thick) 4

4. Paraphyses not persistent (dissolving into a poorly differentiated hymenial gelatin); hymenial gelatin I+ pinkish orange, orange-red or bluish; almost always growing on rock ..... **III. A.Verrucariaceae**, page 64
4. Paraphyses or paraphysoids persistent; hymenium K/I- (non-amyloid); mostly growing on bark, old wood, leaves or bryophytes, rarely on rock 5
5. Ascospores simple, hyaline ..... ***Thrombium***
5. Ascospores septate, hyaline or brown ..... **III. B. Non-verrucarioid Pyrenolichens**, page 65

III. A.Verrucariaceae (ascospores simple or with true septa; asci thin-walled; almost all lichenized, with coccoid green algae; sometimes with hymenial algae)

by O. Breuss and B. D. Ryan

1. Perithecia pale or hyaline; ascospores with transverse septa and/or with additional longitudinal septa (muriform, Fig. 25) ..... ***Psoroglaena*** (Vol. II)
1. Perithecia dark brown to black or perithecia with involucrellum 2

2. Hymenial gelatin containing algae; ascospores muriform (Fig. 25), usually brown at maturity 3
2. Hymenial gelatin not containing algae; ascospores septation and coloration various 4

3. Thallus squamulose (squamules developing individually from a prothallus, not by cracking, distinctly set off from the substratum), attached by rhizoidal hyphae or rhizines; usually on soil or moss ..... ***Endocarpon***
3. Thallus crustose, continuous to warty rimose-areolate, deriving from the cracking of a primarily continuous crust (most clearly seen in young thallus parts); usually within or upon rocks ..... ***Staurothele***

4. Thallus mostly squamulose to rarely umbilicate; distinctly detachable from the substratum [i.e., revealing an underside, thalli developing individually, not by cracking], with or without rhizines or rhizoid hyphae 5

4. Thallus crustose, often endolithic, evanescent to thickly areolate, the areoles deriving from the cracking of a primarily continuous crust; not detachable from the substrate; without rhizines or rhizoid hyphae 12

5. Thallus small (less than 1 mm across), pale greenish blue, the curved-up margin ± sorediate; mostly over mosses and other lichens [The perithecia occasionally present on this species are by most authors regarded as belonging to those of a lichenicolous fungus] ..... ***Normandina* (*pulchella*)** (Vol. II)
5. Thallus usually larger; gray to greenish gray or a shade of brown; not sorediate; on various substrates 6

6. Ascospores not septate (rarely with a pseudoseptum) 7
6. Ascospores with transverse septa and/or with additional longitudinal septa (muriform, Fig. 25) 11

7. Thallus umbilicate, or if appearing squamulose then squamules attached by a central point; lower cortex of anticlinally arranged, strongly conglutinated hyphae with cells in distinct vertical columns ..... ***Dermatocarpon*** (Vol. II)
7. Thallus squamulose; squamules ± broadly attached by rhizoidal hyphae or areolate-subsquamulose (i.e., thallus cracked into areoles, the margins of which may become incised-lobed) with stipe-like attaching organs; lower cortex, if present, not as above 8

8. Thallus squamulose; rhizohyphal felt usually well developed and penetrating the substratum, some species with additional rhizines; mostly on soil, moss or bark (*Catapyrenium* s.l.) 9
8. Thallus areolate-subsquamulose; without rhizohyphal felt, attachment by constricted bases or stipes (if rhizine-like structures present, then not penetrating the substratum); on rock ..... ***Placopyrenium* (*heppioides*)**

9. Upper cortex thin (< 30 µm), indistinctly delimited [in section: unevenly delimited against algal layer with algal cells ± protruding into the cortex], of small (5-8 µm) roundish-angular cells; asci clavate (club-shaped) ... ***Catapyrenium*** s.str.
9. Upper cortex thicker (25-100 µm), distinctly delimited (section: the border against the algal layer forms a straight distinct line), of larger cells (7-14 µm); asci clavate (club-shaped) or cylindrical 10

10. Asci clavate (club-shaped) even when young; ascospores biseriate (aligned in two rows); medulla prosoplectenchymatous (± filamentous) and with well delimited blackish brown basal zone (however without a paraplectenchymatous lower cortex); exciple dark ..... ***Clavascidium* (*umbrinum*)**

10. Asci at least when young distinctly cylindrical; ascospores uniseriate (aligned in a single row); medulla not as above; exciple colorless or light brown ..... ***Placidium***

11. Ascospores muriform (Fig. 25), usually 2 per ascus; thallus finely squamulose, paraplectenchymatous throughout, with tiny hyphal cortical hairs ..... ***Agonimia***
11. Ascospores 1-septate, 8 per ascus; thallus not as above ..... ***Placidiopsis* (*cinerascens*)**

12. Ascospores simple or with 1 (-3) transverse (median) septa 13
12. Ascospores weakly to strongly muriform, often becoming brownish ..... ***Polyblastia*** (Vol. II)

13. Thallus within the substrate or thinly superficial, continuous to rimose-areolate, rarely granular or subsquamulose; areoles usually broadly appressed to the substratum, not corticate below; pycnidia of *Staurothele* type; ascospores simple ..... ***Verrucaria*** (Vol. II)
13. Thallus thickly crustose, rimose-areolate or subsquamulose or placodioid; areoles with lateral and lower cortices, attached by stipe-like holdfasts; pycnidia of *Dermatocarpon* type; ascospores simple or 1 (-3) septate ..... ***Placopyrenium***

III. B. Non-verrucarioid Pyrenolichens

by A. Aptroot and B. D. Ryan

1. Ascospores only with transverse (median) septa 2
1. Ascospores muriform (Fig. 25) at maturity 15

2. Ascospores remaining hyaline (only overmature ascospores sometimes becoming brown 3
2. Ascospores deep brown at maturity 12

3. Ascospores distoseptate, with lenticular (lens-shaped) lumina ..... ***Pseudopyrenula* (*subnudata*)**
3. Ascospores euseptate, with angular lumina 4

4. Ascospores more than 5 times as long as wide 5
4. Ascospores less than 5 times as long as wide 7

5. Ascospores 1-septate; thallus not lichenized ..... ***Leptorhaphis* (*atomaria*)**
5. Ascospores 3-17-septate; thallus lichenized 6

6. Interascal filaments branched; asci with a distinct tholus; conidia with gelatinous appendages (best observed in India Ink) ..... ***Strigula* (*stigmatella*)**
6. Interascal filaments unbranched; asci without a tholus, with a minute refractive ring; conidia without gelatinous appendages ..... ***Porina***

7. Hamathecium almost pseudoparenchymatous; asci globose 8
7. Hamathecium consisting of thread-like interascal filaments; asci clavate (club-shaped) to cylindrical 9

8. Ascocarps 2-8 aggregated below a blackened clypeus ..... ***Tomasellia***
8. Ascocarps usually solitary, only occasionally aggregated ..... ***Mycoporum* (*hippocastani*)**

9. Asci cylindrical and ascospores short-ellipsoid (Fig. 25), ornamented; Sonoran species on (usually calciferous) rock 10
9. Not at the same time with cylindrical asci and short-ellipsoid and ornamented ascospores; Sonoran species on bark or wood 11

10. Photobiont trentepohlioid; terrestrial species ..... ***Acrocordia* (*conoidea*)**
10. Photobiont cyanobacterial; maritime-aquatic species ..... ***Pyrenocollema***

11. Hamathecium consisting of paraphysoids, anastomosing above the asci ..... ***Anisomeridium***
11. Hamathecium consisting of tapering or moniliform cellular pseudoparaphyses or nearly pseudoparenchymatous, not anastomosing above the asci ..... ***Arthopyrenia***

12. Ascospores distoseptate 13
12. Ascospores euseptate 14

13. Ascospores 1-septate; thallus not lichenized ..... ***Distopyrenis* (*americana*)**
13. Ascospores 3- (or more)-septate; thallus lichenized ..... ***Pyrenula***

14. Perithecioid ascomata with a continuing wall below the hamathecium, with elongated cells in the "corners" ..... ***Kirschsteiniothelia***
14. Perithecioid ascomata with a dimidiate wall (covering only the upper half of the ascoma)..... ***Peridiothelia* (*fuliguncta*)**

15. Ascospores distoseptate, brown when mature; thallus lichenized ..... ***Pyrenula***
15. Ascospores euseptate, usually remaining hyaline; thallus lichenized or not 16

16. Thallus not lichenized; interascal filaments not anastomosing ..... ***Julella***
16. Thallus lichenized; interascal filaments anastomosing 17

17. Ascus tips K/I+ strong blue (amyloid) ..... ***Protothelenella* (*sphinctrinoidella*)**
17. Ascus tips K/I- (non-amyloid) 18

18. Periphysoids present; ascus with an indentation at the apex ..... ***Chromatochromys* (*muscorum*)**
18. Periphysoids absent; ascus apex without indentation ..... ***Thelenella***

V. LICHENS WITH TRENTEPOHLIOD PHOTOBIONTS

by B. D. Ryan

[**Note:** Trentepohlioid photobionts are true (eukaryotic) algae and characterized by a ± yellow to orange color when fresh (fades in the herbarium). The thallus of free-living or cultured trentepohlioid algae is arranged in ± elongated cells forming long filaments. The cell wall always show a strongly react violet with chlor-zinc iodine. However, no pyrenoids can be found and the cell content thus never reacts with iodine (non-amyloid, I-). The keys in this set are primarily for the members of the Arthoniales, which are classified by Tehler (1996) as "bitunicate ascoloculars" (except for the Chrysothrichaceae and some species in the Arthoniaceae, which have coccoid green algae). Although these keys are primarily aimed towards crustose lichens with roundish, disc-like ascomata, arthonialean genera with other types of ascomata or thallus are included here. Cross-reference with other keys in this flora is made with groups of lichens having trentepohlioid algae.]

1. Thallus fruticose, subfruticose, or subfoliose or placodioid ..... **II. A. Roccellaceae**, page 62
1. Thallus crustose 2

2. Ascomata, asci, and ascospores absent (or apparently so) ..... **XI. STERILE CRUSTOSE LICHENS** (Vol. II)
2. Ascomata (or at least asci and ascospores), present 3

3. Ascomata perithecioid (roundish, opening by a small pore) ..... **V. A. Opegraphaceae** (a few species only), page 68
3. Ascomata (if present) otherwise 4

4. Ascomata calicioid (with a mazaedium of loose, dark ascospores and/or often distinctly stalked) .... **IV. CALICIOID LICHENS** (Vol. II)
4. Ascomata otherwise 5

5. Ascomata lirellate (± elongated, closed or open) ..... **II. LIRELLATE LICHENS**, page 61
5. Ascomata apothecioid (roundish, with ± exposed disc) 6

6. Ascospores simple ..... ***Hymenelia*** (Vol. II)
6. Ascospores septate to muriform (Fig. 25) 7

7. Ascospores muriform to submuriform, with transverse (median) as well as occasional longitudinal (or diagonal) septa 8
7. Ascospores with transverse septa only 12

8. Well developed ascomata absent; asci loosely scattered across the thallus; rarely aggregated in distinct thallus patches (stromata), but then always separated by hydrophobic (water resistant) plectenchyma; asci globose on a distinct stalk. [Arthoniales: Arthoniaceae s.l.] .....***Cryptothecia*** **(**"sp.", Vol. II**)**
8. Well developed ascomata present or at least asci in well-delimited patches (stromata) which are usually hydrophilic (soaking up water); asci mostly clavate (club-shaped) or pyriform (pear-shaped, Fig. 25) and without a distinct stalk 9

9. Ascomata without distinct exciple, ascolocular [Arthoniales: Arthoniaceae] ..... ***Arthothelium*** (Vol. II)
9. Ascomata with distinct exciple, ascohymenial 10

10. Ascospores with ± lenticular (lens-shaped) or globose cell lumina, mostly attenuate; ascocarps with thalline margin surrounding a proper margin (in some species with both margins distinctly separated) 11
10. Ascospores with ± cylindrical cell lumina; ascocarps with a single margin, or zeorine but without a distinct separation of the two margins ..... ***Gyalecta*** (Vol. II)

11. Exciple with periphysoids on the inside; columella always lacking ..... ***Thelotrema*** (Vol. II)
11. Exciple without periphysoids; columella often present and carbonaceous ..... ***Ocellularia*** (Vol. II)

12. Ascospores ± distinctly brown when mature 13
12. Ascospores hyaline (at most slightly brownish when overmature) 15

13. Ascospores 1-septate; thallus immersed, often evanescent or scarcely apparent .... ***Melaspilea*** **(*constrictella*)** (Vol. II) ..... Opegraphaceae
13. Ascospores 3- or more-septate; thallus superficial and well developed 14

14. Thallus sorediate; ascus lecanoralean; ascospores 3-septate ..... "***Sclerophyton" occidentale*** ..... (**Note:** not treated in the flora; only known north of the region, but may eventually be found farther south)
14. Thallus [at least in Sonoran region species] not sorediate; ascus arthonialean (bitunicate with apical pore apparatus); ascospores 4-9-septate .....***Sclerophyton***

15. Ascospores 1-septate 16
15. Ascospores 3- or more-septate 17

16. Ascomata with distinct exciple, ascohymenial ..... ***Dimerella*** **(*lutea*)** (Vol. II)
16. Ascomata without distinct exciple, ascolocular [Arthoniales: Arthoniaceae] ..... ***Arthonia*** (Vol. II)

17. Ascomata ascohymenial; hamathecium of simple to sparsely branched or anastomosed paraphyses; hypothecium and proper exciple usually pale; asci various [not belonging to the Arthoniales] 18

17. Ascomata "ascolocular"; hamathecium of ± branched and anastomosing paraphysoids; hypothecium and/or proper exciple usually dark, ± black and friable, or if pale then proper exciple absent; asci with hemiamyloid (I+ reddish, K/I+ pale blue) layer in endoascus, bitunicate [Arthoniales] 20

18. Ascospores with ± cylindrical cell lumina; ascocarps with a single margin, or zeorine but without a distinct separation between the two margins 19
18. Ascospores with ± lenticular (lens-shaped) or globose cell lumina, mostly attenuate; ascocarps with thalline margin surrounding a proper margin, the two margins distinctly separated ..... ***Thelotrema* (*californicum*)** (Vol. II)

19. Ascomata at first deeply immersed, remnants of the cortex remaining attached to the disc margin after emerging through the thallus cortex; periphyses present ..... ***Ramonia* (*ablephora*)** (Vol. II)
19. Ascomata soon sessile, without cortical remnants after breaking through the thallus surface; periphyses absent .... ***Gyalecta*** (Vol. II)

20. Asci globose to pyriform (pear-shaped, Fig. 25) or broadly clavate (club-shaped) [Arthoniaceae] 21
20. Asci cylindrical or cylindrical-clavate (club-shaped) ["Roccellaceae" sensu Grube 1998] 22

21. Paraphysoids densely entwining asci; ascomata ± stromatoid (assembled in a group and surrounded by a plectenchyma of sterile, darkened hyphae) and with irregular ascus development; epithecium eroding; ascospores usually muriform (Fig. 25) ..... **(see *Arthothelium*)**
21. Paraphysoids ± loosely arranged around asci; ascomata not stromatoid, and with ± synchronized ascus development; epithecium layers persistent; ascospores only with transverse (median) septa ..... ***Arthonia*** (Vol. II)

22. All ascomatal plectenchyma hyaline or pale brown ..... "***Chiodecton*" *ochroleucum*** (Vol. II)
22. At least some ascomatal plectenchyma carbonaceous (strongly blackened) 23

23. Ascomata with thalline margin ..... **II. A. Roccellaceae**, page 62
23. Ascomata with "lecideine" margin ..... **V. A. Opegraphaceae**, page 68

V. A. Opegraphaceae

(sensu Eriksson and Hawksworth 1986)

by B. D. Ryan

[**Note:** These keys are based primarily on the information and keys provided by Egea and Torrente (1989 & 1994).]

1. With a ± differentiated layer of carbonaceous sterile hyphae ("hypothecium") directly below the asci; ascomata emerging from the thallus, usually with a pale thalline margin, the proper exciple reduced and narrow (usually not visible externally, formed by prolongation of the hypothecium), and the ascogenous layer ("subhymenium") little evident (*pitardi*-type ontogeny) ..... **II. A. Roccellaceae**, page 62
1. Without a differentiated "hypothecium"; ascomata (except in some species of *Lecanographa*) without a thalline margin, either immersed with a scarcely developed exciple and hyaline "subhymenium" (*crassa*-type ontogeny), or becoming sessile with an often prominent carbonaceous proper exciple and a ± distinct brown or yellowish "subhymenium" (*vulgata*- or *abietina*-type ontogeny) 2

2. Ascomata perithecioid, poriform or lirellate, ± immersed in the thallus, with a scarcely developed margin and a hyaline "subhymenium" (ontogeny *crassa*-type) 3

2. Ascomata apothecioid or lirellate, sessile (less often immersed), with ± well developed "lecideine" margin (dark exciple), and often brownish or yellowish "subhymenium" (ontogeny *vulgata*-type or *abietina*-type) 4

3. Ascospores distinctly dark (at least when mature), not curved, constricted at least at the transverse (median) septum, ± thick walled and rounded at the ends, with gelatinous sheath (*circumscriptum*-type); hamathecium of thick paraphysoids; ascus *circumscriptum*-type (cylindrical-clavate, with thin amyloid (I+ blue) layer on the tip of the endoascus, not extending upwards) ..... ***Sclerophyton*** **(**excluding **"*S. occidentale*")**
3. Ascospores hyaline (at most brownish when old), often slightly curved, not constricted, thin-walled with ± narrowed ends and gelatinous sheath (*vulgata*-type) or thick-walled with rounded ends and without gelatinous sheath (*enterographa*-type); hamathecium of very slender paraphyses; ascus *enterographa*-type (cylindrical, with endoascus strongly hemiamyloid (I+ reddish, K/I+ pale blue) when young, and apex of mature asci with thick amyloid (I+ blue) structure extending upwards) ..... ***Enterographa*** (Vol. II)

4. Ascomata ± elongated, lirellate; ascospores with gelatinous sheaths ..... (**II. LIRELLATE**: **LICHENS *Opegrapha*** and ***Lecanographa*** page 62, choice 9)
4. Ascomata roundish, apothecioid; ascospores (except in *Lecanographa*) without gelatinous sheaths 5

5. Paraphysoids easily separated, with dispersed dichotomous branches, little anastomosing; hamathecium without distinct strands of interascal filaments (monocarpocentral); discs epruinose; asci *Bactrospora*-type (with a large amyloid (I+ blue) apical dome), easily separated from ascogenous hyphae when squashed in K .. ***Bactrospora*** (Vol. II)
5. Paraphysoids conglutinated, weakly to ± moderately but irregularly branched and anastomosing; hamathecium with distinct strands of interascal filaments (pluricarpocentral); discs pruinose; asci *abietina*-type or *grumulosa*-type, not easily separated from the ascogenous hyphae 6

6. Asci *grumulosa*-type [the entire endoascus weakly hemiamyloid (I+ reddish, K/I+ pale blue); apex with a ring-structure little or not differentiated, at most a tiny amyloid (I+ blue) structure present]; ascospores with gelatinous sheath; ascomata immersed or sessile, not or scarcely constricted at base; interascal filaments paraphysoids, much branched and anastomosed ..... ***Lecanographa*** (Vol. II)
6. Asci *abietina*-type [the internal endoascus strongly hemiamyloid (I+ reddish, K/I+ pale blue); apex with a conspicuous and relatively wide ring-structure]; ascospores without gelatinous sheath; ascomata sessile, constricted at base; interascal filaments paraphyses, weakly to moderately branched and anastomosed 7

7. Ascomata epruinose or with brightly colored pruina and only on the disc; margin shiny; exciple carbonaceous (strongly blackened), the hyphae smooth, with gelatinized walls, not distinguishable in K; granules of the pseudoepithecium yellowish to reddish, K+ yellow or purple; ascospore wall thick; perispore thick; endospore differentiated ..... ***Cresponea*** (Vol. II)
7. Ascomata with pruina of the same color as that of the thallus, and present on both disc and margin; margin dull; exciple hyphae verrucose (warty), those in the outer part distinguishable in K; granules of the pseudoepithecium K-; ascospore wall thin; perispore thin; endospore not differentiated ..... ***Lecanactis*** (Vol. II)

VII. FRUTICOSE LICHENS

(with coccoid green algae)

by B. D. Ryan

1. Thallus orange, K+ purple, or at least with orange, K+ purple apothecia (containing anthraquinones) ..... **VI. ORANGE LICHENS** (Vol. II)
1. Thallus not orange, usually brown, olive or black (if yellow, then K- or K+ weakly reddish, no anthraquinones) 2

2. Thallus distinctly brown (pale to very dark), olive or reddish ..... **VII. Group A**, page 70
2. Thallus not brown, olive or reddish 3

3. Thallus bright yellow (pulvinic acid derivatives) or yellow green, KC+ yellow (usnic acid) ..... **VII. Group B**, page 71
3. Thallus not yellow or yellow green; rather white or a shade of gray ..... **VII. Group C**, page 72

VII. Group A. Thallus distinctly brown, olive or reddish

1. Branches distinctly flattened and thin in cross section (but often rolled inward) 2
1. Branches terete to irregularly flattened in cross-section (not rolled inward) 3

2. Growing loosely on soil, at high elevations, very rare in the Sonoran region ..... ***Cetraria*** (***ericetorum***)
2. Growing attached to bark at low to moderate elevations, fairly common in the Sonoran region .... see **VIII. FOLIOSE LICHENS** (*Kaernefeltia merrillii* and *Tuckermannopsis*)

3. Thallus with cyphellae; ascospores brown, muriform (Fig. 25); Mexico, barely reaching the southern edge of the Sonoran region ..... ***Oropogon***
3. Thallus without cyphellae (but sometimes with pseudocyphellae); ascospores hyaline, or if brown then simple; mostly in northern parts of the region 4

4. Thallus with central cord; medulla reddish (surface relatively pale yellowish) ..... ***Usnea*** (***rubicunda***) (Vol. II)
4. Thallus without central cord; medulla white (surface dark, some shade of brown) 5

5. Thallus tomentose or pubescent (with fine hair); coastal ..... ***Tornabaea*** (***scutellifera***)
5. Thallus neither tomentose nor pubescent 6

6. Thallus forming horizontally compressed mats or rosettes, closely appressed to rock and attached over most parts of the thallus; usually alpine, or at least at higher elevations ..... ***Pseudephebe***
6. Thallus forming basally attached tufts or becoming pendent, usually on bark or wood (Sonoran region); mostly at low or intermediate elevations (not alpine) 7

7. Thallus (in Sonoran region) usually with soralia; containing phenolic substances (at least the soralia frequently P+ orange-red); and mostly 3-5 cm or more long; surface often shiny; cortex 25-65 µm thick, its surface ± smooth in cross-section, crust-like when viewed from above, with hyphal cells periclinally elongated and straight-walled throughout; apothecia and pycnidia rare or absent; mostly in Arizona or inland parts of Mexico ..... ***Bryoria***
7. Thallus without soredia and lacking phenolic substances (spot tests negative); Sonoran region material $\leq$ 2 (-3) cm long; surface ± dull; cortex $\leq$ 25 (-27) µm thick, its surface knobby or rough in cross section, and with cells ± isodiametric or irregularly wavy in outline (viewed from above; cells below surface periclinally elongated and straight-walled); apothecia or at least pycnidia often present, sometimes abundant; coastal region, mostly California and northern Baja California 8

8. Thallus reddish brown, very brittle; cortical surface knobby in cross-section, forming a jigsaw pattern (with cell walls wavy and interdigitating) when viewed from above (best seen on thinner branches); paraphyses tips in K distinctly capitate and remaining yellow-brown; cell walls of thallus without lichenan ..... ***Nodobryoria***
8. Thallus grayish to pale olive brown or greenish black, not very brittle; cortical surface rough (to knobby in places), areolate (with cell walls straight); paraphyses tips in K only slightly swollen and turning from ± grayish olive to purplish or strong brown; cell walls of thallus with lichenan ..... ***Kaernefeltia* (*merrillii*)**

VII. Group B. **Thallus pale to bright yellow or yellow-green** (K-, rarely weakly reddish)

1. With squamules at the base or on distinct stalks (podetia); stalks usually hollow; apothecia, if present, lacking a thalline margin, red or brown; usually on soil, moss, detritus, or decaying wood ..... ***Cladonia***
1. Without squamules; thallus usually solid (except in some *Ramalina* spp.); apothecia, if present, with a thalline margin, never red; usually on bark, wood, or rock 2

2. Thallus bright greenish yellow, KC- (vulpinic acid or other pulvinic acid derivatives) ..... ***Letharia***
2. Thallus pale to dark yellowish or yellowish green, usually KC+ yellow (usnic acid, sometimes only in traces) 3

3. Thallus entirely ecorticate, with granular to powdery surface throughout; forming dense, low (< 0.5 cm high) mats or mounds of tiny (< 0.5 mm diameter) stalks; ± firmly attached to soil (or rock), usually in coastal areas (rare in montane areas of Arizona) ..... ***Leprocaulon* (*microscopicum*)**
3. Thallus corticate, sometimes becoming sorediate or at least partly decorticate, but never entirely granular or powdery; usually forming larger, thicker, tufted to pendent growths, mostly with coarser stalks; substrate and distribution various, but if growing on soil then very loosely attached and quite coarse 4

4. Thallus usually with distinct central cord which becomes visible when the cortex is broken by stretching or bending, or sometimes (tropical species outside the Sonoran region) with a hollow central axis; ± rounded in cross-section, often with numerous short side branches (fibrils) ..... ***Usnea*** (Vol. II)
4. Thallus without central cord or hollow axis, terete to angular or flattened; without fibrils 5

5. Branches ± rounded in cross-section (to angular or flattened near the axil); pseudocyphellae abundant, conspicuous, markedly raised; cortical hyphae with long cells running ± parallel to surface; apothecia (in Sonoran material) usually present; discs usually brown to black; ascospores brown at maturity, with a thick hyaline outer layer, non-septate, 2-4 per ascus ..... ***Alectoria***
5. Thallus ± flattened or angular in cross-section, or if terete then pseudocyphellae absent or not raised (pale striae abundant in some *Ramalina* spp.); cortical hyphae, if evident, ± perpendicular to the surface, or at least not primarily parallel to it; apothecia present or not; discs pale, yellowish, orangish, or whitish; ascospores hyaline, without thick outer layer, septate or not, usually 8 per ascus 6

6. Branches usually soft, limp; medulla ± loose; chondroid strands lacking, but medulla with several tougher cords (of denser consistency) running through it; one surface often paler and sometimes becoming decorticate; apothecia in Sonoran material absent or very rare 7
6. Branches (at least when dry) usually firm, leathery, or brittle; medulla compact to loose or hollow; chondroid strands present or absent; all surfaces usually concolorous and corticate; apothecia common in some species; ascospores 1- or more-septate [*Ramalina* s.l.] 8

7. Medulla fibrous to arachnoid, ± loose but with cords of denser consistency; with evernic acid (UV- or faint) or divaricatic acid (UV+ ice blue); cephalodia absent; one side sometimes paler, but usually with thin but distinct cortex, common in southern California and central Arizona ..... ***Evernia***
7. Medulla arachnoid but dense, cottony; with bourgeanic acid (UV-); orangish cephalodia present; one side often becoming decorticate; rare, southern California ..... ***Ramalina* (*lacera*)** (Vol. II)

8. Exterior cortex with palisade cell lines usually overlying supportive plectenchyma; chondroid strands absent or indistinct (medulla "fluffy"), or free from the cortex; pycnidia often present and conspicuous, black, chambered; branches terete to angular or flattened but not canaliculate (channeled), usually > 1 mm thick at least near the base; surface often rather distinctly yellowish, opaque, dull; pseudocyphellae (in North American species) and striae absent; sometimes with triterpenes (and the associated mold-like material on the surface). 9

8. Cortex otherwise; chondroid strands usually present and at least partly continuous with the cortex (medulla "cobwebby"); pycnidia absent or inconspicuous, pale (rarely black, but not chambered); branches flattened to canaliculate, less often terete, usually ≤ 0.5 mm thick; surface usually with grayish or greenish tones predominating, sometimes slightly translucent or shiny, often with pseudocyphellae or striae; without triterpenes 10

9. Medulla with chondroid strands free from the cortex; lichen substances primarily ß-orcinol depsidones (salazinic, hypoprotocetraric, norstictic, or protocetraric acids) or depsides (divaricatic or sekikaic acids), rarely without depsides or depsidones; triterpenes absent or present as accessory constituents; skyrin (red-orange pigment) concentrated at the base of the thallus; cortex with an additional palisade layer; irregular reticulate surface ridges usually conspicuous ..... ***Niebla*** (Vol. II)

9. Medulla lacking chondroid strands; lichen substances primarily terpenes ([-] -16-hydroxykaurane and/or zeorin), rarely without lichen substances or with meta-depside (3,5-dichlorolecanorate); ß-orcinol depsidones (hypoprotocetraric, salazinic, norstictic, or psoromic acids) absent or present as accessory secondary metabolites; skyrin absent; cortex without an additional palisade layer; surface ridges, if visible, indistinct, appearing more like internal ribs that form from outer medullary hyphae ..... ***Vermilacinia*** (Vol. II)

10. With black, hair-like marginal projections (cilia) conspicuous; cortex 75-250 (-400) µm thick; thallus solid; coast of Baja California and southern California..... ***Trichoramalina* (*crinita*)** (Vol. II)

10. Without such projections; cortex usually < 100 µm thick; thallus solid or ("*Fistulariella*") hollow and perforated; widely distributed, coastal or inland ..... ***Ramalina*** (Vol. II)

VII. Group C. Thallus Whitish, Gray, Bluish, Greenish, or pale Brownish (often K+ yellow, with atranorin)

1. Lichen cladoniiform (consisting of a secondary thallus of numerous, ± erect, simple or branched terete stalks arising from a horizontally spreading squamulose or crustose primary thallus); usually on the ground, soil or moss over rock, or on decaying wood 2

1. Lichen not cladoniiform but "tufted" (± branching from a basal part attached directly to the substrate) or pendent (hanging down); usually attached to bark or rock 6

2. Stalks podetia, usually hollow or inflated, richly branched, or if simple or sparingly branched then often with squamules at the base or on the stalks; phyllocladia lacking but sometimes with schizidia, soredia, or other vegetative propagules; without cephalodia and tomentum..... ***Cladonia***

2. Stalks pseudopodetia, solid, simple to ± branched, usually without distinct squamules, but often with squamule-like structures (schizidia, phyllocladia, etc.), with or without cephalodia, tomentum, or both 3

3. Pseudopodetia usually ± branched, entire surface(including a horizontal thallus when present) with powdery-granular to coralloid or somewhat squamule-like outgrowths (phyllocladia or phyllocladioid structures) 4

3. Pseudopodetia unbranched or rarely sparsely branched, without phyllocladia, but sometimes with schizidia or soredia 5

4. Pseudopodetia minute, without a cortex, 0.3-1.0 cm high; phyllocladia granular or powdery; cephalodia and tomentum lacking; often sterile ..... ***Leprocaulon***

4. Pseudopodetia coarse, usually > 1 cm high; phyllocladia distinct, corticate; cephalodia and tomentum present; often fertile ..... ***Stereocaulon* (*sasakii*)**

5. Apothecia pink to whitish, plane or soon swollen and with out a margin; thallus, stipes and apothecia K+ yellow, P+ yellow to orange (baeomycesic acid) ..... ***Dibaeis* (*absoluta*)**

5. Apothecia brownish, concave to flat and marginate at first, later swollen and margin becoming excluded; thallus, stipes and apothecia K+ yellow/red, P+ yellow/orange (stictic and/or norstictic acid) ..... ***Baeomyces* (*rufus*)**

6. Ascocarps, if present, with a mazaedium (a powdery mass of dark ascospores) inside globular swellings at the tips of branches; thallus richly branched, bushy, ± erect, stiff, the branches rounded to flattened in cross section, with coralloid branchlets ..... ***Sphaerophorus* (*globosus*)** (Vol. II)
6. Ascocarps, if present, without a mazaedium; thallus morphology various, but without coralloid branchlets [at least in the Sonoran region] 7

7. Branches about 1 mm wide, flattened, ± linear, with cilia or "marginal rhizines" visible without a lens; underside pale . ..... see **VIII. FOLIOSE LICHENS (Physciaceae:** *Physcia* and *Heterodermia*, page 75**)**
7. Branches mostly 2 mm or more wide, terete or flattened, linear or not, always without cilia or "marginal rhizines"; underside pale or dark 8

8. Branches ± flat in section (or rolled upward or downward), or inflated, but usually distinctly dorsiventral 9
8. Branches rounded in section, if flattened or angular then the same (± pale) color on all sides 13

9. Branches hollow, inflated, not canaliculate (channeled); lower side black ..... ***Hypogymnia***
9. Branches solid, not inflated, often canaliculate; lower side pale or black 10

10. Thallus usually loosely attached, without a main trunk or holdfast; lower surface with well developed prosoplectenchymatous cortex and a few scattered rhizines; if branches canaliculate (channeled), then curved upward; medulla containing only a fatty acid (caperatic); conidia sublageniform (± tear-shaped, Fig. 25) ..... ***Platismatia***
10. Thallus with a single main basal trunk and holdfast; lower surface without rhizines; if branches canaliculate, then curved downward; medulla containing depsides or depsidones; conidia, if present, bifusiform (dumb-bell-shaped, Fig. 25) 11

11. Thallus soft and limp, only weakly dorsiventral, grayish or whitish on lower surface; on broad-leafed plants or on wood, California; medulla with evernic acid ..... ***Evernia* (*prunastri*)**
11. Thallus ± tough and stiff, distinctly dorsiventral, usually tan to brown or black on lower surface; usually on conifers; Arizona or Mexico; medulla without evernic acid 12

12. With marginal cilia and sometimes also rhizines on the lower surface ..... ***Everniastrum***
12. Without marginal cilia and without rhizines ..... ***Pseudevernia***

13. Thallus surface distinctly pubescent-tomentose or with shaggy hairs; on shrubs, coastal, Baja California or southern California 14
13. Thallus surface glabrous; on various substrates (usually coniferous trees), at higher elevations, mostly inland .... ***Bryoria*** (various pale species or forms)

14. Thallus tomentose or pubescent (with fine hair), corticate on both surfaces; apothecia rare; discs brown-black .... ***Tornabaea* (*scutellifera*)**
14. Thallus (especially upper surface and younger parts) densely covered with shaggy hairs, ecorticate on lower surface; apothecia infrequent; discs orange ..... ***Teloschistes* (*californicus*)** (Vol. II)

VIII. FOLIOSE LICHENS

(foliose, non-umbilicate lichens with coccoid green algae)

by B. D. Ryan

1. Lower surface fibrous or cottony (lens), with raised to flat, pale to dark veins (sometimes indistinct or fused); upper surface bright green when wet ..... ***Peltigera* (*aphthosa* group and *venosa*)**
1. Lower surface corticate, or fibrous and cottony, but without veins; upper surface not bright green when wet 2

2. Thallus or at least apothecial disks yellow, orange, or red, K+ purple (anthraquinones); ascospores hyaline, polarilocular (Fig. 25) ..... **VI. ORANGE LICHENS** (Vol. II)
2. Thallus and apothecia not orange or red; if yellow then upper cortex K-; ascospores brown and 1-septate but not polarilocular, or hyaline and simple 3

3. Upper surface bright yellow, KC-, with pulvinic acid derivatives 4
3. Upper surface not yellow, or if yellow-green then ± pale or dull yellow and with usnic acid (KC+ yellow) 5

4. Lobes narrow (0.1-0.5 mm wide); ascospores (8-)16-32 per ascus; pycnidia laminal ..... ***Candelaria***
4. Lobes to 5 mm or more wide; ascospores 8 per ascus; pycnidia marginal ..... ***Vulpicida***

5. Perithecia present; paraphyses soon dissolving ..... ***Dermatocarpon*** (Vol. II)
5. Perithecia absent (but pycnidia may be present); paraphyses persistent 6

6. Fertile (with apothecia) 7
6. Sterile ..... **VIII. C. Sterile foliose lichens**, page 78

7. Ascospores brown, 1-septate; disks brown-black to black ..... **VIII. A. Physciaceae**, page 75
7. Ascospores hyaline, simple; disks pale to deep yellowish or reddish brown, less often becoming brown-black (Parmeliaceae s.l.) 8

8. Lower surface with a thick spongy layer of tomentum; without rhizines and without cortex ..... ***Anzia* (*americana*)**
8. Lower surface moderately to sparsely rhizinate or bare, always with cortex 9

9. Lobes ± hollow and inflated, or if solid then at least partly rounded in cross-section; rhizines absent 10
9. Lobes not hollow and flattened; rhizines present or not; on various substrates, lowland or montane to subalpine (**Parmeliaceae** s.str.) 11

10. Thallus [at least in species from the Sonoran region] hollow and ± inflated; usually on bark or wood; coastal regions or upper montane inland ..... ***Hypogymnia***
10. Thallus not hollow and inflated (but lobes, especially the smaller ones, at least partly rounded in cross section); on rocks, alpine ..... ***Brodoa* (*oroarctica*)**

11. Thallus "parmelioid" (closely appressed throughout, or appressed in center and margins somewhat ascending or undulate; lobes linear to sublinear to subirregular with truncate to subrotund to rotund apices; pycnidia, in present laminal) 12
11. Thallus "cetrarioid" (± loosely attached with at least the margins strongly ascending and often undulate; lobes mostly irregular, often broad, with subrotund rotund apices, pycnidia common and mostly marginal) 14

12. Thallus small (2-5 cm diameter), ± tightly adnate; lobes narrow (mostly 0.5-1 mm wide); pseudocyphellae absent 13
12. Thallus frequently larger (a few small species also occur), tightly or loosely adnate; lobes mostly > 1 mm wide; pseudocyphellae present or absent ..... **VIII. B. *Parmelia*** s.l., page 76

13. Medulla with thamnolic acid only; upper surface gray; conidia not curved (bacilliform, bifusiform or ampuliform, Fig. 25) ..... ***Imshaugia***
13. Medulla with divaricatic acid; upper surface gray or yellow green; conidia curved (falcate to sigmoid, Fig. 25) ..... ***Parmeliopsis***

14. Upper surface white, light gray or gray, K+ yellow, with atranorin 15
14. Upper surface greenish yellow or brown, usually K- 16

15. Pseudocyphellae absent or indistinct; medulla with fatty acids (caperatic acid) only ..... ***Platismatia* (*glauca*)**
15. Pseudocyphellae always present, distinct, punctiform; medulla with phenolic substances, or with fatty acids (other than caperatic acid) ..... ***Cetrelia***

16. Medulla bright yellow, with pulvinic acid derivatives; upper cortex greenish to bright yellow, K-, KC+ stronger yellow, with usnic acid (KC+ yellow)..... ***Vulpicida***
16. Medulla white, without pulvinic acid derivatives; upper cortex brown (sometimes greenish, or blackish) 17

17. Pseudocyphellae present ..... ***Cetraria* (*ericetorum*)**
17. Pseudocyphellae absent 18

18. Ascospores globose; asci cylindrical ..... ***Tuckermannopsis*** (Vol. II)
18. Ascospores ellipsoid to oblong-ellipsoid (Fig. 25); asci clavate (club-shaped) or broadly clavate 19

19. Thallus loosely adnate; surface often foveolate or knobby; paraphyses tips distinctly capitate, dark brown; ascospores oblong-ellipsoid (Fig. 25); conidia bifusiform (dumb-bell-shaped, Fig. 25) ..... ***Kaernefeltia* (*merrilii*)**
19. Thallus closely adnate; surface smooth; paraphyses tips slightly swollen, pale brown; ascospores ellipsoid; conidia disc-bar-shaped ..... "***Cetraria fendleri***" group (Vol. II)

VIII. A. Physciaceae (foliose genera)

by T. L. Esslinger and B. D. Ryan

1. Upper surface whitish to gray-white, upper cortex K+ yellow, with atranorin 2
1. Upper surface gray-white to dark gray or brownish, upper cortex K-, without atranorin 5

2. Lobes tightly appressed, often crowded or confluent; lower surface dark brown to black (sometimes difficult to ascertain on very closely appressed thalli), rhizines present or absent [see also *Diploicia* and *Dimelaena,* **XII. CRUSTOSE DISCOLICHENS** (Vol. II)] 3
2. Lobes more loosely adnate, discrete, not confluent and crowded; lower surface white (sometimes with orange pigmentation) to dark brown or black, rhizines present (although sometimes only on the lobe margins) 4

3. Rhizines present; upper surface sometimes ± weakly reticulately ridged and white-spotted, especially towards lobe tips (lens); mature apothecia, if present, lecideine (some younger ones may have a thalline margin); medulla often pigmented, UV- (without divaricatic acid); upper cortex often UV+ yellow (lichexanthone) ..... ***Pyxine***
3. Rhizines absent; upper surface smooth, without white spots; apothecia, if present, lecanorine; medulla white (not pigmented), UV+ whitish blue (divaricatic acid); upper cortex UV- (without lichexanthone) ..... ***Dirinaria*** (Vol. II)

4. Upper cortex prosoplectenchymatous (consisting of dense periclinal hyphae); lower surface mostly white or tan (sometimes with orange pigmentation), occasionally darkening in oldest parts, lower cortex often missing .... ***Heterodermia***
4. Upper cortex paraplectenchymatous (consisting of a pseudoparenchyma of more or less isodiametric to rather angular cells); lower surface white to black, lower cortex present ..... ***Physcia***

5. Lobes tightly appressed, narrow (0.1-0.2 mm wide), dull, dingy brown or gray, greenish when wet; rhizines absent, or if present, short, few, and inconspicuous; ascospores of *Pachysporaia*-type (one-septate, brown, ellipsoid to broadly ellipsoid with very thick cell wall and small angular lumina); on bark or wood, less often on rock [**Note:** If lower cortex lacking, and growing on rock, compare with *Dimelaena* and "*Caloplaca*" *demissa*] ..... ***Hyperphyscia***

5. Lobes more loosely adnate, often over 0.2 mm wide; rhizines present, usually longer, relatively numerous and conspicuous 6

6. Upper cortex prosoplectenchymatous (consisting of dense periclinal hyphae) ..... ***Anaptychia***
6. Upper cortex paraplectenchymatous (having isodiametric to rather angular, thin-walled cells) or scleroplectenchmatous (having thick-walled cells that are not periclinally arranged) 7

7. Rhizines, at least when mature, squarrosely branched; upper surface pruinose, at least on the lobe ends; medulla white to pale yellow, never red or orange; ascospores of the *Physconia*-type (one-septate, brown, ellipsoid, cell wall strongly thickened at the septum) ..... ***Physconia***
7. Rhizines simple to fasciculate or furcate, never squarrose; upper surface usually lacking pruina or only irregularly produced; medulla usually white, but red or orange in some species; ascospores of the *Physcia*-type (one-septate, brown, ellipsoid to narrowly ellipsoid, cell wall strongly thickened at the septum as well as the apices) or *Pachysporaria*-type (one-septate, brown, ellipsoid to broadly ellipsoid with very thick cell wall and small angular lumina) . 8

8. Lower surface usually darkening to brown or black, at least in the oldest parts; lower cortex paraplectenchymatous .. .. ***Phaeophyscia*** (Vol. II)
8. Lower surface white to pale tan; lower cortex prosoplectenchymatous ..... ***Physciella*** (Vol. II)

VIII. B. *Parmelia* s.l.

by B. D. Ryan and T. H. Nash III

1. Upper cortex with usnic acid, generally K- (but KC+ yellow; K+ yellow if usnic acid is accompanied by atranorin); thallus usually pale to dark yellowish-green 4
1. Upper cortex without usnic acid; thallus brown or gray 2

2. Upper cortex without atranorin (K-), pigmented pale brown to brown-black or greenish-black 3

2. Upper cortex with atranorin (then K+ yellow); rarely this cortical substance is replaced by lichexanthone (and the thallus surface is K- but UV+). Thallus generally gray or greenish gray, sometimes with a brown tinge or medium brown, but in this case the upper cortex is always K+ yellow (with atranorin) **[Parmelia** s.l. with gray upper surface, page 77**]** 11

3. Upper cortex N+ blue-green (rarely + violet); pseudocyphellae absent; on rock ..... ***Neofuscelia***
3. Upper cortex N-; pseudocyphellae present or absent; on bark or rock ..... ***Melanelia***

4. Upper surface of thallus with punctiform pseudocyphellae (often very poorly developed in *F. soredica*)..... ..... ***Flavopunctelia*** (Vol. II)
4. Thallus without pseudocyphellae 5

5. Lower surface velvety (with small papillae), dull; upper cortex K+ yellow (with atranorin and usnic acid as major secondary metabolites) ..... ***Arctoparmelia* (*subcentrifuga*)**
5. Lower surface not velvety but smooth (to wrinkled, but not papillate), glossy or dull; atranorin absent, present as traces or in large amounts 6

6. Lobes with dark cilia ("marginal rhizines"); Sinaloa ..... ***Parmotrema***
6. Lobes without cilia; mostly farther north 7

7. On bark or wood 8
7. On rock or soil 10

8. Lobes 0.5-1(-1.5) mm broad, with soredia ..... ***Parmeliopsis* (*ambigua*)**
8. Lobes 2-6 mm broad, with or without soredia 9

9. Medulla P- (fatty acids present); ascospores, if present, less than 6 µm long ..... ***Ahtiana* (*sphaerosporella*)**
9. Medulla P+ orange; ascospores, if present, more than 15 µm long ..... ***Flavoparmelia***

10. Lobes mostly more than 5 mm wide, ascospores, if present more than 15 µm long; cell walls with isolichenan (I+ blue); coastal or inland canyons of intermediate elevation ..... ***Flavoparmelia***
10. Lobes mostly less than 5 mm wide; ascospores, if present less than 15 µm long; cell walls with *Xanthoparmelia*-type lichenan (I+ red); very common in deserts and in open habitats up to the alpine zone ***Xanthoparmelia*** (Vol. II)

[*Parmelia* s.l. with gray upper surface]

11. Upper surface with pseudocyphellae (punctiform or elongate) 12
11. Upper surface without pseudocyphellae (but often with maculae) 13

12. Pseudocyphellae mainly punctiform; lobe tips subrotund to rotund; medulla K- ..... ***Punctelia*** (Vol. II)
12. Pseudocyphellae mainly linear-elongate, effigurate to almost reticulate; lobe tips truncated; medulla K+ yellow turning dark red (Sonoran species) ..... ***Parmelia*** s.str.

13. Thallus subcaespitose, formed of elongate dorsiventral lobes in a very loose imbricate pattern resembling superficially a fruticose lichen [also refer to Key **VII. FRUTICOSE LICHENS**, page 69] 14
13. Thallus circular, formed of sublinear to subirregular lobes forming a single plane with minimal overlapping of lobes 15

14. Lobe margins with long cilia and truncate lobe tips, lower surface lacking involute margins; medulla K+ yellow to orange or deep red and C- (norstictic and/or salazinic acids) ..... ***Everniastrum***
14. Lobe margins without cilia with rotund (rounded) or subtruncate (± squared) lobe tips, lower surface with involute margins, medulla K- and C+ red (lecanoric acid) ..... ***Pseudevernia***

15. Lobe margins with cilia..... 16
15. Lobe margins without cilia 22

16. Cilia bulbate (with enlarged, rounded base and short, thin tips) ..... ***Bulbothrix***
16. Cilia not bulbate, rather long and slender 17

17. Lobes narrow, 0.5-2.0 mm wide, subtruncate tips, tightly adnate ..... ***Parmelinopsis***
17. Lobes broad, 3.0-10.0 mm wide, subrotund to rotund tips, adnate to loosely adnate 18

18. Upper surface stippled with prominent effigurate or punctiform (dot-like) maculae; conidia filiform (thread-like, Fig. 25) >10 µm long; rhizines usually fairly dense and extending to the margin 19
18. Upper surface lacking maculae (at most faint dots present); conidia shorter (<10 µm long); rhizines usually few, often lacking near the margin 20

19. Upper surface conspicuously effigurate or stippled-maculate, becoming irregularly cracked; rhizines dimorphic (short, simple or rarely branched and long, coarse, and ± grouped); upper cortex palisade paraplectenchymatous; cell walls with *Cetraria*-type lichenan ..... ***Canomaculina***
19. Upper surface with reticulate maculae forming a regular network of cracks; rhizines only of one kind (not dimorphic); upper cortex vaulted paraplectenchymatous; cell walls with intermediate-type lichenan ..... ***Rimelia***

20. Lobes usually broad (8-20 mm wide); lower surface black in the center and a conspicuous, brown, naked zone along the margin; cell walls with *Cetraria*-type lichenan ..... ***Parmotrema***
20. Lobes usually narrow (1.5-4 mm wide); lower surface black throughout; cell walls containing isolichenan 21

21. Thallus sorediate; medulla at least partly (especially under the soralia) orange-yellow, C+ and KC+ deep yellow [due to secalonic acid A, terpenes (zeorin and leucotylic acid) also present] ..... ***Myelochroa* (*aurulenta*)**
21. Thallus not sorediate; medulla white, without secalonic acids and without terpenes, but with lecanoric acid (C+ reddish, KC+ red) ..... ***Parmelina* (*quercina*)**

22. Rhizines mostly dichotomously branched; lobes usually sublinear with subtruncate apices ..... ***Hypotrachyna***
22. Rhizines simple; lobes subirregular to irregular with broadly rotund apices 23

23. Lobes 2-6 mm wide; lower surface with a narrow (<1 mm wide) brown margin lacking rhizines; cell wall with isolichenan ..... ***Canoparmelia***
23. Lobes 8-20 mm wide; lower surface with a broad (>1 mm wide) brown margin lacking rhizines; cell wall with *Cetraria*-type lichenan ..... ***Parmotrema***

VIII. C. Sterile Foliose Lichens

1. Upper surface pale (or bright) greenish yellow, K- (but KC+ yellow, with usnic acid) ..... **VIII. C. Group 1**, page 78
1. Upper surface whitish to gray (if yellowish, then usually with atranorin or lichexanthone), greenish, or brown 2

2. Medulla bright greenish yellow ..... ***Vulpicida* (*pinastri*)**
2. Medulla white [or, if pigmented, then very pale or some color other than greenish-yellow] .... **[*Parmelia* s.l. with gray upper surface**, page 77, choice 11**]**

3. Upper surface always K- (without atranorin), usually ± brown (to gray-brown or greenish or blackish; rarely pale gray-white, but still K-) ..... **VIII. C. Group 2**, page 79
3. Upper surface K+ yellow (with atranorin), ± gray (to whitish or greenish; rarely brownish, but still K+ yellow)..... 4

4. Lobes broad ([1.0-] 1.5 – 4.0 cm wide), with rotund apices ..... **VIII. C. Group 3**, page 80
4. Lobes narrow (0.3-1.0 [-1.5] cm wide), with truncate or subacute apices ..... **VIII. C. Group 4**, page 82

VIII. C. Group 1. Sterile foliose lichens with a yellow-green upper surface (e.g. usually with usnic acid present, KC+ yellow)

by T. H. Nash III

1. Thallus with isidia 2
1. Thallus with soredia (including pustules) 3

2. Lobes broadly rotund, usually at least 8 mm wide; usually on trees, Sinaloa ..... ***Parmotrema***
2. Lobes narrowly rotund or subtruncate, usually less than 3 mm wide; primarily on rocks, widely distributed throughout the Sonoran region ..... ***Xanthoparmelia*** (Vol. II)

3. Upper surface pseudocyphellate (either punctiform or as long linear fissures) 4
3. Upper surface not pseudocyphellate 6

4. Upper cortex with long, linear pseudocyphellae, rare on rocks in scree slopes at moderately high elevations .... ***Parmelia* (*fraudans*)**
4. Upper cortex with punctiform rather than linear pseudocyphellae, widespread at various elevations 5

5. Soredia primarily laminal, lobes rotund, pseudocyphellae abundant, primarily on trees in coastal regions and rocks at mid-elevations in interior mountains ..... ***Flavopunctelia* (*flaventior*)** (Vol. II)

5. Soredia primarily marginal, lobes subrotund, pseudocyphellae occasional (often poorly developed), primarily on trees at mid-elevations in interior mountains ..... ***Flavopunctelia* (*soredica*)** (Vol. II)

6. Thallus lobes primarily less than 2 mm wide 7
6. Thallus lobes primarily more than 3 mm wide 9

7. Medulla P+ red (protocetraric acid present), on coastal shrubs in southern California and Baja California …..... ..... ***Flavoparmelia* (*subcapitata*)**
7 Medulla P-, at high elevations on rocks or conifers 8

8. Thallus usually less than 3 cm in diameter, usually on conifers ..... ***Parmeliopsis* (*ambigua*)**
8. Thallus usually more than 3 cm in diameter, on rock scree (SE Arizona) ..... ***Arctoparmelia* (*subcentrifuga*)**

9. Medulla pale yellow (secalonic acid present), P- 10
9. Medulla white (secalonic acid absent), P+ orange 11

10. Cortex often broken revealing a yellow medulla; on rocks ..... ***Parmotrema* (*xanthopustulata*)**
10. Cortex not broken covering a pale yellowish medulla; on trees ..... ***Myelochroa* (*aurulenta*)**

11. Thallus with globose ± corticate outgrowth (pustules), usually with secondary gyrophoric acid (KC/C+ rose to red, usually restricted to rocks ..... ***Flavoparmelia* (*baltimorensis*)**
11. Thallus with granular soredia, always lacking gyrophoric acid (KC/C-), usually on trees but secondarily on rocks .... ***Flavoparmelia* (*caperata*)**

VIII. C. Group 2. **Brown sterile foliose lichens** (upper surface K-)

by T. Esslinger

1. Thallus with soredia 2
1. Thallus without soredia (with or without isidia) 9

2. Upper surface distinctly pruinose, at least towards lobe ends 3
2. Upper surface epruinose 5

3. Upper cortex prosoplectenchymatous (consisting of dense periclinal hyphae) ..... ***Anaptychia* (*elbursiana*)**
3. Upper cortex paraplectenchymatous (consisting of isodiametric to rather angular, thin-walled cells) or scleroplectenchymatous (consisting of thick walled cells that are not periclinally arranged) 4

4. Rhizines distinctly squarrose, lower surface pale tan to dark brown or black ..... ***Physconia***
4. Rhizines simple to furcate, lower surface largely pale or with a bluish-green, K+ violet pigment (also present in parts of the upper cortex) ..... ***Culbersonia* (*nubila*)**

5. Thallus loosely appressed to somewhat erect ..... ***Tuckermannopsis* (*chlorophylla*)** (Vol. II)
5. Thallus closely appressed 6

6. Thallus olive-brown to pure brown or blackish-brown, the medulla with various depsides, and frequently C+ rose or red ..... ***Melanelia***
6. Thallus gray to brown, occasionally very pale gray-white, the medulla lacking secondary substances or only with terpenoids or anthraquinones (always C-) 7

7. Lobes very tightly appressed, rhizines absent, or if present, short, few, and inconspicuous; lobes narrow (0.1-0.2 mm wide), dull, dingy brown or gray, greenish when wet [If lower cortex lacking, and growing on rock, compare with "*Caloplaca*" *demissa*] . ..... ***Hyperphyscia***
7. Lobes more loosely adnate, rhizines present, usually longer, relatively numerous and conspicuous; lobes often over 0.2 mm wide 8

8. Lower surface often darkening to brown or black, at least in the oldest parts; lower cortex paraplectenchymatous .... ***Phaeophyscia*** (Vol. II)
8. Lower surface white to pale tan; lower cortex prosoplectenchymatous ..... ***Physciella*** (Vol. II)

9. Upper surface olive-brown to pure brown and N+ blue-green, or greenish black and N+ violet ..... ***Neofuscelia***
9. Upper surface N- 10

10. Thallus with isidia 11
10. Thallus without isidia .... **VIII. A. Physciaceae**, page 75 or **VIII. B.** ***Parmelia*** s.l. with gray upper surface, page 77, choice 11

11 Rhizines distinctly squarrose, the lower surface mostly pale, upper surface ± pruinose ..... ***Physconia* (*elegantula*)**
11. Rhizines simple to fasciculate or furcate 12

12. Thallus dark olive-brown to greenish black and shiny, at least on the lobe ends; lobes narrow (< 1 mm) and finely divided; growing almost always on decorticate wood, rarely on bark ..... "***Tuckermannopsis" coralligera*** (Vol. II)
12. Thallus colored otherwise and/or with larger lobes; usually growing on bark or rock 13

13. Lobes mostly 1-5 mm in diameter, olive-brown to true brown or dark brown, shiny or not; some species with C+ depsides in the medulla; on bark or rock, less often on wood ..... ***Melanelia***
13. Lobes mostly 1 mm or less in diameter, gray to dark or brownish gray, usually dull; depsides lacking; on rock or mosses over rock ..... ***Phaeophyscia* (*sciastra*)** (Vol. II)

VIII. C. Group 3. Sterile foliose lichens with ± gray upper surface and broad lobes ([1.0-] 1.5 – 4.0 cm wide)

by T. H. Nash III

1. Thallus ciliate 2
1. Thallus not ciliate 4

2. Cilia bullate (expanded at the base) ..... ***Bulbothrix***
2. Cilia not bullate 3

3. Thallus lobes usually less than 3 mm broad, lobe tips truncate to narrowly rotund ..... ***Heterodermia***
3. Thallus lobes usually more than 3 mm broad, lobe tips broadly rotund 4

4. Upper surface reticulately cracked ..... ***Rimelia***
4. Upper surface not reticulately cracked 5

5. Upper surface with effigurate maculae; simple and furcate rhizines ..... ***Canomaculina***
5. Upper surface without effigurate maculae; simple rhizines only ..... ***Parmotrema***

6. Thallus isidiate 7
6. Thallus sorediate 16

7. Thallus subfruticose, lobes canaliculate (channeled) below ..... ***Pseudevernia* (*consocians*)**
7. Thallus essentially in one plane (foliose), lobes not canaliculate below 8

8. Rhizines dichotomous; lobes usually subtruncate (± square) and dichotomously branched ..... ***Hypotrachyna***
8. Rhizines usually simple (rarely furcate); lobes usually rotund (rounded) and irregularly branched 9

9. Isidia short, granular; thallus whitish ..... ***Heterodermia* (*granulifera*)**
9. Isidia narrowly cylindrical; thallus some shade of gray 10

10. Isidia tips ciliate, lobe width rarely exceeding 2 mm ..... ***Parmelinopsis* (*minarum*)**
10. Isidia tips not ciliate, lobe width usually more than 3 mm 11

11. Upper surface with strongly reticulate maculae and often reticulately cracked ..... ***Rimelia* (*subisidosa*)**
11. Upper surface without maculae (or weakly maculate) and not reticulately cracked 12

12. Medulla K+ yellow turning orange or red (stictic or salazinic acid major secondary metabolites) 13
12. Medulla K- (stictic or salazinic acid absent) 14

13. Medulla K+ yellow turning deep red (salazinic acid as major, norlobaridone often as accessory secondary metabolite) ..... ***Canomaculina* (*subtinctoria*)**
13. Medulla K+ yellow turning orange (stictic acid major secondary metabolites; norlobaridone absent) ..... ***Parmotrema* (*crinitum*)**

14. Medulla C+ red (lecanoric acid major secondary metabolite), UV- ..... ***Parmotrema* (*tinctorum*)**
14. Medulla C- (lecanoric acid absent) 15

15. Medulla UV+ white (alectoronic acid major secondary metabolite) ..... ***Parmotrema* (*mellissii*)**
15. Medulla UV- (divaricatic acid major secondary metabolite) ..... ***Canoparmelia* (*caroliniana*)**

16. Medulla pale yellow 17
16. Medulla white 18

17. Cortex often broken, revealing yellow medulla, on rocks ..... ***Parmotrema* (*xanthopustulata*)**
17. Cortex not broken, pale yellowish medulla not visible without sectioning, on trees ..... ***Myelochroa* (*aurulenta*)**

18. Upper surface with punctiform pseudocyphellae ..... ***Punctelia* (*subrudecta*)**
18. Upper surface without pseudocyphellae 19

19. Lower cortex absent ..... ***Heterodermia***
19. Lower cortex present 20

20. Lower surface with a mottled white margin and a blackened center 21
20. Lower surface either black throughout or with a brown margin and black center 25

21. Medulla P+ orange 22
21. Medulla P- 23

22. Medulla with stictic acid major secondary metabolite ..... ***Parmotrema* (*hypoleucinum*)**
22. Medulla with norstictic acid major secondary metabolite ..... ***Parmotrema* (*hypotropum*)**

23. Medulla UV+ white (alectoronic acid present); thallus surface smooth ..... ***Parmotrema* (*louisianae*)**
23. Medulla UV- (caperatic acid present); thallus often strongly rugose ..... ***Platismatia* (*glauca*)**

24. Rhizines dichotomous; lobes usually subtruncate and dichotomously branched ..... ***Hypotrachyna***
24. Rhizines usually simple (rarely furcate); lobes usually rotund (rounded) and irregularly branched 25

25. Upper surface yellowish, KC+ yellow (usnic acid present) ..... ***Arctoparmelia* (*subcentrifuga*)**
25. Upper surface whitish or some shade of gray, without yellow tinge 26

26. Upper surface strongly reticulate maculae and often reticulately cracked 27
26. Upper surface without maculae (or weakly maculate) and not reticulately cracked 28

27. Medulla K+ yellow turning deep red (salazinic acid present) ..... ***Rimelia* (*reticulata*)**
27. Medulla K- (fatty acids present) ..... ***Rimelia* (*simulans*)**

28. Lobes usually less than 5 mm in diameter ..... ***Canoparmelia***
28. Lobes usually more than 5 mm in diameter ..... ***Parmotrema***

VIII. C. Group 4. Sterile foliose lichens with ± gray upper surface and narrow lobes (0.3-1.0 [-1.5] cm wide)

by T. H. Nash III

1. Thallus subfruticose 2
1. Thallus essentially in one plane although lobes may become closely imbricate (overlapping) 4

2. Lower surface canaliculate (channeled); thallus margin without cilia ..... ***Pseudevernia***
2. Lower surface not canaliculate; thallus margin with cilia 3

3. Upper cortex prosoplectenchymatous, genus widespread ..... ***Heterodermia***
3. Upper cortex paraplectenchymatous, southern part of the Sierra Madre Occidental ..... ***Everniastrum***

4. Thallus UV+ yellow (lichexanthone present) ..... ***Pyxine***
4. Thallus UV- (lichexanthone absent) 5

5. Thallus with cilia 6
5. Thallus without cilia 8

6. Cilia bullate (expanded at the base) ..... ***Bulbothrix***
6. Cilia not bullate (rather relatively uniform in diameter throughout) 7

7. Upper cortex prosoplectenchymatous ..... ***Heterodermia***
7. Upper cortex paraplectenchymatous ..... ***Physcia***

8. Thallus without rhizines 9
8. Thallus with rhizines 10

9. Lobes more than 0.4 mm wide, ± rounded in cross-section, alpine ..... ***Brodoa* (*oroarctica*)**
9. Lobes usually less that 0.2 mm wide, ± flattened in cross section, lower elevations, particularly in riparian areas ..... ***Hyperphyscia***

10. Thallus with prominent linear pseudocyphellae that may form deep fissures in the thallus surface ..... ***Parmelia***
10. Thallus without pseudocyphellae 11

11. Thallus isidiate [including pustulate isidia (polysidiangia) in the case of *Pyxine*] 12
11. Thallus sorediate (not isidiate) 18

12. Isidia predominately globular; upper cortex prosoplectenchymatous ..... ***Heterodermia* (*granulifera*)**
12. Isidia cylindrical, upper cortex paraplectenchymatous 13

13. Isidia becoming pustulate at the tip (polysidiangia) ..... ***Pyxine* (*mexicana*)**
13. Isidia not becoming pustulate 14

14. Isidia with apical cilia ..... ***Parmelinopsis* (*horrescens*)**
14. Isidia without apical cilia 15

15. Rhizines dichotomous; lobes usually subtruncate and dichotomous ..... ***Hypotrachyna***
15. Rhizines simple (or at most sparingly furcate) 16

16. Medulla C/KC+ rose to red (gyrophoric acid present) ..... ***Parmelinopsis* (*minarum*)**
16. Medulla C/KC- (gyrophoric acid absent) 17

17. Medulla P+ deep yellow (thamnolic acid present) ..... ***Imshaugia* (*aleurites*)**
17. Medulla usually P- (rarely P+ yellow, atranorin) ..... ***Physcia***

18. Lobes hollow (inflated) ..... ***Hypogymnia***
18. Lobes ± solid (at least filled with some medullary hyphae) 19

19. Lower cortex lacking ..... ***Heterodermia***
19. Lower cortex present 20

20. Thallus dark gray or greenish gray ..... ***Pyxine* (*sorediata*)**
20. Thallus light gray 21

21. Upper cortex prosoplectenchymatous ..... ***Heterodermia***
21. Upper cortex paraplectenchymatous 22

22. Rhizines dichotomous; lobes usually subtruncate and dichotomous ..... ***Hypotrachyna***
22. Rhizines simple (or at most furcate); lobes usually rotund and irregularly branched 23

23. Medulla P+ orange (stictic acid) ..... ***Canoparmelia* (*carneopruinata*)**
23. Medulla usually P- (rarely P+ yellow, atranorin) 24

24. Medulla UV+ white (divaricatic acid present); predominately in spruce-fir zone ..... ***Parmeliopsis* (*hyperopta*)**
24. Medulla UV- (divaricatic acid absent); widely distributed in all major plant communities ..... ***Physcia***

IX. UMBILICATE LICHENS

by B. D. Ryan

1. Perithecia present; paraphyses soon dissolving ..... ***Dermatocarpon*** (Vol. II)
1. Perithecia absent (but pycnidia may be present); paraphyses persistent 2

2. Thallus with distinct pustules (conspicuous convex “blisters” with corresponding concavities on the lower surface) . ..... ***Lasallia*** (Vol. II)
2. Thallus without pustules 3

3. Apothecia absent **or** without a thalline margin; discs black; upper surface of thallus brown, gray, or blackish .... ***Umbilicaria*** (Vol. II)
3. Apothecia (usually present) with a thalline margin or immersed in the thallus; disc color various (sometimes sterile or with black discs in *Rhizoplaca*, and then upper surface of thallus always distinctly green-yellow) 4

4. Ascospores *c.* 100 per ascus; on basic rocks; apothecial compound, the individual discs scabrid (roughened) but epruinose, with a pruinose net between ..... ***Glypholecia* (*scabra*)**
4. Ascospores 8 per ascus (or sometimes sterile, in *Rhizoplaca*); apothecia single, the discs smooth or pruinose but not scabrid 5

5. Thallus large (usually over 10 cm wide); upper surface ridged, coarsely papillate; cell walls with lichenan ..... ***Omphalora* (*arizonica*)**
5. Thallus smaller (to 1-4 cm wide); upper surface not ridged or papillate; cell walls without lichenan ..... ***Rhizoplaca***

X. SQUAMULOSE AND LOBATE LICHENS

(with apothecia and coccoid green algae)

by B. D. Ryan

1. Thallus upper surface orange (to red or yellow), K+ purple (anthraquinones), always C-, KC- ..... **VI. ORANGE LICHENS** (Vol. II)
1. Thallus upper surface not orange; if yellow or reddish then K- or K+ yellow (sometimes K+ faint reddish in *Candelina* or *Candelariella*, but then with pulvinic acid derivatives rather than anthraquinones), occasionally KC/C+ rose to red (gyrophoric or lecanoric acids in addition to the cortical pigments) 2

2. Thallus upper surface bright yellow, golden or yellowish green, KC- (pulvinic acid derivatives), KC+ yellow or orange (usnic acids and/or xanthones), or C+, KC+ red 3
2. Thallus upper surface whitish, grayish, brownish or blackish, KC- or C+, KC+ red; if tinged yellowish or greenish then without acetone-soluble pigments (detected by thin-layer chromatography) ..... **X. Group A**, page 84

3. Thallus surface ± bright or deep yellow (to very slightly greenish or brownish), KC- (pulvinic acid derivatives) or C+, KC+ red; if thallus appearing pale (some *Acarospora* spp.) then distinctly pruinose ..... **X. Group B**, page 86
3. Thallus surface ± pale and often distinctly greenish or brownish, KC+ yellow (usnic acids) or KC+ orange (xanthones), or C+, KC+ red ..... **X. Group C**, page 87

X. Group A. Thallus upper surface whitish, gray, brown or blackish

1. Thallus sorediate; apothecia rarely present 2
1. Thallus not sorediate; apothecia almost always present 3

2. Thallus UV+ orange-red (diploicin); lower cortex absent (± crustose); common in coastal areas ... ***Diploicia*** (Vol. II)
2. Thallus UV-; lower cortex present (foliose but very closely appressed); common in inland desert riparian areas ..... ***Hyperphyscia* (*adglutinata*)**

3. Mature ascospores brown, one-septate 4
3. Mature ascospores colorless, simple or septate 6

4. Thallus subsquamulose; on soil; alpine ..... ***Phaeorrhiza*** (Vol. II)
4. Thallus lobate; on rock or bark; coastal to intermediate montane 5

5. Thallus crustose (areolate in the center and lobate along the margin); ascospores thin walled; on rocks ..... ***Dimelaena*** (Vol. II)
5. Thallus distinctly foliose but very closely appressed; ascospores thick walled; on bark ..... ***Hyperphyscia***

6. Ascospores many (*c.* 100) per ascus, mostly >4 µm long 7
6. Ascospores to 8 per ascus, mostly < 6 µm long 8

7. Apothecia lacking a distinct thalline exciple (in section, microscope); apical dome of asci K/I+ blue; prothallus distinct ..... ***Sporastatia* (*testudinea*)** (Vol. II)
7. Apothecia with a thalline exciple (in section, microscope) or immersed and bordered by the thallus; apical dome of asci well developed, but K/I- (non-amyloid, attention: the hymenial gelatin usually reacts blue); prothallus absent ..... ***Acarospora*** (Vol. II)

8. Asci *Teloschistes*-type; ascospores ± polarilocular (but septum sometimes very thin and without a distinct isthmus, Fig. 25); apothecial discs yellow, orange or red and K+ purple, or brown to black but then epihymenium often K+ violet in section (microscope) ..... ***Caloplaca*** (Vol. II)
8. Asci not *Teloschistes*-type; ascospores not polarilocular; apothecial discs and epihymenium ± brown or black, not K+ red-violet 9

9. Apothecia lecanorine (with algae present in margin and/or below the hypothecium, at least in young apothecia) 10
9. Apothecia lecideine or biatorine 16

10. Ascospores septate (Fig. 25) 11
10. Ascospores simple 12

11. Asci ± *Catillaria*-type, the tips entirely I+ blue, at most with a small ocular chamber; conidia bacilliform (cylindrical, Fig. 25), formed pleurogenously (endobasidial); thallus (in all species definitely known to occur in the Sonoran region) P+ orange, with pannarin ..... ***Solenopsora***
11. Asci *Bacidia*-type, the tips K/I+ blue (amyloid) with an K/I- (non-amyloid) axial mass and usually a distinct ocular chamber; conidia usually filiform (thread-like, Fig. 25) and formed acrogenously (exobasidial); thallus P-, or at least without pannarin ..... ***Lecania*** s.l. (Vol. II)

12. Apothecial margin conspicuously warty; thallus with cephalodia; on moss and/or soil ..... ***Psoroma***
12. Apothecial margin not warty; thallus without cephalodia;. on soil or rock 13

13. Ascospores over 14 µm long; apothecia frequently sunken, with a ± indistinct margin; asci K/I- (non-amyloid) or pale blue (hemiamyloid), without a distinct tholus 14
13. Ascospores generally less than 14 µm long; apothecia usually sessile, with a distinct margin; ascus with a distinct I+ blue tholus 15

14. Uppermost part of hymenium greenish, N+ green; paraphyses often moniliform; lobes indistinct or narrow, thin ..... ***Aspicilia*** (Vol. II)
14. Uppermost part of hymenium brownish, N-; paraphyses not moniliform; lobes distinct, broad, thick ..... ***Lobothallia*** (Vol. II)

15. Thallus subsquamulose or indistinctly lobed at margin; thallus and apothecia usually distinctly brown, shiny ..... ***Protoparmelia*** (Vol. II)
15. Thallus with distinct, elongated, radiating marginal lobes; thallus usually yellow green, KC + yellow (usnic acid) although some species are white or brownish tinged or even yellowish- to reddish brown, shiny or dull ..... ***Lecanora*** subg. ***Placodium*** s.l. (Vol. II)

16. Ascospores septate (Fig. 25) 17
16. Ascospores simple 18

17. Ascospores 1-septate, 4-5.5 µm wide; alpine; on acidic rocks ..... ***Psorinia* (*conglomerata*)**
17. Ascospores 2 or more septate, less than 4 µm wide; desert to high elevations; commonly on soil, occasionally on rock ..... ***Toninia***

18. On bark or wood ..... ***Hypocenomyce*** **(**including **"*Biatora*" *anthracophila*)**
18. On rock, or soil, detritus or mosses 19

19. Growing directly on rock; thallus tightly appressed, subsquamulose to weakly lobed along margin 20
19. Growing on soil (sometimes over soil in rock crevices); thallus often ± loosely appressed and frequently distinctly squamulose or lobate 21

20. Asci ± *Lecanora*-type (but apical cushion often weakly defined and ocular chamber weakly developed); usually with miriquidic acid (± peacock-blue to greenish spots in TLC after charring) ..... ***Miriquidica*** (Vol. II)
20. Asci *Lecidea*-type (with tiny, scarcely detectible amyloid (I+ blue) structures in the tip); without miriquidic acid; ... . ***Lecidea*** (Vol. II)

21. Upper surface of thallus KC/C+ red; ascus apical dome K/I- (non-amyloid), or weakly I+ blue (hemiamyloid) .... ***Trapeliopsis*** (Vol. II)
21. Upper surface of thallus KC/C- (but some *Psora* spp. may be KC/C+ rose to red and contain gyrophoric acid); ascus apical dome I+ (or at least K/I+) blue with a deeper blue axial tube 22

22. Squamules dark green, surrounded by cyanobacteria (free-living or lichenized: *Spilonema*)..... ***Psorula*** **(*rufonigra*)**
22. Squamules not dark green, free of cyanobacteria 23

23. Thallus crustose to areolate-squamulose; apothecia dark red-brown; on acidic soil, montane to alpine .... ***Lecidoma*** **(*demissum*)** (Vol. II)
23. Thallus distinctly squamulose; apothecia black or red-brown; often on ± calcareous soil, deserts to alpine in open habitats 24

24. Apothecia plane to weakly convex, hymenial gelatin K/I+ blue (amyloid) ..... ***Lecidea*** **(*lurida*)** (Vol. II)
24. Apothecia strongly convex to ± hemispherical, hymenial gelatin K/I- (non-amyloid) ..... ***Psora***

X. Group A. Thallus surface ± bright yellow (KC- or KC+ red, not purple)

1. Ascospores present, brown, 1-septate (Fig. 25) ..... ***Catolechia*** **(*wahlenbergii*)** (Vol. II)
1. Ascospores (if present) hyaline, simple or rarely 1-septate 2

2. Thallus with elongate, radiating, appressed lobes at the margin and an areolate center 3
2. Thallus squamulose with at most short lobes 5

3. Ascospores 8 per ascus; cortex containing calycin, pulvinic dilactone, or related substances (if small foliose, then *Candelaria*) ..... ***Candelina***
3. Ascospores 50 (-100) per ascus; cortex containing rhizocarpic acid 4

4. Asci with K/I- (non-amyloid) apical cap, hymenium often over 80 µm; cortex paraplectenchymatous .... ***Acarospora*** (Vol. II)
4. Asci *Lecanora*-type, with apical amyloid (I+ blue) ring; hymenium mostly under 80 µm; cortex of thallus short-celled prosoplectenchymatous ..... ***Pleopsidium*** (Vol. II)

5. Ascospores 8 per ascus, cortex containing calycin, pulvinic dilactone, or related substances 6
5. Ascospores 50 (-100) per ascus ..... ***Acarospora*** (Vol. II)

6. On soil; apothecia lacking a thalline margin ..... ***Psora*** **(*icterica*)**
6. On rock, apothecia with a thalline margin ..... ***Candelariella*** (Vol. II)

KEY TO THE GENERA

X. Group C. Thallus ± pale yellow to yellowish green (KC+ yellow or orange, usnic acids and/or xanthones)

1. Thallus without a cortex, granular or powdery leprose, sterile ..... ***Leproloma*** (Vol. II)
1. Thallus with a cortex, not granular or powdery, usually fertile; apothecia (at least when young) lecanorine or immersed 2

2. Mature ascospores (usually present) brown, 1-septate; discs brown-black; thallus crustose with ± weakly lobed margin ..... ***Dimelaena*** (Vol. II)
2. Mature ascospores (if present) colorless, non-septate; discs pale or dark; thallus squamulose or crustose and weakly to strongly lobed at the margin 3

3. Ascus tips ± entirely I+ blue, without a distinctly K/I- (non-amyloid) axial mass; medulla dense and chalky; lower cortex absent; usually on ± calcareous soil, in deserts ..... ***Squamarina (lentigera)***
3. Ascus tips with a distinctly K/I- (non-amyloid) axial mass; medulla usually rather loose (except "*Petroplaca*") and not chalky; lower cortex at least partly developed; almost always growing on rock 4

4. Thallus squamulose-peltate, subunits ± stipitate, usually without distinctly radiating marginal lobes; lower cortex well-developed over the entire lower surface, thicker and more gelatinized than upper cortex; medulla ± loose..... ***Rhizoplaca***
4. Thallus areolate-subsquamulose to lobate; areoles subsquamulose to substipitate, usually with distinctly radiating, marginal lobes; lower cortex, if present, ± thin or poorly developed and confined to areas near the margins or tips; medulla dense or loose ..... ***Lecanora*** subg. ***Placodium*** s.l. [including "***Squamarina*** sect. ***Petroplaca***"] (Vol. II)

Generic and species description formats

by T.H. Nash III

Generic and species descriptions in floras contain considerable information in condensed form. For users less familiar with such descriptions the following explanation is provided.

Genera are always capitalized and species not. Within the text use of genus and species names are italicized. The names following genus and species names refer to the authors (abbreviated by convention according to Kirk and Ansell [1992]) for the name, and following the comma an abbreviated reference is given for where the name was published. Generic concepts have evolved considerably over the past 250 years such that an original description is frequently published under a different genus name than what is accepted today. In this case the author(s) for the species is given in parentheses and the author(s) responsible for transferring the species to genus used today follow the parentheses. The reference for the most recent name is given thereafter. In a few cases, there was not time to publish a new species description elsewhere, and consequently Latin descriptions are included and "sp. nov." is written afterwards. For a few other species (e.g. *Candelaria "pacifica"*) there was not sufficient time to research all potentially valid old names, and consequently they are given provisional names, followed by "in prep." To be validated these names will have to be published with a Latin description after this Flora appears.

At the beginning of the next paragraph the name used in the original description (the "basionym") is given and literature reference for that name follows (also in abbreviated form). In cases where there has been no name change, then the basionym is the same as the accepted name and there is no need to list it again.

Nomenclature can for some species be quite complex. For example, synonyms (given under the species name) arise when either (1) a species has been described more than once, or (2) a species has been placed in multiple genera over the years. Full lists of synonyms and their references are usually given in monographs. We primarily provide synonyms (before the species description) that have been used in recent literature for western North America. Nomenclature is governed by the Botanical Code (Greuter et al. 1994), a set of rules established by periodic, international botanical congresses. In cases

where the currently accepted name is the one used in the original species description, then there are no synonyms.

Books with excellent illustrations of lichens have proliferated in recent years. Consequently, we did not feel it necessary to include as many photographs as would have been ideal. Rather, references for photos are given for most species. However, photographs are provided for a number of the rarer species and for most of the newly described ones.

Under the genus name, the family to which the genus belongs is given. By convention a hierarchal classification system is used: e.g species belong within genera, genera within families, families within orders and orders within classes. An approximation of the higher level classification will be given in Vol. II, but readers should be aware than higher level taxonomy is a very active area of modern research and that lichen systematists are not in universal agreement.

Under the genus "type" refers to the name that typifies the genus (Greuter et al. 1994). In addition, an approximation for the number of species world-wide is also given.

In the "Literature Cited" section at the end of the book, we provide the references for the most recent name of each species, the references listed after "Selected lit." and "Illustrations" and those that are cited in the introduction and notes within the descriptions. However, we do not provide all the basionym citations because many of these are relatively obscure and may be books or journals that are not readily available. The latter references can usually be found in monographs, such as the ones often listed after "Selected lit."

Generic descriptions may look very similar to species descriptions in that many of the major categories (**bold face**) are repeated. But there are major differences. Ideally generic description should cover the range of variation across species; whereas the species description are, of course, restricted to the species in question. In some cases there are generic characters that apply to all species within the genus (e.g. anatomy of the upper cortex within the parmelioid genera). Such characters may only be mentioned within the generic descriptions.

No flora is ever complete in that new records are invariably discovered after publication. If the genus for a new record is included in the flora, then it is hoped that the user can get to the genus. In some cases information about species not currently recognized from the Sonoran region is given in the "Notes" following the generic description.

Within the generic and species descriptions major categories are highlighted in **bold print**. This should allow the user to make rapidly comparisons across species (or across similar genera). Because of the heterogeneity of characters among genera, the choice of major categories must necessarily change among dissimilar genera. Within the major categories a further hierarchy is employed by using or not using capitalization. For example, within foliose species "Thallus" includes "lobes", "upper and lower surfaces", "upper and lower cortices", "medulla", etc. Thus, "Thallus" is capitalized and the other subcategories are not. By convention in taxonomic descriptions verbs in the usual sense of English sentences are omitted. The words that follow a major category are a series of modifiers applying to that category. Semi-colons are used at the end of each set of modifiers and are followed by a different noun (new attribute, not always bolded). Following each noun, a colon is used and descriptors follow thereafter (adjectives, phrases) until the next attribute occurs. Periods are only used at the end of paragraphs or for abbreviations (e.g. diam. = diameter; *c.* = *circa* [approximately in Latin]).

In cases where a species is known from more than one or two localities, distribution maps are provided. Exact locality information can be found in our database (http://cochise.asu.edu/collections/index.html). As time progresses, the database will become more comprehensive as more collections are added.

ACROCORDIA

by A. Aptroot

Acrocordia A. Massal., Geneacaena: 17 (1854).

Family: Monoblastiaceae; Type: *Acrocordia conoidea* (Fr.) Körb.; No. species: 10 world-wide; Selected lit.: Harris (1995), and Purvis et al. (1992).

Life habit: lichenized;**Thallus:** crustose, thin, mostly immersed in substrate; **upper surface:** whitish or pale; **cortex:** lacking; **photobiont:** primary one a trentepohlioid alga, secondary photobiont absent; **Ascomata:** perithecial, almost entirely immersed to sessile, black (rarely pink or whitish), compound, **involucrellum:** brown-black, hemispherical to globose, surrounding exciple; **ascomatal wall:** black, continuous below the hamathecium; **exciple:** ± globose, colorless or pale brownish; **hamathecium:** branched pseudoparaphyses, anastomosing above the asci, non-amyloid; **asci:** bitunicate, cylindrical, K/I-; apical dome: with a broad ocular chamber surmounted by a hemispherical, meniscus-like structure, non-amyloid, (4-) 8-spored; **ascospores:** uniseriate, hyaline, ellipsoid, 1(-3)-septate with a median euseptum, 11-60 x 5.5-23 µm; walls: ornamented with tiny warts; **Conidiomata:** pycnidial; **conidia:** formed acrogenously, ellipsoid to narrowly ellipsoid, simple, hyaline; **Secondary metabolites:** none detected; **Geography:** mostly temperate on both hemispheres; **Substrate:** mostly on bark, but also on calcareous rock.

Notes: It is characterized by its cylindrical asci with an unusual ascal tip structure and ellipsoid, 1-septate ascospores with a warted epispore.

The Species

Acrocordia conoidea (Fr.) Körb., Syst. Lich. Germ.: 358 (1855).

Basionym: *Verrucaria conoidea* Fr., Lich. Eur.: 432 (1831); Illustrations: Harris (1975a), p. 237; Wirth (1995), pp. 115 & 139.

Thallus: continuous to rimose, areolated with the margins of the areoles often upturned, not immersed in the substrate; **upper surface:** pale sand-colored brown; **photobiont:** a trentepohlioid alga; **Perithecia:** hemispherical, black, immersed in the thallus, 0.4-0.8 mm diam.; **ascomatal wall:** black, continuous below the hamathecium; **hamathecium:** branched pseudoparaphyses, anastomosing above the asci; filaments: *c.* 1 µm wide, not inspersed with oil droplets; **asci:** cylindrical, *c.* 120 x 12 µm, with 8, uniseriately arranged ascospores, tip with a conspicuous tholus; **ascospores:** hyaline, broadly ellipsoid, 1-septate with a median euseptum, 14-18 x 7-9 µm; walls: ornamented with tiny warts, without a gelatinous sheath; **Pycnidia:** frequent to numerous, 0.14-0.20 mm diam.; **conidia:** ellipsoid to narrowly ellipsoid, simple, hyaline; **Spot tests:** all negative, UV negative; **Secondary metabolites:** none detected.

Substrate and ecology: on calcareous, disintegrating, sandstone and shale; **World distribution:** mostly temperate in the Northern Hemisphere; **Sonoran distribution:** only known from the Channel Islands in California.

Notes: The related *Acrocordia cavata* (Ach.) R. C. Harris, that occurs on bark, has been erroneously reported from the area, as *Arthopyrenia sphaeroides* (Wallr.) Zahlbr.

AGONIMIA

by O. Breuss

Agonimia Zahlbr., Őster. Bot. Z. 59: 350 (1909).

Family: Verrucariaceae; Type: *Agonimia tristicula* (Nyl.) Zahlbr.; No. species: nine world-wide; Selected lit.: Coppins and James (1978), Sérusiaux et al. (1999).

Life Habit: lichenized; **Thallus:** smooth or granular to finely digitate or minutely squamulose; **upper surface:** green, grayish green, olivaceous or brownish; **anatomy:** paraplectenchymatous throughout, composed of ± papillate cells; **photobiont:** primary one a chlorococcoid alga, secondary photobiont absent; algal cells: 5-11 µm in diam., distributed over most of thallus; **Ascomata:** perithecial, subglobose or pyriform to barrel-shaped, often between squamules or granules, superficial to half-immersed, without an involucrellum; exciple: thick, paraplectenchymatous, ± distinctly 3-layered, black externally, paler or colorless internally, outer surface matt or subnitid, plicate-rugose or smooth; periphyses: present, simple or sparingly branched; interascal filaments absent; hymenial gel I+ blue or orange-red; **asci:** clavate, thin-walled (I-), with slightly thickened apex that lacks an ocular chamber, (1-) 2- or (4-) 8-spored; **ascospores:** strongly muriform, hyaline to pale brownish, ellipsoid to elongate-ellipsoid; **Conidiomata:** pycnidial (known only in one species) small, black; **conidia** bacilliform; **Secondary metabolites:** none detected; **Geography:** temperate regions of the world; **Substrate:** soil, detritus, mosses, bark of old trees.

Notes: The genus is closely related to *Polyblastia*, from which it is separated by ± papillate cortical cells and multi-layered perithecial walls.

Key to the species of ***Agonimia*** from the Sonoran region:

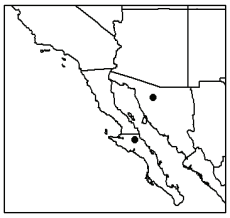
1. Squamules mainly flattened, without cortical hairs; perithecia usually present ..... ***A. tristicula***
1. Squamules distinctly segmented, bud-like, with hyaline cortical hairs; usually sterile ..... ***A. opuntiella***

The Species

Agonimia opuntiella (Buschardt & Poelt) Vězda, Lich. rar. exs. 330 (1997).

Basionym: *Physcia opuntiella* Buschardt & Poelt, Flora 169: 24 (1980); Synonym: *Phaeophyscia opuntiella* (Buschardt & Poelt) Hafellner; Illustrations: Vězda (1997), nr. 330; Poelt (1980), pp. 24 & 25.

Thallus: minutely squamulose; **squamules:** loosely attached, with ± ascending, segmented, yeast-like thallus fragments with finger-like papillae; segments: 0.1-0.25 mm wide, rounded, flat or convex, **upper surface:** grayish green or brown, with delicate hyaline cortical hairs, **anatomy:** paraplectenchymatous throughout, composed of polygonal cells (c. 6-10 µm in diam.,) with no distinct cortices; algal cells: up to 15 µm diam., distributed throughout most of the thallus; **lower surface:** similar as upper or paler; **Perithecia:** not seen in Sonoran material; elsewhere pyriform, up to 0.4 mm high and 0.3 mm broad; wall: black, with rugose surface; **asci**: clavate, 2-spored; **ascospores:** muriform, brownish when old, 60-70 x 25-28µm; **Pycnidia:** unknown; **Spot tests:** all negative; **Secondary metabolites:** none detected.



Substrate and ecology: over mosses, lichens or detritus over soil or rock on dry sites; **World distribution:** Europe (Alps, central Spain), Canary Islands, SW North America; **Sonoran distribution:** known from a few localities in Baja California Sur and Sonora.

Notes: The formation of segmented, bud-like propagules with hyaline hyphal hairs is distinctive.

Agonimia tristicula (Nyl.) Zahlbr., Österr. bot. Z. 59: 351 (1909).

Basionym: *Verrucaria tristicula* Nyl., Flora 48: 356 (18 65); Synonym: *Polyblastia tristicula* (Nyl.) Arnold.

Thallus: delicately squamulose, forming small aggregates several mm across; **squamules:** 0.1-0.5 mm wide, ± crowded, adnate to ascending, flat or convex, roundish to elongate, more rarely digitiform or divided into coarsely subgranular segments; **upper surface:** grayish brown or green-brown to fawn, green when wet, dull; **anatomy:** paraplectenchymatous throughout, with no distinct cortices; algal cells: distributed throughout most of the thallus; **lower surface:** pale; **Perithecia:** prominent, black, barrel-shaped, up to 0.5 mm broad, surface rough and wrinkled; **asci:** clavate, 2-spored; **ascospores:** strongly muriform, elongate-ellipsoid, hyaline to pale yellow-brown, *c.* 80-120 x 30-50 µm; **Pycnidia:** unknown; **Spot tests:** all negative; **Secondary metabolites:** none detected. **Substrate and ecology:** over soil, mosses or debris, mainly over calciferous ground, rarely on nutrient-rich bark, mainly upland; **World distribution:** Europe, Macaronesia, North America, Pacific islands; **Sonoran distribution:** very rarely found in Arizona, but certainly overlooked.

AHTIANA

by B. D. Ryan

Ahtiana Goward, Bryol. 88: 370 (1985).

Family: Parmeliaceae; Type: *Ahtiana sphaerosporella* (Müll. Arg.) Goward; No. species: three world-wide; Selected lit.: Brodo et al. (2001), p. 150; Goward (1985); Thell et al. (1995).

Life habit: lichenized; **Thallus:** foliose, ± closely adpressed, to 8 cm across, broadly lobate; **lobes:** 0.5-10 mm wide; cilia present or absent; **upper surface:** pale yellow to pale yellow-green, rugose and subplicate, continuous, without pseudocyphellae, maculae, soredia or pustulae; isidia: present or absent; **upper cortex:** paraplectenchymatous, 15-25 µm thick, composed of *c.* 3 cell layers; with non-pored epicortex; **medulla:** white; medullary hyphae: 3-4 µm thick; cell walls: containing *Cetraria*-type lichenan (medulla I+ blue); **photobiont:** primary one a trebouxioid alga, secondary photobiont absent; **lower cortex:** paraplectenchymatous, 15-20 µm thick, composed of 2-3 layers of somewhat brownish cells; **lower surface:** usually light tan or pale brown (to olive-black), with sparse to abundant simple rhizines to the margins; **Ascomata:** apothecial, frequent, with prominent thalline exciple, laminal or marginal, sessile, ± circular, up to 13 mm across; disc: brown, non-perforate; exciple: hyaline or grayish, 2-layered; upper layer: 10-30 µm thick, composed of periclinally arranged hyphae; lower layer: 35-50 µm thick, paraplectenchyamtous; hymenium: (including ascogenous layer) 50-60 µm high, uppermost part brown or ochraceous-yellowish; paraphyses: straight, somewhat branched, not (or scarcely) anastomosing; hypothecium: hyaline; **asci:** narrowly to rather broadly clavate, 45-60 µm high, *Lecanora*-type; axial body 2-5 µm wide, 8-spored; **ascospores:** ± uniseriate, simple, globose or subglobose, 4-6 µm diam.; wall: hyaline, smooth, without distinctly developed endospore thickening, not amyloid; **Conidiomata:** pycnidial, laminal or marginal, emergent, often abundant, black, conspicuous, to 0.2 mm across; **conidia:** usually bifusiform or occasionally bacilliform, citriform or sublageniform, 5-7 (-9) x *c.* 1 µm; **Secondary metabolites:** upper cortex with usnic acid, medulla with aliphatic acids; **Geography:** montane coniferous forests in western North America; **Substrate:** on bark or wood.

Notes: It was initially segregated as a monotypic genus from *Parmelia*, and later two additional species were transferred from *Cetraria* and *Tuckermannopsis*. It is characterized by its yellow-green upper cortex (usnic acid), absence of pseudocyphellae, presence of caperatic acid in the medulla and globose ascospores. It differs from *Flavoparmelia* in having a paraplectenchymatous upper cortex, non-pored epicortex, a medulla lacking dep-

sides and depsidones and with *Cetraria*-type lichenan (not isolichenan) in the cell walls, and much smaller and ± globose (rather than large and ellipsoid) ascospores.

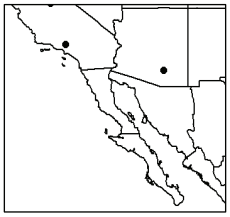
The Species

Ahtiana sphaerosporella (Müll. Arg.) Goward, Bryol. 88: 370 (1985).

Basionym: *Parmelia sphaerosporella* Müll. Arg., Flora 74: 378 (1891); Illustrations: Hale (1979), p. 45; Hale and Cole (1988), plate 1; McCune and Geiser (1997), p. 19; Goward, et al. (1994), p. 30 and Vitt et al. (1988), p. 221; St. Clair (1999), p. 30.

Thallus: foliose, closely adnate, frequently tightly wrapped around small twigs or tightly appressed to larger stems, (2-) 4-6 (-8) cm across, lobate; **lobes:** 2-3 (-5) mm wide, ± linear-elongate, apically rounded; margins aprèssed; cilia absent; **upper surface:** light yellowish green (often rather more yellowish than green, occasionally becoming dark olive green), strongly and finely wrinkled except near the margins, to more often becoming folded; without pseudocyphellae; **upper cortex:** thin walled; **medulla:** white; **lower cortex:** thin walled; **lower surface:** white to buff or partly olivaceous, reticulately wrinkled, rhizines sparse to more often abundant to the lobe tips, concolorous with or slightly darker than lower surface, usually simple; **Apothecia:** numerous, laminal, mostly restricted to thallus center, 1-4 mm diam.; disc: light brown to greenish or yellowish or darkening; exciple: 2-layered, upper layer composed of horizontally arranged hyphae, lower layer thin walled; **asci:** rather broadly clavate, 40-50 x 13-18 µm; axial body 3-5 µm; **ascospores:** spherical, 4-6 µm diam.; **Pycnidia:** laminal, generally conspicuous, often abundant, black; **conidia:** formed pleurogenously, bifusiform, 5-7 (-9) x *c.* 1 µm; **Spot tests:** upper cortex K-, C-, KC+ yellow, P-, UV-; medulla K-, P-, KC-, P-; **Secondary metabolites:** upper cortex with usnic acid; medulla with caperatic acid (major).

Substrate and ecology: on conifers in montane to subalpine forests, 1500-2400 m in its southern range, rarely on hardwoods (*Quercus*); **World distribution:** common NW North America, particularly near the Pacific coast, but rarer to the south; **Sonoran distribution:** formerly known from the southern California mountains and one location in Santa Cruz County in SE Arizona.



Notes: The one occurrence in Arizona is a disjunct from its other extant populations, and occurs on an unusual bark type. In the Sonoran region *Ahtiana sphaerosporella* might be confused with the more southerly *Flavoparmelia rutidota*, from which *A. sphaerosporella* can be easily distinguished by its mostly pale discs and its P- medulla (lacking protocetraric acid). *Flavopunctelia* species are also yellow-green and are much more common in the Sonoran region, but they have white pseudocyphellae on the upper surface (not in *A. sphaerosporella*) and a C+ red medulla.

ALECTORIA

by B. D. Ryan

Alectoria Ach., Tent. Hist. Lich. 95 (1810) [see Hawksworth, et al. 1995].

Family: Alectoriaceae; Type: *Alectoria sarmentosa* (Ach.) Ach.; No. species: eight known world-wide. Selected lit.: Brodo and Hawksworth (1977).

Life Habit: lichenized; **Thallus:** fruticose, erect, decumbent (prostrate), subpendent or pendent, markedly elongate, attached by a basal holdfast; branches: ± terete, or occasionally somewhat expanded and dorsiventrally compressed, or angular to foveolate towards the base and at branch axils; **surface:** greenish yellow or occasionally streaked greenish-black, or in one species (*A. nigricans*)

grayish to pinkish or brown-black, continuous, generally smooth, occasionally becoming striately ridged towards base and axils; pseudocyphellae: always present, often conspicuous, fusiform, white, flat to markedly raised; soredia: present or absent; isidia: absent (but pseudocyphellae becoming sorediate and bearing spinules in one species); true lateral spinules: absent; **cortex:** composed of longitudinal, periclinal, arachnoid, conglutinated hyphae immersed in ± large amount of matrix; **medulla:** loose, arachnoid; hyphae: longitudinal, distinctly segmented, usually ornamented; cell walls with isolichenan, *Cetraria*-type lichenan, and sometimes traces of intermediate types of lichenan; **photobiont:** primary one a trebouxioid alga, secondary photobiont absent; **Ascomata:** apothecial, lateral, sometimes appearing geniculate owing to the death of the branch distal to them, sessile, slightly stalked, circular; thalline exciple: persistent and often markedly incurved, concolorous with thallus; disc: concave, brown to dark brown or black; exciple: gray or hyaline; hymenium: hyaline below, brown, green, blue-green, gray above, I+ very strongly blue; paraphyses: 1.5-3 µm wide, somewhat branched and anastomosing, the tips weakly pigmented, 70-140 µm; hypothecium: hyaline or pale, 20-40 µm, over an algal layer; **asci:** clavate-oval, 65-130 x 25-50 µm, *Lecanora*-type; wall: 6-12 µm thick; tholus: I+ blue, the ocular chamber and axial body short and broad, 2-4 (-8)-spored; **ascospores:** simple, broadly ellipsoid, 20-45 x 12-25 µm; wall: 3-4 µm thick, at first hyaline, becoming pale brownish, grayish to dark brownish or blackish at maturity, smooth, with distinct, pale, gelatinous outermost layer, I-; **Conidiomata:** pycnidial, usually rare, (sub-) marginal-(sub-)terminal, immersed in thalloid warts; **conidia:** bacilliform, pleurogenously formed, 7-8 x 0.8 µm; **Secondary metabolites:** cortex usually with usnic acid (except in *A. nigricans*); medulla and/or cortex often with orcinol and ß-orcinol depsides and depsidones and an unidentified K+ red, C+ green-black metabolite occurs in the cortex of the basal parts of the thalli of most species; **Geography:** circumbipolar, arctic-alpine to boreal-montane; **Substrate:** on bark, wood, soil, or detritus.

Notes: *Alectoria* is readily separable from other genera, including *Bryoria* and *Pseudephebe*, by its characteristic yellow-green color (due to usnic acid) in most species, the cortical structure and the abundance and structure of the pseudocyphellae. It differs from most species of *Usnea* (which are also yellow green due to usnic acid) by the lack of a central strand. According to Tucker and Jordan (1978), the reports of *A. ochroleuca* (Hoffm.) A. Massal. from southern California by (Orcutt 1907 & 1909, as *Usnea ochroleuca* Fr.) and Hasse (1913) are based on misidentifications (presumably not species of *Alectoria* at least in the modern, more restricted sense).

Key to species of ***Alectoria*** in the Sonoran region:

1. Thallus caespitose (to prostrate), short (only a few cm long), stiff; apothecia usually common; ascospores 35-45 x 18-24 µm; at higher elevations (> 1500 m), Chihuahua (relatively common) and Sinaloa ..... ***A. lata***
1. Thallus pendent to subpendent, 20-40 (-80) cm long, flaccid except at the base; apothecia generally absent or few; ascospores 23-35 x 14-20 µm; at moderate elevations, mainly boreal, extending south to California .... ***A. sarmentosa*** subsp. ***sarmentosa***

The Species

Alectoria lata (Taylor) Linds., Trans. Roy. Soc. Edinb. 22: 135 (1859), *sensu lato*.

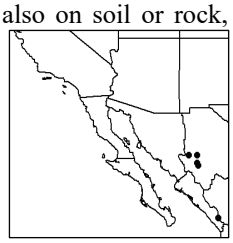
Basionym: *Cornicularia lata* Taylor, Lond. J. Bot. 6: 190 (1847); Synonyms: see Brodo and Hawskworth (1977); Illustrations: Brodo et al. (2001), p. 152; Hale and Cole (1988), fig. 52-a [incorrectly labeled as 52-b, which is actually of *A. imshaugii*] and below.

Thallus: caespitose [to subpendent in non-Sonoran material], occasionally prostrate and entangled, stiff, 1.5-2 cm long [usually 5-8 cm long in non-Sonoran material], apparently dying at the base [looser and more irregular, often with persistent base, in non-Sonoran material]; **branching:** mainly isotomic dichotomous from the base, sometimes becoming anisotomic dichotomous towards the apices, sometimes with short perpendicular lateral branches; axils: mostly acute; ultimate branchlets sometimes curved but not distinctly drooping; **branches:** terete [usually somewhat angular in cross-section in non-Sonoran region material], not flattened, even to uneven in diam., 0.5-1.5 (-2.0) mm diam.; **surface:** grayish green to

pale greenish yellow throughout [in non-Sonoran material, more distinctly yellow or green, without grayish cast, and sometimes streaked greenish-black, especially towards the base]; soralia**:** absent; true lateral spinules absent; **pseudocyphellae:** white, raised, ± abundant and conspicuous, mostly ellipsoid and 0.1-0.2 mm long [in non-Sonoran region material, elongate fusiform and mainly 0.5-1.0 mm long], without isidia-like spinules; **Apothecia:** frequent, lateral but sometimes appearing geniculate due to the death or disintegration of the branch distal to the ascocarps, (0.6-) 2-4 mm in diam. [to 10 mm elsewhere]; thalline exciple: concolorous with thallus, incurved; disc: light yellowish brown to grayish yellowish brown [brown to black in non-Sonoran material], concave to plane; **asci:** clavate-oval, 2-spored; **ascospores:** ellipsoid, simple, 35-45 x 18-24 µm; **Pycnidia:** not seen; **Spot tests:** cortex K- or sometimes K+ red, C- or sometimes C+ green-black, KC+ yellow, P-, UV-; medulla K-, C-, KC+ red, CK-, P-, UV+ ice-blue; **Secondary metabolites:** cortex: with usnic acid and occasionally a K+ red unknown; medulla with alectoronic acid.

Fig.37. *Alectoria lata*, photograph by R. Schoeninger.

Substrate and ecology: on pine bark in oak-pine and oak-pine-cypress forests, elsewhere also on soil or rock, usually at high altitudes; **World distribution:** western North America (central Mexican highlands northward along the Sierra Madre Occidental, then disjunct to the Cascade range in Pacific NW), Central America (Guatemala) and eastern Asia; **Sonoran distribution:** Chihuahua and Sinaloa, 1800-2300 m.



Notes: Although the material from the Sonoran region differs in some respects from the description given by Brodo and Hawksworth (1977), it clearly fits *A. lata* in chemistry, ascospores, and various other features. The species was originally described from Mexico and was previously reported from Chihuahua. It differs from *A. sarmentosa*, with which it can sometimes be confused, by its caespitose habit, its generally more abundant ascocarps and its larger spores. It differs from *A. mexicana* in chemistry (C-, with alectoronic rather than olivetoric acid; both KC+ red), and in its mainly acute axils, and ± concave discs. Brodo and Hawksworth (1977) described *A. mexicana* as being ± pendent and 10-12 (-22) cm long, but an examination of a set of Beharrel collections from Oaxaca suggests that the species can be much shorter and caespitose. The ASU exsiccati, distributed as *A. mexicana*, from Chihuahua, contain alectorialic rather than olivetoric acid, and are included here under *A. lata*.

Alectoria sarmentosa (Ach.) Ach.
subsp. **sarmentosa**, Lich. Univ.: 595 (1810).

Basionym: *Lichen sarmentosus* Ach., K. Vet. Acad. Handl. 16: 212 (1795); Synonyms: see Brodo and Hawksworth (1977); Illustrations: Brodo et al. (2001), p. 155; Hale and Cole (1988), fig. 52c; McCune and Geiser (1997), pp. 21 & 23; Goward (1999), p. 47; Wirth (1995), p. 119.

Thallus: pendent, flaccid except at the base, 20-40 (-80) cm long, with a persistent base; **branching:** mainly isotomic dichotomous, frequent from the base, axils acute or obtuse, often rounded; **branches:** terete often becoming compressed and angular to foveolate towards the base and at the axils, 0.5-2.0 (-2.5) mm diam.; **surface:** greenish gray to bright golden yellow, sometimes becoming striately blackened in parts; lateral spinules: absent; **soredia:** in irregularly tuberculate soralia, rare in North American material; **pseudocyphellae:** white, abundant, conspicuous, raised, elongate fusiform to ovoid and tuberculate,

clearly delimited, usually *c.* 1 mm long; **Apothecia:** often abundant, lateral; thalline exciple: concolorous with thallus, usually persistent; disc: orange-yellow to dark brown or black, 2-3 (-5) mm in diam., **asci:** clavate-ovoid, 2-3 (-4)-spored; **ascospores:** ellipsoid, simple, 23-35 (-48) x (12-) 15-20 (-25) µm; **Pycnidia:** sometimes frequent, mainly apical, up to *c.* 2.0 mm diam., black and shining; **conidia:** not seen; **Spot tests:** cortex K-, C-, KC+ yellow, P-, UV- (sometimes K+ red, C+ green-black near the base); medulla K- (rarely K+ yellow), C- or slowly becoming yellow, KC+ red or KC-, P- (rarely P+ yellow), UV+ ice-blue or UV-; **Secondary metabolites:** cortex with usnic acid, and occasionally an unidentified K+ red, C+ green-black substance; medulla usually with alectoronic acid (major), thamnolic, squamatic and barbatic acids (all accessory) but a common chemotype lacks all secondary metabolites except usnic acid.

Substrate and ecology: on a variety of conifers, particularly in moist, lowland forests along the west coast, less often inland; **World distribution:** central and northern Europe, North America and South America (Patagonia); **Sonoran distribution:** probably extinct, reported from collections in the San Bernardino Mountains of southern California in 1929.

ANAPTYCHIA

by T. L. Esslinger

Anaptychia Körb., Grundriss der Kryptogamen-Kunde (1848) [not seen].

Family: Physciaceae; Type: *Anaptychia ciliaris* (L.) Körb.; Species No.: *c.* 15 world-wide; Selected lit.: Kurokawa (1962), Poelt (1965 & 1966) Poelt and Wunder (1970).

Thallus: foliose to subfruticose, small to medium sized, moderately to very loosely attached, lobate; **lobes:** linear-elongate to shorter and rounded or flabellate; **upper surface:** dingy white or gray to dark brown, totally bare in some species but other species may have a weak and partial to almost complete pruina, or a tomentum of fine cortical hairs, or larger tapering cortical hairs near lobe ends, or marginal cilia; **upper cortex:** prosoplectenchymatous; **medulla:** white; **photobiont:** primary one a chlorococcoid alga, secondary photobiont absent; **lower cortex:** lacking or prosoplectenchymatous, but then sometimes only weakly organized and poorly differentiated from the medulla; **lower surface:** pale or darkening; sparsely to rather densely rhizinate, the rhizines pale or darkening, simple or furcate to densely squarrosely branched; **Apothecia**: with thalline exciple; **asci:** subclavate to clavate, 8-spored; **ascospores:** *Physconia*-type, brown, 1-septate, 25-46 x 13-23 µm; **Pycnidia:** blackened and immersed; **conidia:** bacilliform to short-cylindrical, 3.5-6 x ± 1 µm; **Secondary metabolites:** terpenoids; apparently lacking typical phenolic substances; **Geography:** primarily temperate, North America, Europe, Asia and Africa**; Substrate:** bark or wood, rock or rarely soil.

Notes: *Anaptychia* (*sensu lato*, including *Heterodermia*) has long been recognized by most authors as distinct from *Physcia*, based largely on the presence of a prosoplectenchymatous upper cortex (rather than paraplectenchymatous) and also by the different types of spores (Kurokawa 1962). Poelt (1965) segregated the genus *Heterodermia*, leaving in *Anaptychia* all those species with *Physconia*-type spores and lacking atranorin in the upper cortex. One genus at times confusable with *Anaptychia* is *Physconia*, which shares the distinctive spores and a K- upper cortex. Although these two genera don't seem extremely closely related, for some of their species there is really only one conclusive character that can be used to separate them: a prosoplectenchymatous cortex in *Anaptychia*, and a paraplectenchymtous or scleroplectenchymatous cortex in *Physconia*.

Key to the species of ***Anaptychia*** occurring in the Sonoran region:

1. Thallus with soredia, primarily in terminal, labriform soralia ..... ***A. elbursiana***
1. Thallus without soredia ..... ***A. ulotrichoides***

The Species

Anaptychia elbursiana (Szatala) Poelt, Nova Hedwigia 12: 132 (1966).

Basionym: *Physcia elbursiana* Szatala, Ann. Hist. Nat. Mus. Nat. Hung. 8: 243 (1957); Synonym: *Physconia thomsonii* Essl., Mycotaxon 51: 97 (1994); Illustrations: Esslinger (1994), p. 98 as *Physconia thomsonii* and Fig. 38 below.

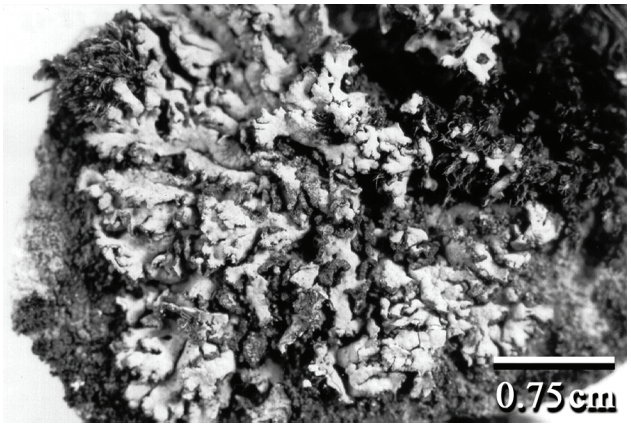
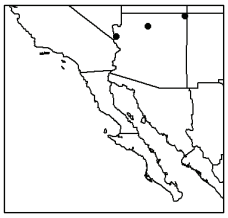


Fig.38. *Anaptychia elbursiana,* photo by T.L. Esslinger.

Thallus: foliose, up to 5 cm in diam., irregular to somewhat orbicular; **lobes:** mostly irregular-flabellate, ± contiguous to slightly overlapping, 0.8-2 mm broad, ± flat at the tips but often becoming somewhat convex inwardly; **thallus surface:** gray to gray-brown, usually with a ± complete pruina; **sorediate:** the soredia primarily in marginal and terminal soralia on lateral lobes, becoming labriform, scattered punctiform laminal soralia sometimes forming in older thallus parts; individual soredia coarsely granular, mostly becoming distinctly darkened, to almost black; **upper cortex:** prosoplectenchymatous, irregularly so in parts; **medulla:** white; **lower cortex:** very thin, poorly organized to weakly prosoplectenchymatous, intergrading with the medulla; **lower surface:** almost white on the lobe tips, inward becoming pale tan to deep tan; rhizines scattered, simple to irregularly furcate, concolorous with the lower surface; **Apothecia:** not seen; **Pycnidia:** infrequent, dark brown to blackened and flush with the surface; **conidia:** cylindrical (a few becoming slightly curved), 5-6 x 1 µm; **Spot tests:** all negative for both cortex and medulla; **Secondary metabolites:** small amounts of unidentified terpenoids (2 or 3).



Substrate and ecology: rock or very thin soil or mosses over rock, in open areas **World distribution:** western North America and central Asia. **Sonoran distribution:** northern half of Arizona, in the mountains

Notes: The presence of labriform soralia distinguishes this species from *A. ulotrichoides*, which is the only other member of the genus in the Sonoran region. Occasional immature or poorly developed specimens may have very few or no soralia, and will cause troubles in determination. *Anaptychia elbursiana* is a somewhat larger and coarser species than *A. ulotrichoides*, but this too may not be apparent in young or poorly treated specimens.

Because of its general form and often heavy pruinosity, the typical form of this species is most likely to be mistaken for a species of *Physconia*. The upper cortex is prosoplectenchymatous but much less clearly so than is the upper cortex of more typical species of *Anaptychia* such as *A. ciliaris* (L.) Körber or *A. palmulata* (Michaux) Vain. The upper cortex is easily misinterpreted as being scleroplectenchymatous, as I did when I described the synonymous *Physconia thomsonii*. Many of the early collections of this species were identified as *Physconia grisea*, which has a similarly colored lower surface and also mostly non-squarrose rhizines, but has not been found in North America.

Anaptychia ulotrichoides (Vain.) Vain., Bot. Tidskr. 26: 245 (1904).

Basionym: *Physcia ulotrichoides* Vain., Act. Hort. Petrop. 10: 553 (1888); Illustrations: Moberg (1980a), p. 252 and Fig. 39 below.

Thallus: foliose, up to 2 cm in diam., irregular to somewhat orbicular; **lobes:** mostly ± linear and elongate, often somewhat overlapping or entangled, 0.3-1 mm broad, ± flat or weakly convex in older parts, with sparse to rather numerous cortical hairs on or near lobe ends, the hairs tapered, darkening and sometimes intergrading with the darkening rhizines on underside of lobe ends;

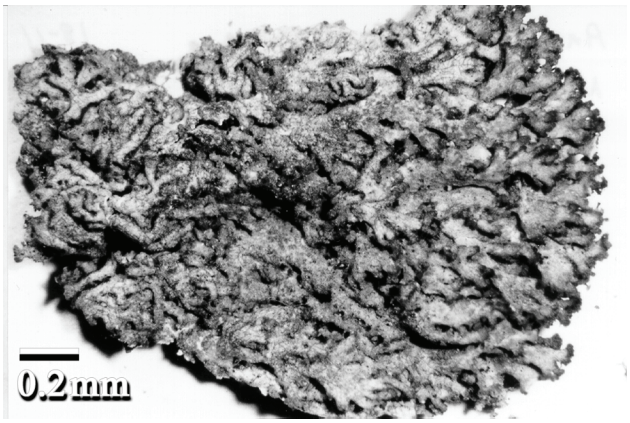


Fig.39. *Anaptychia ulotrichoides*, photo by T.L. Esslinger.

thallus surface: dingy white to tan-brown or darker brown, usually pruinose at least near the lobe ends and sometimes ± continuously; without soredia or isidia; **upper cortex:** prosoplectenchymatous, **lower cortex** missing or poorly differentiated and intergrading with the medulla; **medulla:** white; lower surface: white to tan, without well developed cortex (noticeably absent at lobe ends, but with some agglutinated hyphae developing inward), sparsely to moderately rhizinate, the rhizines simple to sparsely furcate (very sparse, short, perpendicular side branches sometimes present), mostly concolorous with the lower surface, up to 1 mm long; **Apothecia:** rare, up to 1 mm in diam., sessile to short stipitate, the margin entire to irregularly crenate; **ascospores:** 25-31 x 13-14 µm; **Pycnidia:** rare, immersed; **conidia:** bacilliform, 3.5-5 x <1 µm; **Spot tests:** all negative for both cortex and medulla; **Secondary products:** trace unknown terpenoids (2 or 3).

Substrate and ecology: rock or soil over rock, mostly in open areas; **World distribution:** North America, Europe, north Africa and Asia; **Sonoran distribution:** not yet found in the Sonoran Region, but known from just outside Arizona, in Utah (Kane Co.: 18 mi. NNW of Page, Arizona, Nash 6611), and so included here for comparison, since it is likely yet to be found in the region.

Notes: The lack of soralia make this species easily distinguishable from *A. elbursiana*, the only other member of the genus occurring in the Sonoran region, but *A. ulotrichoides* has been most commonly misidentified as a species of *Phaeophyscia* or, less often, as *Physconia*. The presence of the rather coarse but sparse cortical hairs, and the pale, almost ecorticate lower surface will distinguish it from most species in both those genera. At times, it may be necessary to section the thallus to check the upper cortex anatomy, which, however, is open to the same misinterpretation as that described for *A. elbursiana* (discussed above).

ANEMA

by M. Schultz

Anema Nyl. *ex* Fóriss., Nova Acta Reg. Soc. Sci. Ups., ser. 3, 16: 91 (1885).

Family: Lichinaceae; Type: *Anema decipiens* (A. Massal.) Fóriss.; No. species: *c.* 10 world-wide; Selected lit.: Moreno and Egea (1992a).

Life habit: lichenized; **Thallus:** umbilicate-rosette shaped, squamulose, crustose-squamulose, subfruticose, gelatinous when wet; **surface:** black, rarely grayish pruinose, smooth, sometimes nodulose or granulose; **anatomy:** ecorticate, homoiomerous, loose network of hyphae surrounding large photobiont cells; **photobionts:** primary one a chroococcoid cyanobacterium, secondary photobiont absent; **Ascomata:** apothecial, laminal on thallus, or-

bicular, semi-immersed to sessile, margin distinct, with thick thalloid rim; **ontogeny:** hemiangiocarpous, forming pycnoascocarps from ascogonia beneath the pycnidia; **anatomy:** exciple: hyaline; epithecium: brownish yellow; hypothecium: hyaline, **asci:** prototunicate, wall thin, non-amyloid, 8-spored; **ascospores:** simple, ellipsoid, broadly ellipsoid or globose; 8-14 µm long, 4-11 µm wide; walls: thin, hyaline; **Conidiomata:** pycnidial, laminal, immersed; **conidia:** ellipsoid or bacilliform, *c.* 3 x 1 µm; **Secondary metabolites:** none detected; **Geography:** arid, semi-arid to warm temperate regions; **Substrate:** limestone and calcareous rock.

Notes: Species of the *Phylliscum macrosporum* group are similar. Formally, the separation is based on the gelatinous sheath coloration of the photobiont cells which may not be a reliable character. Species of the *Phylliscum demangeonii* group differ in the lack of paraphyses and possess tapered ascus tips. *Paulia* is also similar but lacks an exciple and the ascomata arise from a web of generative hyphae.

The Species

Anema progidulum (Nyl.) Henssen, Lichenologist 22: 139 (1990).

Basionym: *Omphalaria progidula* Nyl., Flora 62: 353 (1879); Synonym: *Thyrea progidula* (Nyl.) Zahlbr.; Illustrations: Moreno and Egea (1992a), p. 55; and Fig. 40 to right.

Thallus: black, crustose to squamulose, areoles/squamules small, 0.5-1 mm wide, ± angular or roundish in outline, not rosette-shaped, **surface:** black, rough, **attachment:** by a central bundle of rhizohyphae; **Apothecia:** sessile, zeorine, 1-3 (-5) per squamule, *c.* 0.5 mm wide; disc: dark red, slightly depressed, open; thalline margin: persisting, smooth; exciple: 10-20 µm thick, hyaline, composed of loosely interwoven thin hyphae; epihymenium: faintly yellowish-brown; hymenium: hyaline, amyloid, up to 125 µm high; paraphyses: distinctly septate, sparingly branched and anastomosing; apical cells: *c.* 3 µm thick; hypothecium: *c.* 12.5 µm thick; **asci:** 8-spored; **ascospores:** simple, hyaline, globose to broad ellipsoid, 7.5-10 x 7.5 µm; walls: thin; in old, deformed spores *c.* 2.5 µm wide; **Pycnidia:** immersed, simple, globose, *c.* 0.1 mm wide; **conidia:** small, bacilliform or ellipsoid, *c.* 3 x 1 µm; **Spot tests:** all negative; **Secondary metabolites:** none detected.

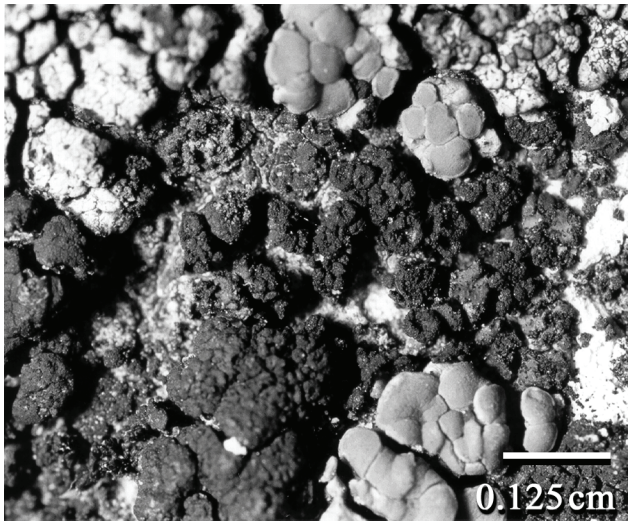


Fig. 40. *Anema progidulum,* photo by M. Schultz.

Substrate and ecology: on limestone, on sheltered, steep or exposed faces of boulders on rocky slopes; chaparral woodlands and pine-oak forests; **World distribution:** southern Europe, NW Africa and SW North America; **Sonoran distribution:** limestone deposits in central Arizona.

Notes: This is the smallest species of the genus with an almost crustose-areolate growth form. Similar genera are *Psorotichia* and *Porocyphus*, both of which have a paraplectenchymatous anatomy composed of smaller cells. *Phloeopeccania* is similar in anatomy but either has polysporous asci or large apothecia with thick (*c.* 125 µm), prominent thalline margins, depressed to urceolate discs, no exciple and a different type of ascoma ontogeny (groups of coiled ascogonia). *Gloeoheppia polyspora* differs in the subgelatinous thallus with cavities, the dark brownish thallus color, and polysporous asci.

ANISOMERIDIUM

by A. Aptroot

Anisomeridium (Müll. Arg.) M. Choisy, Icon. Lich. Univ. Fasc. 3 (1926).

Family: Monoblastiaceae. Type: *Arthopyrenia xylogena* Müll. Arg.; No. species: *c.* 100 world-wide; Selected lit.: Harris (1995), and Purvis et al. (1992).

Life habit: lichenized or non-lichenized, saprobic; **Thallus:** crustose, mostly immersed in substrate, lacking a cortex; **upper surface:** whitish or pale gray; **photobiont:** primary one trentepohlioid alga or absent, secondary photobiont absent; **Ascomata:** perithecial, almost entirely immersed to sessile, black (rarely pink or whitish), simple to compound; **involucrellum:** often present, brown-black, hemispherical to ± globose; **ascomatal wall:** black, not continuous below the hamathecium, composed of ± cellular hyphae without bark cells; **exciple:** globose, surrounding the center, colorless or pale brownish; **hamathecium:** long-celled pseudoparaphyses, slender, branched, anastomosing above the asci, non-amyloid; **asci:** bituncate, cylindrical to clavate, with an apical dome and with an indistinct or short and broad ocular chamber, non-amyloid, 4-8 spored; **ascospores:** uniseriate, hyaline, ellipsoid to clavate-fusiform, 1 (-3)-septate with eusepta, 11-22.5 x 4.5-6.5 µm; walls: occasionally ornamented with tiny warts; **Conidiomata:** pycnidial, immersed to sessile, ± globose or conical, black; **conidia:** ovoid to ellipsoid to bacilliform, simple, hyaline; **Secondary metabolites:** none detected; **Geography:** cosmopolitan in temperate and tropical regions but most diverse in the tropics; **Substrate:** usually on bark, but also on calcareous or non-calcareous rock.

Notes: It differs from *Arthopyrenia* in several features, particularly in the structure of the involucrellum, which is not clypeate. *Acrocordia* has a different ascal structure and ellipsoid ascospores with a warted epispore.

Key to the species of ***Anisomeridium*** from the Sonoran region:

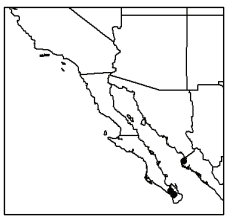
1. Ascospores 3-septate; 14-16 x 4.5-5.5 µm .... ***A. quadricoccum***
1. Ascospores 1-septate 2
2. Ascospores uniseriate, 13-15 x 5-6 µm .... ***A. biforme***
2. Ascospores biseriate to irregularly arranged 3
3. Ascospores more than 2.5 times longer than broad, 14-20 x 5-6 µm; thallus lichenized or not .. ***A. subprostans***
3. Ascospores less than 2.5 times longer than broad, 15-17 x 7-8 µm; thallus not lichenized ..... ***A. anisolobum***

The Species

Anisomeridium anisolobum (Müll. Arg.) Aptroot, Biblioth. Lichenol. 57: 21 (1995).

Basionym: *Arthopyrenia anisoloba* Müll. Arg., Flora 66: 305 (1883); Illustration: Harris (1975a), p. 243 (as *A. feeanum*).

Thallus: continuous, immersed in the substrate; **upper surface:** whitish, smooth; **photobiont:** usually a trentepohlioid alga, but absent in Sonoran material; **Perithecia:** hemispherical, black, semi-immersed in the thallus, 0.3-0.5 mm diam.; **perithecial wall:** black, continuous below the hamathecium; **hamathecium:** branched pseudoparaphyses, anastomosing above the asci; filaments: *c.* 1 µm wide, not inspersed with oil droplets; **asci:** clavate, *c.* 75-100 x 10-15 µm, with 8, irregularly arranged ascospores; **ascospores:** hyaline, ovoid, 1-septate with a submedian euseptum, 15-17 x 7-8 µm; walls: slightly ornamented with warts when old, without a gelatinous sheath; **Pycnidia:** not observed; **Spot tests:** all negative, UV-; **Secondary metabolites:** none detected.



Substrate and ecology: on bark of various woody plants; **World distribution:** pantropical; **Sonoran**

distribution: only found in Baja California Sur and Sinaloa, but there not rare.

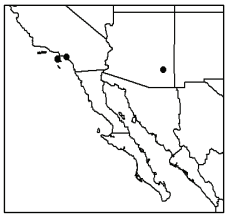
Notes: It is a common, pantropical species, which is especially abundant in coastal regions. Remarkably, the Sonoran Desert material was not lichenized.

Anisomeridium biforme (Borrer) R. C. Harris, in Vězda, Lich. sel. exs. fasc. 61: 1305 (1978).

Basionym: *Verrucaria biformis* Borrer, in Hooker & Sowerby, Suppl. Engl. Bot. 1: pl. 2617, f. 1 (1831); Synonyms: *Arthopyrenia biformis* (Borrer) A. Massal., *Arthopyrenia conformis* (Nyl.) Müll. Arg., *Arthopyrenia parvula* Zahlbr.; Illustration: Harris (1975a), p. 241.

Thallus: continuous, not immersed in the substrate, effuse or delimited by a thin, blackish hypothallus; **upper surface:** whitish to greenish gray, smooth; **photobiont:** a trentepohlioid alga; **Perithecia:** hemispherical, black, semi-immersed in the thallus, 0.3-0.6 mm diam.; **perithecial wall:** black, with a well differentiated involucrellum, 50-100 µm thick; lower wall: pale or colorless, continuous below the hamathecium; **hamathecium:** branched pseudoparaphyses, anastomosing above the asci; filaments: *c.* 1 µm wide, not inspersed with oil droplets; **asci:** cylindrical, *c.* 70-100 x 10 µm, with 8, uniseriately arranged ascospores; **ascospores:** hyaline, ovoid, 1-septate with a slightly submedian euseptum, 13-15 x 5-6 µm, not ornamented, without a gelatinous sheath; **Pycnidia:** two types: 100-200 µm diam. or 40-100 µm diam.; **conidia:** respectively either subglobose to ellipsoid macroconidia, 2.3-4 x 1.8-2.7 µm or globose microconidia, 1-1.5 µm diam.; **Spot tests:** all negative, UV-; **Secondary metabolites:** none detected.

Substrate and ecology: on bark of various woody plants; **World distribution:** nearly cosmopolitan; **Sonoran distribution:** SW Arizona and California, including the Channel Islands, but there not rare.



Anisomeridium quadricoccum R. C. Harris, More Florida Lichens: 129 (1995) [as '*quadrococcum*'].

Thallus: continuous, immersed in the substratum; **upper surface:** whitish, smooth; **photobiont:** a trentepohlioid alga; **Perithecia:** hemispherical, *c.* 0.2 mm diam., immersed in bark, below black, often fused clypeus of 0.4-0.7 mm diam.; **perithecial wall:** pale, continuous below the hamathecium, ostiole white; **asci:** clavate, *c.* 70-90 x 13-16 µm, with 8, irregularly arranged ascospores, tip with a conspicuous tholus; **hamathecium:** branched pseudoparaphyses, anastomosing above the asci; filaments: *c.* 1 µm wide, not inspersed with oil droplets; **ascospores:** hyaline, narrowly ovate, 3-septate (starting with a median euseptum), 15-17 x 6-7 µm; wall: not ornamented, without a gelatinous sheath; **Pycnidia:** not observed; **Spot tests:** all negative, UV-; **Secondary metabolites:** none detected.

Substrate and ecology: on bark of various woody plants; **World distribution:** possibly nearly endemic; so far known only from the USA (Florida and Georgia) and Mexico (Baja California Sur); **Sonoran distribution:**. only recorded twice from Baja California Sur.

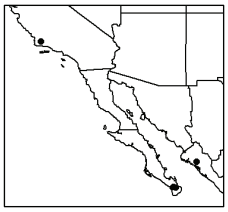
Notes*:* It is a rare species, which only recently has been described.

Anisomeridium subprostans (Nyl.) R. C. Harris, in S. C. Tucker & R. C. Harris, Bryologist 83: 4 (1980).

Basionym: *Verrucaria subprostans* Nyl., Expos. syn. Pyrenocarp.: 56 (1858); Illustration: Harris (1975a), p. 247.

Thallus: continuous, immersed in the substrate; **upper surface:** whitish or absent, smooth; **photobiont:** a trentepohlioid alga or absent; **Perithecia:** hemispherical, black, superficial or semi-immersed in the thallus, 0.2-0.5 mm diam.; **perithecial wall:** black, continuous below the hamathecium; **hamathecium:** branched pseudoparaphyses, anastomosing above the asci; filaments: *c.* 1 µm wide, not inspersed with oil droplets; **asci:** clavate, *c.* 75-95 x 10-13 µm, with 8, irregularly arranged ascospores; **ascospores:** hyaline, narrowly ovoid, 1-septate with a slightly submedian euseptum, 14-20 x 5-6 µm, not orna-

mented, without a gelatinous sheath; **Spot tests:** all negative, UV-; **Secondary metabolites:** none detected.



Substrate and ecology: on bark of various woody plants; **World distribution:** pantropical or possibly nearly cosmopolitan, abundant especially in coastal regions; **Sonoran distribution:** recorded from Baja California Sur (several times), southern California and Sinaloa.

Notes: Remarkably, the Sonoran Desert material was partly lichenized and partly not (Aptroot 1997).

ANZIA

by I. Yoshimura

Anzia Stizenb., Flora 44: 390 (1861).

Family: Parmeliaceae; Type: *Anziia colpodes* (Ach.) Stizenb.; No. species: 34 world-wide; Selected lit.: Yoshimura and Sharp (1968), Yoshimura (1987) and Yoshimura (1995).

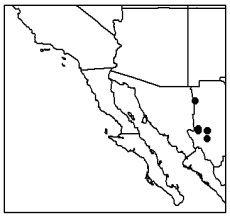
Life habit: lichenized; **Thallus:** foliose, circular in outline or irregularly spreading, 2-30 cm wide, loosely to tightly adnate, lobate; **lobes:** flat to convex, discrete, often loosely imbricate, elongate, mostly <2 mm wide, tips often ascending, eciliate; **upper surface:** pale whitish gray, greenish gray or bluish gray, dull or somewhat shiny, emaculate and lacking pseudocyphellae; with or without soredia or isidia; **upper cortex:** paraplectenchymatous with a non-pored epicortex; **medulla:** white, with or without a chondroid strand; hyphal walls: containing *Cetraria*-type lichenan; **photobiont:** primary one a trebouxioid alga, secondary photobiont absent; **lower cortex:** absent; **lower surface:** brown-black, with a continuous or discontinuous, prominent, dense spongiostratum (spongy hypothallus), with or without rhizines; rhizines: simple or or sparingly branched, stout, apically with a squarrose tuft; **Ascomata:** apothecial, lecanorine, laminal, sessile to substipitate: disc: brown to black, eperforate; epithecium: pale brown; hymenium and hypothecium colorless; paraphyses: simple or forked above, apices clavate, pale brown with a dark brown cap; **asci:** cylindrical, many (more than 20) spored, *Lecanora*-type; **ascospores:** simple, curved; **Conidiomata:** pycnidial, brown-black, immersed, punctiform; **conidia:** simple, bacilliform, colorless; **Secondary metabolites:** depsides, depsidones and aliphatic acids; **Geography:** world-wide, except Europe, most common in east Asia in temperate to subtropical regions, extending to New Guinea, and Oceania, Central and South America (Andes), eastern North America; **Substrate:** common on bark of trees and on rocks.

The Species

Anzia americana Yoshimura & Sharp, Bryologist 71: 110 (1968).

Illustrations: Yoshimura and Sharp (1968), p. 111; Yoshimura (1987), p. 188.

Thallus: foliose, pendulous (appearing superficially fruitcose due to strongly upturned lobe tips), circular in outline or irregularly spreading, up to 5 cm wide, loosely adnate, lobate; **lobes:** flat to convex, discrete, loosely imbricate, dichotomously branched, short linear, 2.5 mm long, mostly 0.5-2 mm wide, tips strongly ascending, eciliate; **upper surface:** pale gray to greenish gray, dull or somewhat shiny; without soredia or isidia; **upper cortex:** paraplectenchymatous, 40-60 µm thick, hyaline to brownish; **medulla:** white, with a chondroid strand; **lower surface:** dark brown, with a continuous, dense spongiostratum 1 mm thick, erhizinate; upturned tips erupting into soredia; **Apothecia:** not seen; **Pycnidia:** not seen; **Spot tests:** cortex K+ yellow, C-, KC-, P+ yellow; medulla K-, C-, KC-, P-;



Secondary metabolites: upper cortex with atranorin and chloroatranorin; medulla with divaricatic acid.

Habitat and ecology: on bark or rock in very humid microclimates; **World distribution:** SE USA (Smoky Mountains) and Mexico south to Venezuela; New Guinea, the Philippines; **Sonoran distribution:** *c.* 2000 m in the Sierra Madre Occidental region of Chihuahua

ARCTOPARMELIA

by T. H. Nash III and J. A. Elix

Arctoparmelia Hale, Mycotaxon 25: 251 (1986).

Family: Parmeliaceae; Type: *Arctoparmelia centrifuga* (L.) Hale; No. species: five world-wide; Selected lit.: Hale (1986b) and Elix (1993a).

Life habit: lichenized; **Thallus:** foliose, *c.* circular in outline, lobate; **lobes:** usually subirregular; tips: usually subrotund, eciliate; **upper surface:** pale yellow green to whitish or gray, smooth, plane to rugulose, dull, usually strongly pruinose, with or without soredia, emaculate; pseudocyphellae: absent; **upper cortex:** palisade plectenchymatous, pored epicortex; **medulla:** white, cell walls containing *Cetraria*-type lichenan; **photobionts**: primary one a *Trebouxia*, secondary photobiont absent; **lower surface:** ivory white to light brown or purplish black, velvety, frequently with a gray margin (like mouse fur), attachment by sparse, simple rhizines, cyphellae, pseudocyphellae and tomentum absent; **Ascomata:** apothecial, imperforate, laminal on thallus, orbicular, cup-shaped, sessile, margin prominent with thalloid rim; exciple gray or hyaline, hypothecium hyaline, epithecium brown or brownish yellow; **asci:** lecanoral, wall layers apex thickened, apex amyloid, with wide, axial body divergent towards apex; **ascospores:** *c.* 8 per ascus, simple, ellipsoid; 10-12 µm long, 4-6 µm wide; wall thin, hyaline; **Conidiomata:** absent or present, pycnidial, laminal, immersed; **conidia:** bifusiform, 6 x *c.* 1 µm; **Secondary metabolites:** upper cortex with usnic acid and atranorin and chloroatranorin; medulla with an orcinol depsidones and (higher) aliphatic acids; **Geography:** throughout arctic and northern boreal regions of the Northern Hemisphere and extending southwards in high montane areas; **Substrate:** mostly on non-calciferous rocks.

Notes: Among the *Parmelia* generic segregates, *Arctoparmelia* is most similar to the southern hemispheric *Psiloparmelia* in cortical chemistry and color of the lobe tips and the lower side, but the later genus has only a rudimentary epicortex, isolichenan in the cell walls and lacks rhizines. Among the yellow-green, non-pseudocyphellate parmelioids occurring in the Sonoran region, *Flavoparmelia* has broader lobes, larger spores, isolichenan in the cell walls and brown lobe tips on the lower side and the ubiquitous genus *Xanthoparmelia* has a shiny, epruinose upper surface, *Xanthoparmelia*-type lichenan in the cell walls, shiny brown or black lobe tips on the lower side, only usnic acid in the upper cortex and a far more complex medullary chemistry.

The Species

Arctoparmelia subcentrifuga (Oxner) Hale, Mycotaxon 24: 25 (1986).

Basionym: *Parmelia subcentrifuga* Oxner, Journ. Bot. Acad. Sci. RSS Ukraine 1: 39 (1940); Synonyms: *Parmelia groenlandica* Lynge and *Xanthoparmelia subcentrifuga* (Oxner) Hale; Illustration: Hale (1986b), p. 253.

Thallus: tightly adnate to adnate, foliose, 4-8 cm in diam., lobate; **lobes:** narrow, sublinear to subirregular, contiguous to imbricate, somewhat elongate, convex, separate, 0.6-3 mm wide, lobe tips subrotund; **upper surface:** pale greenish to yellowish gray, smooth but cracked with age, dull, becoming rimose, emaculate, becoming strongly rugulose; **soredia:** coarse, in linear to irregular pustulae, coarse, becoming diffuse, submarginal, isidia absent; **me-**

dulla: white; **lower surface:** purplish black centrally, gray marginally, sparsely rhizinate, rhizines black, simple; **Apothecia:** not seen; **Pycnidia:** not seen; **Spot tests:** cortex K- or K+ yellow (depending on atranorin concentration), C-, KC+ yellow, P+ yellow; medulla K-, C-, KC-, P-; **Secondary metabolites:** upper cortex with atranorin, chloroatranorin and usnic acid, medulla with alectoronic acid (major).

Substrate and ecology: open boulder fields in arctic, upper montane to alpine areas; **World distribution:** arctic North America southwards at scattered localities throughout the Rocky Mountains and in the Great Lakes area; **Sonoran distribution:** only known from one location on rocks in an upper montane scree slope in the Chiricahua Mountains of SE Arizona.

ARTHOPYRENIA

by A. Aptroot

Arthopyrenia A. Massal., Ric. auton. lich. crost.: 166 (1852).

Family: Xanthopyreniaceae; Type: *Arthopyrenia cerasi* (Schrad.) A. Massal.; No. species: 50 world-wide; Selected lit.: Harris (1973 & 1995), and Purvis et al. (1992).

Life habit: lichenized or saprobic; **Thallus:** crustose, mostly immersed in substrate, or byssoid with black subiculum, or absent; **photobiont:** a trentepohlioid alga or absent; **Ascomata:** perithecial, circular to ellipsoid in surface view; **involucrellum:** clypeate, dark brown, composed of compacted hyphae and bark cells; true **ascomatal wall:** black, not continuous below the hamathecium; **exciple:** thin, usually colorless, surrounding center; **hamathecium:** usually branched, anastomosing, ± moniliform pseudoparaphyses, non-amyloid, or disappearing and than sometimes amyloid; periphysoids: also present; **asci:** bitunicate, pyriform to clavate, with tholus, non-amyloid, 8-spored; **ascospores:** usually hyaline but sometimes brownish with age, pyriform to clavate, 1-3-septate with eusepta, 4-16 x 12-50 µm; walls: sometimes ornamented with tiny warts; **Conidiomata:** pycnidial, blackish; **conidia:** simple to 1-3-septate, oblong, ovoid, bacilliform or thread-like; **Secondary metabolites:** absent; **Geography:** cosmopolitan; **Substrate:** mostly on bark, but also on non-calcareous rock.

Notes: Sonoran species of this genus have recently been classified in four different genera in three different families (Harris 1995a), but the differences between species of *Arthopyrenia* are not very discrete and do not warrent a separation at the generic (let alone familial) level. The genus is, in this wide concept, characterized by the branched, but not anastomosing pseudoparaphyses, which may disappear in later stages, and the usually somewhat sole-shaped ascospores, which always have a broader and shorter upper cell and a longer but more slender lower cell.

Key to the species of ***Arthopyrenia*** in the Sonoran region:

1. Ascospores 3-septate when mature 2
1. Ascospores remaining 1-septate 3

2. Ascocarps inbedded in a thick, hyphal, black subiculum ..... ***A. rhyponta***
2. Ascocarps on a smooth, gray crust ..... ***A. antecellans***

3. Ascospore cells usually both constricted, more or less equally 4
3. Ascospore cells not constricted, upper cell much shorter and broader than lower cell 5

4. Ascospores ornamented with warts; thallus white, lichenized ..... ***A. lyrata***
4. Ascospores smooth; thallus gray, not lichenized ..... ***A. plumbaria***

5. Hamathecium consisting of pseudoparaphyses, with broadened threads (moniliform) ..... ***A. punctiformis***
5. Hamathecium up to 3 µm broad below, with tapering to slender threads above ..... ***A. analepta***

The Species

Arthopyrenia analepta (Ach.) A. Massal., Ric. auton. lic. crost.: 165 (1852).

Basionym: *Lichen analeptus* Ach., Lichenogr. suec. prodr.: 15 (1798); Synonyms: *Arthopyrenia fallax* (Nyl.) Arnold, *Arthopyrenia lapponina* Anzi; Illustration: Harris (1975a), p. 221, as *A. lapponina*.

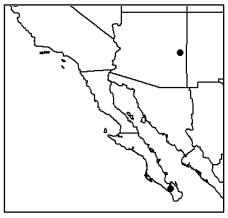
Thallus: discontinuous, mostly immersed in the substrate; **upper surface:** gray, smooth; photobiont: absent; **Perithecia:** hemispherical, black, superficial on the thallus, 0.2-0.4 mm diam.; **ascomatal wall:** black, absent below the hamathecium; **hamathecium:** mostly unbranched pseudoparaphyses, branched above the asci; filaments: *c.* 3 µm wide below, smaller above, not inspersed with oil droplets; **asci:** cylindrical, *c.* 50 x 10 µm, with 8, irregularly arranged ascospores; **ascospores:** hyaline, clavate, 1-septate with a submedian euseptum, 16-20 x 6-7 µm; walls: not ornamented, without a gelatinous sheath; **Spot tests:** all negative, UV negative; **Secondary metabolites:** none detected.

Substrate and ecology: on bark of *Rhus diversiloba*; **World distribution:** northern temperate or possibly nearly cosmopolitan; **Sonoran distribution:** only found once on the Channel Islands of southern California.

Arthopyrenia antecellans (Nyl.) Müll. Arg., Flora 53: 485 (1870).

Basionym: *Verrucaria antecellans* Nyl., Flora 49: 86 (1866); Synonym: *Mycoporum antecellans* (Nyl.) R.C. Harris [as '*antecellens*']; Illustration: Harris (1975a), p. 215.

Thallus: continuous, immersed in the substrate, **upper surface:** whitish to gray, smooth; photobiont: absent; **Perithecia:** hemispherical, black, superficial on the thallus, 0.2-0.3 mm diam.; **ascomatal wall:** black, absent below the hamathecium; **hamathecium:** branched pseudoparaphyses, not anastomosing, dehiscent or becoming unclear; filaments: *c.* 3 µm wide, not inspersed with oil droplets; **asci:** pyriform, *c.* 60-70 x 18-22 µm, with 8, irregularly arranged ascospores; **ascospores:** hyaline but overmature ones brownish, clavate, 3-septate (starting with a supramedian euseptum), 25-30 x 6-9 µm; walls: roughly ornamented with warts, without a gelatinous sheath; **Spot tests:** all negative, UV negative; **Secondary metabolites:** none detected.

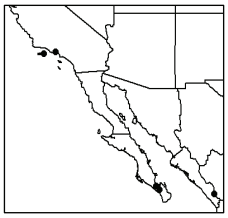


Substrate and ecology: on bark of various woody plants, especially conifers like *Abies* and *Picea*; **World distribution:** northern temperate or possibly nearly cosmopolitan; **Sonoran distribution:** recorded in eastern Arizona and Baja California Sur.

Arthopyrenia lyrata R. C. Harris, in Tucker and R. C. Harris, Bryologist 83: 6 (1980).

Illustrations: Harris (1975a), p. 229; Tucker and Harris (1980), p. 8.

Thallus: continuous, immersed in the substrate; **upper surface:** white to rarely yellowish gray, smooth; photobiont: trentepohlioid; **Perithecia:** hemispherical, black, semi-immersed in the thallus, 0.2-0.5 mm diam.; **ascomatal wall:** black, absent below the hamathecium; **hamathecium:** mostly unbranched pseudoparaphyses, not anastomosing; filaments: up to *c.* 3 µm wide below, not inspersed with oil droplets; **asci:** cylindrical to clavate, *c.* 80-120 x 11-20 µm, with 8, irregularly arranged ascospores; **ascospores:** hyaline, long ellipsoid, 1-septate with a median euseptum, 16-25 x 5-8 µm, with median endospore thickenings in each cell, often breaking into part spores when old; walls: ornamented with warts, without a gelatinous sheath; **Spot tests:** all negative, UV negative; **Secondary metabolites:** none detected.



Substrate and ecology: on bark of various woody plants, most common in the area on *Quercus*; **World distribution:** probably restricted to (sub-) tropical America; **Sonoran distribution:** a rather common species, with numerous

collections from southern California (Channel Islands), Baja California Sur and Sinaloa.

Arthopyrenia plumbaria (Stizenb.) R. C. Harris, in Egan, Bryol. 90: 163 (1987).

Basionym: *Verrucaria plumbaria* Stizenb., in Hasse, Erythrea 3: 44 (1895); Synonym: *Pyrenula herrei* Fink; Illustration: Harris (1975a), p. 225.

Thallus: continuous, immersed in the substrate; **upper surface:** pale gray, smooth; photobiont: absent; **Perithecia:** hemispherical, black, semi-immersed in the thallus, 0.2-0.5 mm diam.; **ascomatal wall:** black, absent below the hamathecium; **hamathecium:** mostly unbranched pseudoparaphyses, not anastomosing; filaments: up to *c.* 3 µm wide below, not inspersed with oil droplets; **asci:** cylindrical, *c.* 50-75 x 10-15 µm, with 8, uniseriately arranged ascospores; **ascospores:** hyaline, long ellipsoid to fusiform, 1-septate with a median euseptum, 15-18 x 4.5-6 µm, with median endospore thickenings in each cell; walls: not ornamented, without a gelatinous sheath; **Spot tests:** all negative, UV negative; **Secondary metabolites:** none detected.

Substrate and ecology: on bark of various woody plants; **World distribution:** tropical to temperate areas of western North America; **Sonoran distribution:** commonly collected in southern California, including the Channel Islands.

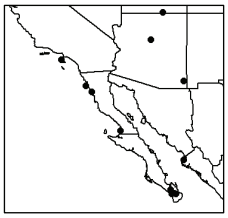
Notes: The species was originally described from the region, and among the studied material was an isotype, which may be the only remaining type specimen. It was not studied by Harris (1973 & 1995a) but agrees with his concept of the species, except that it is non-lichenized. The specimen reported from California as *Arthopyrenia cinereopruinosa* (Schaer.) A. Massal. probably also belongs to this species.

Arthopyrenia punctiformis (Pers.) A. Massal., Ric. auton. lich. crost.: 166 (1852).

Basionym: *Verrucaria punctiformis* Pers., Ann. Bot. (Usteri) 1: 19 (1794); Synonyms: *Arthopyrenia padi* Rabenh., *Naetrocymbe punctiformis* (Pers.) R. C. Harris; Illustrations: Harris (1973), p. 55; Harris (1975a), p. 223 as *A. padi*; Wirth (1995), p. 139.

Thallus: absent or continuous, immersed in the substrate; **upper surface:** gray, smooth; photobiont: absent; **Perithecia:** hemispherical, black, superficial on the thallus or bark, 0.15-0.4 mm diam; **ascomatal wall:** black, absent below the hamathecium; **hamathecium:** unbranched pseudoparaphyses, not anastomosing; filaments: *c.* 2 µm wide, cells often swollen (moniliform), not inspersed with oil droplets, but becoming slimy or oily; **asci:** pyriform, *c.* 45-55 x 15-25 µm, with 8, irregularly arranged ascospores; **ascospores:** hyaline, clavate, 1-septate with a supramedian euseptum, 18-22 x 5-6 µm; walls: not ornamented, with a 1-2 µm thick gelatinous sheath; **Spot tests:** all negative, UV negative; **Secondary metabolites:** none detected.

Substrate and ecology: on bark of various woody plants, including *Acer, Jatropha, Quercus, Punica* and *Rhus*; **World distribution:** northern temperate or possibly cosmopolitan; **Sonoran distribution:** one of the most common corticolous pyrenocarps in the region, collected in California (including the Channel Islands), Arizona, Baja California, Baja California Sur and Sinaloa.



Arthopyrenia rhyponta (Ach.) A. Massal., Ric. auton. lich. crost.: 166 (1852).

Basionym: *Verrucaria rhyponta* Ach., Kongl. Vetensk. Akad. Nya Handl. 30: 150 (1809); Synonym: *Naetrocymbe rhyponta* (Ach.) R. C. Harris; Illustration: Harris (1975a), p. 225.

Thallus: consisting of a filamentous layer on the substrate (a subiculum); **upper surface:** black; photobiont: absent; **Perithecia:** hemispherical, black, immersed in the subiculum, 0.15-0.3 mm diam.; **ascomatal wall:** black, absent below the hamathecium; **hamathecium:** unbranched

pseudoparaphyses, not anastomosing; filaments: up to *c.* 3 µm wide below, cells often swollen (moniliform), not inspersed with oil droplets; **asci:** pyriform, *c.* 50-60 x 22-27 µm, with 8, irregularly arranged ascospores; **ascospores:** hyaline but becoming brown when old,, clavate, 3-septate (starting with a supramedian euseptum), 20-23 x 6-9 µm, often breaking into part spores; walls: not ornamented, with a 2-3 µm wide gelatinous sheath; **Spot tests:** all negative, UV negative; **Secondary metabolites:** none detected.

Substrate and ecology: on bark of *Populus tremuloides*; **World distribution:** northern temperate or nearly cosmopolitan; **Sonoran distribution:** only collected once in Arizona.

BAEOMYCES

by B. D. Ryan

Baeomyces Pers., Usteri, Neue Ann. der Bot. 1: 19 (1794).

Family: Baeomycetaceae; Type: *Baeomyces rufus* (Huds.) Rebent.; No. species: *c.* 8 world-wide; Selected lit.: Thomson (1967a & 1984), and Purvis et al. (1992).

Life habit: lichenized; **Primary thallus:** crustose, granular, verrucose or subsquamulose to squamulose, or marginally almost foliose; **upper surface:** usually brown, gray, or olivaceous, ± continuous; soralia sometimes present; schizidia when present discoid, detachable; **cortex:** with one or more pseudoparenchymatous layers or of interwoven hyphae running ± parallel to the upper surface; **photobiont:** primary one a chlorococcoid alga, secondary photobiont absent; forming a zone at least in the primary thallus; **lower surface:** without special structures; **Secondary thallus:** composed of short stipes (mostly under 2 cm tall), erect, usually unbranched, solid; **Ascomata:** apothecial, borne terminally, 1-several, terminal on stipes, or sometimes almost sessile; disc: pale to dark brown or reddish brown (rarely pinkish), roundish, concave to flat and marginate at first, later swollen and with reflexed margins, often clustered, usually (at least the clusters) distinctly larger than diam. of the stipe; thalline exciple: absent; exciple: ochraceous-yellowish, not distinct from the interior of the stipe; hymenium: hyaline below, ochraceous-yellowish above, hymenial gelatin I-, K/I-; paraphyses: simple or sparingly branched above, not (or scarcely) anastomosing; hypothecium: usually hyaline or pale; **asci:** narrow, unitunicate, thin-walled, the apex truncated, with a single functional wall layer, I-, K/I-, 8-spored; **ascospores:** ellipsoid, obtuse at the poles, simple to indistinctly 1-septate, without an endospore thickening, 8-14 x 2-4 µm; **Conidiomata:** pycnidial, immersed in small warts on the thallus; **conidia:** short, bacilliform; **Secondary metabolites:** ß-orcinol depsidones; **Geography:** cosmopolitan, circumpolar, arctic to tropical regions and Australasia; **Substrate:** acidic rocks or soils, bryophytes, detritus; characteristic of temporary and recently disturbed sites.

Notes: The genus is usually easily recognized (when fertile) by the ± pale brown, often convex and swollen apothecia usually on rather short and slender, solid stipes, arising from ± crustose (to minutely squamulose or lobate) thallus, growing on soil or rock. It differs from *Cladonia* especially in that the stalks are solid and its basal squamules, if present, are mostly tightly appressed and often fused. If the stipes are absent, the genus might be confused with various other crustose genera with ± pale biatorine apothecia. Species with distinctly pinkish apothecia, an amyloid hymenium, a different ascal structure, and containing depsides rather than depsidones, have now been placed in the genus *Dibaeis*. The statement by Thomson (1984) that *B. roseus* (= *Dibaeis baeomyces*) is the type species of the genus *Baeomyces* is now incorrect, because that species is the genus type for *Dibaeis*.

The Species

Baeomyces rufus (Huds.) Rebent., Prodr. Flor. Neomarch.: 315 (1804).

Basionym: *Lichen rufus* Huds., Flora Anglica 443 (1762); Illustrations: Brodo et al. (2001), p. 175; Thomson (1984), p. 52; Wirth (1995), p. 173; McCune and Geiser (1997), p. 27.

Primary thallus: discrete or ± wide-spreading, continuously crustose, nodulose, warty or partly squamulose, the squamules small (to 1 mm broad), somewhat raised, compacted, sometimes imbricate, ± delimited; **surface:** green to dull greenish gray, to whitish gray or sometimes brownish, either not sorediate or with diffuse, coalescing, irregular greenish soralia with powdery soredia; schizidia occasionally present, < 0.2 mm diam., disc-like; **cortex:** lacking where sorediate, composed of three types: 1) mainly in ± vertical paraplectenchyma, 2-3 cells thick or 2) composed of hyphae spreading out from between the algae and becoming ± flat-interwoven, or 3) forming a ± vertical but decomposed layer that is macroscopically whitish and pruinose; **photobiont:** cells 6-13 (-14) µm diam., globose or a few ellipsoid, < 14 x 12 µm; **stipes:** short, rarely more than 6 mm tall, flattened or cylindrical, white, furrowed and almost always fissured, mostly ecorticate but sometimes greenish and corticate towards the base; inner layer: composed of parallel thick-walled hyphae and containing many algal cells; **Apothecia:** almost sessile, dark red-brown, seldom reddish or pale dull pink, ± translucent when wet, concave or flat, becoming slightly convex, often incurved at base, up to 2 mm diam., single or occasionally several together; exciple: distinct from the hypothecium, at edges gradually merging into a palisade plectenchyma; hymenium: 90-105 µm; paraphyses: slender, 1-1.8 µm, the tips scarcely thickened; **asci:** cylindrical, 75-100 x 7-9 µm, I-, KI-, 8-spored; **ascospores:** ellipsoid, often indistinctly 1-septate, 8-13 x 2.5-4.5 µm; **Pycnidia:** often absent; **conidia:** ellipsoid, 4-5 x 1 µm; **Spot tests:** thallus K+ yellow, C-, KC+ yellow, P+ yellow to orange, UV-; **Secondary metabolites:** stictic acid (major), norstictic and constictic acids (both accessory).

Substrate and ecology: on soil in coniferous forests and particularly in recently disturbed, ± moist sites; **World distribution:** circumpolar in temperate and boreal zones in the Northern Hemisphere, extending southwards in the mountains; **Sonoran distribution:** eastern Arizona, 2900 m, on shaded earth in *Picea engelmannii* forest.

Notes: Although it is a distinctive species, mature specimens have not yet been found in the Sonoran region. It was recognized by Dr. J. Hafellner on the basis of its parasite occurring on its crustose thallus.

BRODOA

by B. D. Ryan

Brodoa Goward, Bryol. 89: 222 (1986).

Family: Parmeliaceae; Type: *Brodoa oroarctica* (Krog) Goward.; No. species: three world-wide; Selected lit.: Krog (1974), Thomson (1984), and Goward (1986).

Thallus: foliose to subfruticose, closely adnate to semierect, cushion-forming, up to *c.* 6 cm diam., lobate; **lobes:** rather elongate, ± swollen, stiff, 0.5-1.5 mm wide, contiguous to separate or loosely overlapping; attached by basal holdfasts; **upper surface:** pale gray to nearly black, generally somewhat shiny (at least towards lobe tips), convex; soredia, isidia, and thallus perforations lacking, but regeneration lobules occasionally present; **upper cortex:** paraplectenchymatous and covered in a thin polysaccharide-like layer (nonpored epicortex); **medulla:** white throughout; cell walls containing *Cetraria*-type lichenan; **photobiont:** primary one a trebouxioid alga, secondary photobiont absent; **lower cortex:** palisade plectenchymatous, lacking polysaccharide-like covering; **lower surface:** tan or black, dull, becoming wrinkled, without rhizines; **Ascomata:** apothecial, laminal, circular, sessile with a prominent thalline margin; disc: concave, nonperforate, up to 5 mm diam.; exciple: gray or hyaline; epihymenium: brown or ochraceous-yellowish; hymenium: hyaline, usually with unbranched paraphyses; hypothecium:

hyaline; **asci:** clavate, *Lecanora*-type, 8-spored; **ascospores:** ellipsoid, obtuse at the poles, colorless, simple, 8-12 x 6-8 µm, wall smooth, without distinct endospore thickening, I-; **Conidiomata:** pycnidial, black, laminal-lateral, immersed in upper cortex; **conidia:** normally bifusiform (6 x 1 µm); **Secondary products:** ß-orcinol depside, orcinol and ß-orcinol depsidones; **Geography:** arctic and alpine in the Northern Hemisphere; **Substrate:** on siliceous rocks, not calciferous.

Notes: *Brodoa* differs from *Hypogymnia* in that the lower cortex is palisade plectenchymous without a polysaccharide-like layer, the medulla is always solid, the thallus lacks perforations, the spores are larger, and it grows only on rocks in arctic-alpine areas. Apparently it is related to *Allantoparmelia*, which differs in having a brown upper surface (lacking atranorin) and isolichenan in the cell walls. Superficially it might be confused also with loosely adnate species of *Lobothallia*, but that crustose to subfoliose genus occurs at low to moderate elevations, is usually K+ yellow then red, and has a very different ascocarp anatomy with larger spores.

The Species

Brodoa oroarctica (Krog) Goward, Bryol. 89: 222 (1986).

Basionym: *Hypogymnia oroarctica* Krog, Lichenologist 6: 136 (1974); Illustrations: Brodo et al. (2001), p. 178; Thomson (1984), p. 239; Goward et al. (1995), p. 34; McCune and Geiser (1997), p. 28.

Thallus: foliose, adnate, orbicular, irregularly rosetted and spreading, 2-8 cm diam., lobate, with mostly contiguous to overlapping lobes; **lobes:** up to *c.* 2.5 cm long, 0.5-1 mm broad, terete, or the main ones flattened when on stone, becoming crenate to incised or irregularly branched laterally or towards tips, partly also with ± sparse, discrete, narrow (0.2-0.5 mm) branches or lobules, which arise ± perpendicularly to the tips or margins, or towards the thallus center, and are often more terete and nodulose than the main branches; **upper surface:** epruinose, pale gray, ashy gray, or brown, darkening or blackening especially on the lobules and towards the tips, and there becoming shiny, with conspicuous, reticulate whitish-yellowish maculae at least in the apical 2-3 mm of the lobes or lobules, with the darker areas between the maculae often slightly depressed (shallowly sulcate); otherwise mostly plane, smooth, dull, continuous to irregularly and finely cracked [in material from outside the Sonoran region, becoming distinctly areolate with discontinuous patches of cortex interspersed with black cracks and lines, Thomson 1984]; **medulla***:* white, solid; **lower surface:** black, brown toward the tips, with occasional coarse transverse cracks, smooth to ± irregularly, weakly, and shallowly wrinkled to plicate or foveolate; **Apothecia:** rare [not seen in material from Sonoran region], up to 5 mm diam., with a thin, entire thalloid margin; disc: dark brown; **ascospores:** subglobose to broadly ellipsoid, 10-12 x 8 µm; **Pycnidia:** numerous, conspicuous under lens, immersed, the visible part black to gray-brown, roundish, < *c.* 0.5 mm diam; **Spot tests:** cortex K+ yellow, C-, KC-, P+ yellow; medulla K-, C-, KC+ red, P+ orange in layer close to cortex in apices only, or P-; **Secondary metabolites:** cortex with atranorin and chloroatranorin, medulla with physodic acid (major) and with protocetraric acid (accessory).

Substrate and ecology: alpine, on highly insolated rocks and over mosses in places with winter snow cover; **World distribution:** circumpolar, arctic and northern boreal and alpine regions to the south; **Sonoran distribution:** known only from the alpine zone of the San Francisco Peaks near Flagstaff, Arizona.

BRYORIA

by B. D. Ryan

Bryoria Brodo & D. Hawksw., Opera Botanica 42: 78 (1977).

Family: Parmeliaceae; Type: *Bryoria trichodes* (Michx.) Brodo & D. Hawksw.; No. species: 45 world-wide; Selected lit.: Brodo and Hawksworth (1977), Kärnefelt and Thell (1992), McCune and Goward (1995), Common (1991), McCune and Geiser (1997), and Goward (1999).

Life Habit: lichenized; **Thallus:** shrubby, erect, decumbent or subpendent to pendent; **branches:** ± terete and smooth, often hair-like, occasionally becoming flattened or angular and ± pitted (foveolate) especially on the main branches and towards the base, never markedly expanded and dorsiventrally compressed; **branching:** aniso- or isotomic-dichotomous; **surface:** continuous, usually dark reddish brown, sometimes pale grayish to yellowish brown, greenish to black, or partly greenish yellow (vulpinic acid); soralia: absent to abundant, tuberculate or fissural; pseudocyphellae: absent to abundant, usually sparse and inconspicuous, sometimes elongate and spiralling around in the main stems, usually fusiform, depressed to somewhat raised; soralia and pseudocyphellae: white to greenish or blackish, or rarely bright greenish yellow; isidia: absent but isidia-like spinules arising in tufts from soralia in a few species; true lateral spinules: present or absent; **cortex:** composed of periclinal, conglutinate hyphae immersed in moderate or relatively little matrix; **medulla:** hyphae usually not ornamented; cell walls with *Cetraria*-type lichenan and often also with isolichenan; **photobiont:** primary one a trebouxioid alga, secondary photobiont absent; **Ascomata:** apothecial, infrequent and unknown in some species, lateral, sometimes appearing geniculate, roundish, sessile; thalline exciple: slightly prominent to prominent, persistent to excluded, concolorous with thallus; disc: brown to dark brown, rarely white, sometimes yellowish pruinose; exciple: hyaline; hymenium: hyaline below and yellowish to brown above, I+ strongly blue, 30-55 µm high; paraphyses: septate, scarcely branched and anastomosing, 1-2 µm wide, the tips to 2 µm, strongly pigmented; hypothecium: hyaline; **asci:** clavate, 25-45 x 9-15 µm, *Lecanora*-type, the wall 1-1.5 µm thick, (6-) 8-spored; **ascospores:** broadly ellipsoid to subglobose, simple, hyaline, smooth, without perispore or a distinct endospore thickening, I-, 4-12 (-14) x (2.5-) 4-7.5 µm; **Conidiomata:** pycnidial, immersed, usually rare; **conidia:** cylindrical to fusiform, minute; **Secondary metabolites:** cortex with unknown brown pigments (usnic acid lacking), medulla with orcinol depsides, orcinol depsidones, ß-orcinol depsides, ß-orcinol depsidones, or pulvinic acid derivatives; **Geography:** in the Northern Hemisphere circumarctic and circumboreal, temperate-montane to alpine and with a few species in mountainous areas in the Southern Hemisphere. **Substrate:** on bark, wood, rock or soil.

Notes: The genus is usually easily recognized by its shrubby to vine-like or hair-like, mostly brown to black or grayish thallus, ± terete branches with a loose interior surrounded by arachnoid medullary hyphae. This genus is still very difficult because of challenges doing spot tests (McCune and Rosentreter 1993 and McCune and Goward 1995). In addition, non-sorediate specimens of typically sorediate species occur, and the close intermixing of different species is frequent. Thallus colors are best compared in sunlight, or against a dark or neutral (not pale) background. In separating apparent mixtures, care must also be taken to follow the branches to their basal parts rather than breaking off apical or basal parts that may look quite different from the main parts of the thalli, to which they are connected. Several additional species of *Bryoria*, as well as the similar genus *Sulcaria* (*S. isidiifera* Brodo) have been reported from just north of the Sonoran region in California (Riefner et al. 1995).

Key to species of ***Bryoria*** in the Sonoran region:

1. On rocks or soil, alpine or subalpine; thallus erect or prostrate to decumbent; main branches usually much larger than secondary ones, frequently 0.5-1.0 mm di-

am.; surface ± dark brown to blackish, usually shiny; soralia sparse to absent, P+ red-orange ..... ***B. chalybeiformis***

1. On bark or wood, mostly montane to subalpine; thallus caespitose to subpendent or pendent; main branches slightly to moderately larger than secondary ones, 0.2-0.5 (-0.6) mm diam., often less; surface pale to dark, dull or shiny; soralia various 2

2. Soralia present 3
2. Soralia (at least in Sonoran region material) absent . 7

3. Soralia frequently greenish black, always P-; rare in the Sonoran region [known from New Mexico; unconfirmed report from Arizona] ..... ***B. simplicior***
3. Soralia white or speckled with black, P+ orange-red; common in the Sonoran region 4

4. Soralia with isidioid spinules (usually abundant, clustered, and distinct); thallus caespitose (to subpendent) ..... ***B. furcellata***
4. Soralia without isidioid spinules (or occasionally with few, scattered and poorly developed spinules); thallus usually pendent or subpendent 5

5. Branches very slender, usually less than 0.2 mm diam. 6
5. At least main branches thick, generally over 0.2 mm diam. ..... ***B. fuscescens [s. lato]***

6. Thallus ± dark throughout, olive black, usually dull; soralia virtually all fissural, usually narrower than the branches bearing them; axils acute throughout; branches mostly parallel, often clinging together to form narrow strands; very brittle ..... ***B. lanestris***
6. Thallus usually ± pale, often much more so at base, ± grayish to yellowish brown, dull or shiny; soralia fissural to tuberculate, often wider than the branches bearing them; axils obtuse at least towards base; branches usually more divergent and not clinging together; usually not brittle ..... see ***B. fuscescens***

7. Thallus yellow-brown to red-brown or dark red-brown, often shiny; main branches usually twisted and foveolate; thallus pendulous. [Note: species of *Nodobryoria* will also key out here, but have a dull surface and jigsaw-puzzle like cortex in surface view] ***B. fremontii***
7. Thallus grayish, olive, or blackish, dull or shiny; main branches usually straight and even; thallus caespitose to pendulous ..... ***B. sp.*** [occasional specimens from Arizona, perhaps just poorly developed forms of the sorediate species]

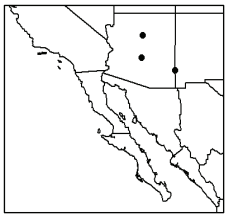
The Species

Bryoria chalybeiformis (L.) Brodo & D. Hawksw., Opera Bot. 42: 81 (1977).

Basionym: *Lichen chalybeiformis* L., *Sp. Pl.* 2: 1153 (1753); Synonyms: *Alectoria chalybeiformis* (L.) Gray; for further synonyms see Hawksworth (1972); Illustrations: Thomson (1984), p. 56; Hansen (1995), p. 17; Goward (1999), p. 56; Jahns (1980), fig. 384; Redón (1985), fig. 65.

Thallus: prostrate or decumbent, usually 8-15 (-20) cm long; **branches:** irregular, often sparse towards the base, main branches: much larger than the secondary ones, sometimes straight but usually becoming twisted and foveolate or sometimes channeled, occasionally flattened, (0.3-) 0.5-1.0 (-2.0) mm diam.; **branching:** isotomic dichotomous towards the base but becoming anisotomic dichotomous towards the apices, often entangled, angles between the dichotomies mainly obtuse; **surface:** dark brown to olive-black, sometimes paler towards base, usually shiny; true lateral spinules absent but irregular, spinulose branches sometimes present; **soralia:** absent or sparse, usually tuberculate, occasionally becoming spinulose, usually narrower than the branches on which they occur; pseudocyphellae absent; **Apothecia:** and **Pycnidia:** unknown; **Spot tests:** cortex and medulla K-, C-, KC-, usually P-, UV-; soralia P+ red; **Secondary metabolites:** fumarprotocetraric acid (usually in the soralia only).

Substrate and ecology: on base-rich or acid rocks and soil, occasionally on lignum, rarely on conifers, in exposed intermontane localities at all elevations, usually montane to alpine, rare in maritime regions; **World distribution:** circumpolar, apparently bipolar; **Sonoran distribution:** rare in Arizona on granite - or soil, 2680-3050 m.



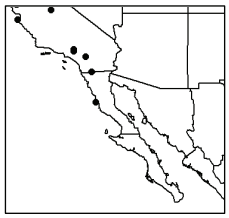
Notes: This species is distinguished from *B. fuscescens* (which normally grows on bark but has been reported to occur occasionally on soil or rock) mainly by the coarser, darker and often shiny main stems (Krog 1980). The few specimens from the Sonoran region that can be assigned to *B. chalybeiformis* are rather poorly developed and somewhat pale and slightly reddish (rather than greenish) tinged, but fit here better than under *B. fuscescens*.

Bryoria fremontii (Tuck.) Brodo & D. Hawksw., Opera Bot. 42: 136 (1977).

Basionym: *Alectoria fremontii* Tuck., Synonyms: see Brodo and Hawksworth (1977); Illustrations: Brodo et al. (2001), p. 180; McCune and Geiser (1997), p. 35; Goward (1999), p. 59; Moberg and Holmåsen (1992), p.103; Jahns (1980), fig. 385 [close-up, with soralia].

Thallus: pendent, filamentous, often very long, 6-45 (-90) cm, often draping tree branches, not brittle; **branches:** uneven in thickness, (0.2-) 0.4-1.5 (-4.0); main branches: foveolate and twisted, sometimes becoming dorsiventrally compressed and expanded toward the base; true lateral spinules: absent; **branching:** anisotomic to submonopodial, usually frequent from the base; **surface:** yellow-brown to red-brown or dark red-brown, often variable within the same specimen, shiny or less frequently dull; pseudocyphellae: absent or sparse (perhaps only torsion cracks), depressed and elongate fusiform, white to pale brown; **soralia:** rare, absent in most specimens, sparse when present (not seen in Sonoran material), tuberculate, pale to bright yellow, usually as wide as the branches on which they occur, up to 2.0 (-4.0) mm long; **Apothecia:** absent or sparse, lateral; thalline exciple: concolorous with thallus, thin and soon becoming excluded, 1.0-2.0 (4.0) mm in diam.; disc: becoming convex at maturity, yellow pruinose; **asci:** clavate, 8-spored; **ascospores:** subglobose, simple, 5-8 x 4-5 µm; **Pycnidia:** not seen; **Spot tests:** cortex and medulla: K-, C-, KC-, P-, UV- (soralia and apothecia may be UV+); **Secondary metabolites:** no lichen substances, or vulpinic acid (in soralia and apothecia only).

Substrate and ecology: on bark or wood, mainly conifers in dry, open forests, occasionally on hardwoods near the coast; **World distribution:** Eurasia and western North America; **Sonoran distribution:** southern California and northern Baja California.



Notes: It is characterized by its usually shiny, broad, foveolate main stems and its characteristic yellowish brown to dark reddish brown color. It often forms long thick beards when dry. Although quite variable, well-developed material is difficult to confuse with any other species in California except possibly *Nodobryoria oregana*, which has a dull surface and jig-saw puzzle-like cortex in surface view and often has a few apothecia with brown discs. Records of *B. fremontii* from Arizona are dubious and are most likely poorly developed, non-sorediate specimens of *B. fuscescens*]. It may be extinct from the Sonoran region, as only one specimen collected in Riverside Co., California, by Hasse in 1904 was found.

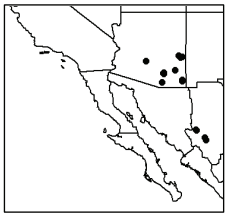
Bryoria furcellata (Fr.) Brodo & D. Hawksw., Opera Bot. 42: 103 (1977).

Basionym: *Cetraria furcellata* Fr., Syst. Orb. Veg. 1: 283 (1825); Synonyms: *Alectoria nidulifera* Norrlin; *Cornicularia fibrillosa* (Ach.) Halsey; and see Brodo and Hawksworth (1977) for additional synonyms; Illustrations: Brodo et al. (2001), p. 181; Hale (1979), p. 171; McCune and Goward (1995), p. 65; Goward (1999), p. 55; Jahns (1980), fig. IVH [SEM of soralium with spinules].

Thallus: caespitose, usually 3-5 (-12) cm long; **branches:** even in thickness, 0.3-0.4 (-0.5) mm diam., sometimes slightly compressed towards base but not twisted or foveolate, somewhat brittle; base persistent; short perpendicular lateral spinulose branches sometimes present, occasionally abundant; **branching:** regularly isotomic dichotomous, axils usually broad towards base and acute towards tips; **surface:** very pale brown to cervine brown or rarely dark brown to black, often darker towards base, smooth, usually shiny; pseudocyphellae: absent; **soralia:** usually abundant, fissural, sometimes slightly raised, usually narrower than the branches on which they occur, white (or speckled blackish with incipient spinules), 0.3-

1.0 mm long, bearing tufts of blackening isidioid spinules 0.5-2.5 mm long; **Apothecia:** very rare lateral, 0.8-2.0 (4.0) mm diam.; thalline exciple: concolorous with thallus, thick, usually becoming sorediate; disc: concave at first but becoming convex and sloughing the margin with age, light brown to reddish brown; **asci:** clavate, 8-spored; **ascospores:** subglobose, 6-7 x 3-4 µm; **Spot tests:** outer cortex K-, C-, KC-, P-, UV-; inner cortex and medulla K-, C-, KC-, P+ red; soralia P+ red; **Secondary metabolites:** fumarprotocetraric and protocetraric acids.

Substrate and ecology: mainly on conifers in sheltered to somewhat exposed sites but also found on rock outcrops or boulders, lignum, and rarely on soil; **World distribution:** circumpolar and circumboreal in the Northern Hemisphere, extending south to Mexico and Central America; **Sonoran distribution:** on *Pinus* and *Pseudotsuga* in Arizona and Chihuahua at 1700-2900 m.



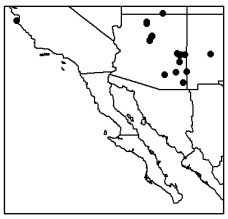
Notes: Although it is somewhat variable, *B. furcellata* is usually easily identified by the groups of isidia-like spinules on the soralia. According to Brodo and Hawksworth (1977) *B. fuscescens* and *B. chalybeiformis* also occasionally have such spinules; however, *B. fuscescens* is usually pendent, with partly anisotomic branching, partly unevenly thickened branches, much paler towards the base and more often dull, and the soralia are often broader than the branch bearing them and partly tuberculate, while *B. chalybeiformis* has coarser branches with obtuse axils, a darker and more olive-blackish color, and sparse, tuberculate soralia, and usually grows on rock. Neither of them normally has a P+ red medulla.

Bryoria fuscescens (Gyeln.) Brodo & D. Hawksw., Opera Bot. 42: 83 (1977).

Basionym: *Alectoria fuscescens* Gyelnik, Nyt. Mag. Naturvid. 70: 55 (1932); Synonym: *Bryopogon pacificus* Gyeln.; for further synonyms see Hawksworth (1972); Illustrations: Brodo et al. (2001), p. 181; McCune and Goward (1995), p. 66; McCune and Geiser (1997), p. 37; Goward (1999), p. 56; Swinscow and Krog (1988), p. 22.

Thallus: pendent (to prostrate in some morphotypes of var. *positiva*), relatively lax, usually 5-15 (-30) cm long, moderately branched; **branches:** terete, to sometimes partly flattened or twisted and occasionally foveolate (in var. *positiva*), somewhat unevenly (to evenly) thickened, (0.2-) 0.3-0.4 (-0.6) mm in diam. near its base, but main or secondary branches often 0.1 mm diam.; **branching:** isotomic or anisotomic at the base, often becoming anisotomic toward the apices, frequent from the base; axils: acute (to obtuse, but generally not broadly rounded); **surface:** pale to medium brown or somewhat grayish or olivaceous, to blackish, usually much paler at the base than at the apices, often with black fragmentation regions, often dull but sometimes quite shiny; pseudocyphellae: lacking; lateral, spinulose branches sometimes present but inconspicuous; true lateral spinules: lacking; **soralia:** sparse or abundant, fissural (sometimes resembling pseudocyphellae when young) or sometimes also tuberculate, often strongly convex at maturity, sometimes becoming spinulose, usually white; **Apothecia** and **Pycnidia:** not seen in North American material; **Spot tests:** cortex and medulla K-, C-, KC-, UV-, P- or P+ red (v. *positiva*); soralia: P+ red-orange; **Secondary metabolites:** fumarprotocetraric and protocetraric acids (and accessory chloroatranorin in specimens from eastern North America).

Substrate and ecology: on bark, mostly of conifers in dry and open forests (*Pinus ponderosa* and *Pseudotsuga* forests); var. *positiva* has also been reported from lignum, and from rocks in highly exposed sites; **World distribution:** circumpolar and boreal and in the East African mountains; **Sonoran distribution:** Arizona, *c.* 2875-3400 m, in pine and spruce-fir forest.



Notes: It is characterized mainly by P+ red-orange soralia, mostly V-shaped axils, and typically grayish brown and often dull surface, which is usually paler at the base. The thallus is often pendulous but rarely forms long, thick beards. It is an extremely variable species and is treated here in a very broad sense. Most material from the Sonoran region tends to have much finer branches than previously described (Brodo and Hawksworth 1977), and is

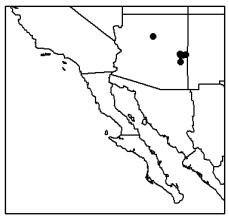
therefore often very difficult to distinguish from the frequently intermixed *B. lanestris*, The only other *Bryoria* known from North America that has P+ red soralia and very narrow branches is *B. subcana*, which has a pale gray to brown, short thallus (up to 5 cm long) and is found in maritime areas well north of the Sonoran region. Some collections included here under *B. fuscescens* appear to be mixtures of short, very pale thalli with ± longer and/or darker ones. The palest (almost whitish) ones may represent basal or dying parts, but have a rather different appearance. Coarser, darker, or shorter forms of *B. fuscescens* from exposed habitats can be similar to *B. chalybeiformis*, that primarily occurs on rock or soil. *Bryoria fuscescens* is usually more grayish brown, and have tuberculate soralia.

Bryoria lanestris (Ach.) Brodo & D. Hawksw., Opera Bot. 42: 88 (1977).

Basionym: *Alectoria jubata* ζ *lanestris* Ach., *Lich. Univ.:* 593 (1810); Synonyms: *Alectoria lanestris* (Ach.) Gyeln.; and see Brodo and Hawksworth (1977) and Hawksworth (1972) for further synonyms; Illustrations: Brodo et al. (2001), p. 182; Thomson (1984), p. 59; Goward (1999), p. 55.

Thallus: pendent to subpendent, 5-10 (-15) cm long, very brittle (fragmenting in herbarium packets); **branches:** most *c.* 0.1 mm diam.; main branches (and basal ones, Sonoran material): 0.1-0.25 (-0.3) mm diam., sometimes becoming compressed toward the base, but straight, neither contorted nor foveolate; **branching:** irregular, isotomic to anisotomic dichotomous, frequent from the base; axils: usually acute; **surface:** brown-black or olive blackish or black, usually concolorous and dull; lacking pseudocyphellae and true lateral spinules; **soralia:** sparse to abundant, fissural, mostly rather inconspicuous in Sonoran material, white or often speckled with black, up to 0.3 mm long; **Apothecia** and **Pycnidia:** unknown; **Spot tests:** cortex and medulla: K-, C-, KC-, UV-, P-; soralia: P+ orange or red; **Secondary metabolites:** fumarprotocetraric acid (and protocetraric acid?).

Substrate and ecology: usually on conifers; **World distribution:** circumboreal in the Northern Hemisphere; reports from Algeria and Mexico are dubious; **Sonoran distribution:** common in Arizona, usually on *Picea engelmannii* or *Abies lasiocarpa* in forests at 2900-3400 m.



Notes: As presently circumscribed this species is often very difficult to distinguish from *B. fuscescens*, with which it is often closely entangled. At least in populations from northern areas, *B. lanestris* characteristically is very unevenly thickened and has quite brittle branches with strictly fissural soralia, that are frequently larger than the branch diameter and is often black-spotted. However, in Sonoran populations the consistently thinner branches and the often dull, uniformly dark olive-blackish surface (without paler basal parts) seem to be the most consistent distinguishing features of *B. lanestris*. Another frequent difference between *B. lanestris* and *B. fuscescens* is that in *B. lanestris* the axils are acute even at the base, such that the branches tend to lie mostly parallel to each other and form narrow (*c.* 3 mm across) strands.

Bryoria simplicior (Vain.) Brodo & D. Hawksw., Opera Bot. 42: 109 (1977).

Basionym: *Alectoria nidulifera* f. *simplicior* Vain., Medd. Soc. Fauna Fl. Fenn. 6: 115 (1881); Synonyms: *Alectoria simplicior* (Vain.) Lynge and see Brodo and Hawksworth (1977); Illustrations: Brodo and Hawksworth (1977), p. 110; Thomson (1984), p. 65; Hansen (1995), p. 18; Goward (1999), p. 55; Moberg and Holmåsen (1992), p. 105.

Thallus: caespitose or sometimes decumbent, 2-4 (-5) cm long, forming small, rather dense tufts to slightly hanging, sometimes attached to the substrate at the tips as well as the base; base persistent; **branches:** even in thickness, 0.2-0.4 mm in diam., straight or slightly curved, round or rarely slightly deformed (foveolate); **branching:** mainly isotomically dichotomous from the base; axils: usually acute, making the thalli appear brush-shaped; **surface:** ± shiny, brown to dark brown to almost black, concolorous, or not much paler towards tips; lateral spinules: with slightly constricted bases, sparse to frequent, sometimes abundant; pseudocyphellae: absent; **soralia:** abundant,

fissural, sharply delimited, usually broader than the branches on which they occur, round or oval, white to brownish black or more usually greenish black; young soredial masses convex, the soralia becoming crateriform as the soredia are shed, lacking isidial spinules but sometimes bearing irregular, often contorted, non-isidiiform spinules; **Apothecia** and **Pycnidia:** unknown; **Spot tests:** cortex and medulla K-, C-, KC-, P-, UV-; soralia P-; **Secondary metabolites:** none detected.

Substrate and ecology: characteristically on well illuminated twigs and small branches, rare on soil or rock but often on lignum, almost always intermixed with *B. lanestris* and frequently also *B. furcellata*; **World distribution:** circumpolar, mainly in continental areas; **Sonoran distribution:** reported from Arizona (St. Clair and Newberry 1992) [not seen].

Notes: The species is characterized by greenish black, tuberculate soralia (rather than pale or at most speckled with brownish black, as in other North American species of *Bryoria*) and is always P-. According to Brodo and Hawksworth (1977) *B. simplicior* is quite frequently mixed with *B. lanestris*, which is similarly colored but has finer, pendulous branches and P+ red soralia.

BULBOTHRIX

by T. H. Nash III and J.A. Elix

Bulbothrix Hale, Phytologia 28: 480 (1974).

Family: Parmeliaceae; Type: *Bulbothrix bicornuta* (Lynge) Hale.; No. species: *c.* 37 world-wide; Selected lit.: Elix (1993a & 1994a) and Hale (1976a).

Life habit: lichenized; **Thallus:** foliose, *c.* circular in outline, lobate, contiguous, rarely imbricate; **lobes:** sublinear to subirregular; lobe tips: usually rotund, with bulbate cilia; **upper cortex:** pored epicortex, palisade parenchymatous, **upper surface:** gray, smooth, plane to rugulose, shiny or dull, maculate or not, usually epruinose; with or without isidia, soredia or lobules; pseudocyphellae: absent; **medulla:** white, loosely packed; cell walls: containing isolichenan; **photobionts:** primary one a *Trebouxia*, secondary photobiont absent; **lower surface:** tan to black, plane to sometimes wrinked, attachment by simple and/or dichotomous rhizines; cyphellae, pseudocyphellae and tomentum absent; **Ascomata:** apothecial, laminal, orbicular, cup-shaped, subpedicellate or sessile; margin: prominent, with thalloid rim; disc: imperforate, pale to dark brown, coronate with black bulbae around inner margin of thalline exciple or ecoronate; exciple: gray or hyaline; epithecium: brown or brownish yellow; hypothecium: hyaline, **asci:** lecanoral, wall layers apex thickened; apex: amyloid, with wide, axial body divergent towards apex, *c.* 8-spored; **ascospores:** simple, ellipsoid or bicornute, curved or semilunate, obtuse at the poles; 6-21 x 4-12 µm; walls: thin, hyaline, not amyloid; **Conidiomata:** absent or present, pycnidial, laminal or marginal, immersed or emergent sessile; **conidia:** bifusiform or rarely bacilliform, 5-10 (-15) x 1 µm; **Secondary metabolites:** upper cortex with atranorin (rarely usnic acid accessory) and chloroatranorin; medulla with some combination of orcinol depsides or depsidones, ß-orcinol depsides or depsidones; **Geography:** predominately pantropical and subtropical with a few species extending to temperate forests and woodlands; **Substrate:** mostly bark or acidic rock.

Key to the species of ***Bulbothrix*** from the Sonoran region:

1. Thallus isidiate; apothecia (if present) ecoronate 3
1. Thallus not isidiate; apothecia coronate 2

2. Apothecia coronate ..... ***B. coronata***
2. Apothecia ecoronate ..... ***B. atrichella***

3. Medulla K- and C+ red ..... ***B. goebelii***
3. Medulla K+ yellow turning deep red and C- . ***B. isidiza***

The Species

Bulbothrix atrichella (Nyl.) Hale, Phytologia 28: 480 (1974).

Basionym: *Parmelia atrichella* Nyl., Flora 68: 614 (1885); Illustration: Hale (1976a), p. 10.

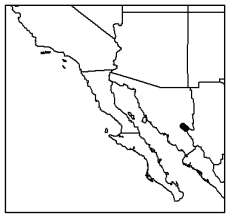
Thallus: adnate, foliose, 3-6 cm in diam., irregularly lobate; **lobes:** sublinear, elongate, moderately imbricate, elongate, plane to subconvex, separate, 0.5-2 mm wide; margin: sometimes lobulate; apices: subrotund with prominently inflated, dense, bulbate cilia; **upper surface:** pale gray to olive-gray (turning olive buff in the herbarium), smooth to rugose, shiny, white maculate; soredia, isidia and pustulae absent; **medulla:** white with continuous algal layer; **lower surface:** black, rhizinate; rhizines: moderately dense, black, simple to branched; **Apothecia:** common, laminal, 1-2.5 mm wide; disc: dark brown; margin: outer rim smooth, inner rim ecoronate; **asci:** clavate, 8-spored; **ascospores:** broadly ellipsoid, 7-8 x 5-6 µm; **Pycnidia:** not seen; **Spot tests:** upper cortex K+ yellow, C-, KC-, P+ yellow; medulla K-, C+ red, KC+ red, P-; **Secondary metabolites:** upper cortex with atranorin and chloroatranorin; medulla with gyrophoric acid (major).

Substrate and ecology: on small trees in open habitats; **World distribution:** neotropics, including Mexico, Colombia and Peru; **Sonoran distribution:** oak forests at intermediate elevations in Sonora.

Bulbothrix coronata (Fée) Hale, Phytologia 28: 480 (1974).

Basionym: *Parmelia coronata* Fée, Essai Crypt. écor. exotiq. off.: 123 (1824); Synonyms: see Hale (1976a); Illustrations: Hale (1976a), p. 13, Swinscow and Krog (1988), p. 24.

Thallus: adnate, foliose, 3-6 cm in diam., irregularly lobate; **lobes:** sublinear, elongate, moderately imbricate, elongate, plane to subconvex, separate, 0.5-2 mm wide; apices: subrotund with prominent inflated, with bulbate cilia; **upper surface:** pale gray, smooth to rugose, shiny, faintly white maculate; soredia, isidia and pustulae absent; **medulla:** white with continuous algal layer; **lower surface:** black, rhizinate, the rhizines moderately dense, black, simple to branched; **Apothecia:** common, laminal, 1-3 mm wide; disc: red-brown to dark brown; margin: outer rim smooth, inner rim coronate; **ascospores:** ellipsoid, 6-10 x 5-6 µm; **Pycnidia:** not seen; **Spot tests:** upper cortex K+ yellow, C-, KC-, P+ yellow; medulla K-, C+ red, KC+ red, P-; **Secondary metabolites:** upper cortex with atranorin and chloroatranorin; medulla with gyrophoric acid (major).



Substrate and ecology: on small trees in open habitats; **World distribution:** neotropics and East and South Africa; **Sonoran distribution:** oak forests at intermediate elevations in Sonora.

Bulbothrix goebelii (Zenker) Hale, Smithsonian Contr. Bot. 32: 14 (1976).

Basionym: *Parmelia goebelii* Zenker, Pharm. Waarenk. 1: 134 (1827); Synonyms: *Parmelia scortella* Nyl. and see Elix (1994a); Illustration: Brodo et al. (2001), p. 191; Hale (1976a), p. 13.

Thallus: adnate, foliose, 2-8 cm in diam., fragile, irregularly lobate; **lobes:** sublinear, moderately imbricate, elongate, plane to subconvex, separate, 0.5-1.5 mm wide; apices: subrotund, sometimes dissected, ciliate; cilia: dense, bulbate, sometimes branched; **upper cortex:** pale gray, smooth to rugose, shiny, faintly or distinctly white maculate; **isidia:** laminal, dense, cylindrical, simple to coralloid, sometimes darkened apically; soredia and pustulae absent; **medulla:** white, with continuous algal layer; **lower cortex:** black centrally, pale marginally, densely rhizinate; rhizines, branched, black to medium brown; **Apothecia:** rare, laminal, 1-2 mm wide, sessile to subpedicellate; disc: red-brown to dark brown; margin: outer rim usually isidiate, inner rim ecoronate, **ascospores:** ellipsoid, 8-10 x 4-6 µm; **Pycnidia:** not seen; **Spot tests:** upper cortex K+ yellow, C-, KC-, P+ yellow; medulla K-, C+ red, KC+ red, P-; **Secondary metabolites:** upper cortex with atranorin and chloroatranorin; medulla with gyrophoric acid (major).

Substrate and ecology: on small trees in open habitats; **World distribution:** pantropical and extending into subtropics; **Sonoran distribution:** oak forests at intermediate elevations in Sonora.

Bulbothrix isidiza (Nyl.) Hale, Phytologia 28: 480 (1974).

Basionym: *Parmelia isidiza* Nyl., Bol. Soc. Brot. 3: 130 (1884); Synonyms: see Hale (1976b); Illustrations: Hale (1976a), p. 17, Swinscow and Krog (1988), p. 27.

Thallus: adnate, foliose, 4-10 cm in diam., irregularly lobate; **lobes:** sublinear to subirregular, moderately imbricate, elongate, plane to subconvex, separate, 1.5-5 mm wide; apices: subrotund, with prominent inflated, bulbate cilia; **upper surface:** pale gray, smooth to rugose, shiny, faintly or distinctly white maculate; **isidia:** laminal, dense, cylindrical, simple to coralloid; soredia and pustulae absent; **medulla:** white with continuous algal layer; **lower surface:** pale brown or darkening, moderately rhizinate, the rhizines, pale to medium brown, simple to branched, concolorous; **Apothecia:**, rare, laminal, 1-4 mm wide; disc: red brown to dark brown; margin: outer rim usually isidiate, inner rim ecoronate; **ascospores:** ellipsoid, 7-14 x 5-8 µm; **Pycnidia:** common, immersed; **conidia:** bacilliform to weakly bifusiform, 5-6 x 1 µm; **Spot tests:** upper cortex K+ yellow, C-, KC-, P+ yellow; medulla K+ yellow turning deep red, C-, KC-, P+ orange; **Secondary metabolites:** upper cortex with atranorin and chloroatranorin; medulla with salazinic acid (major) and consalazinic (minor).

Substrate and ecology: on small trees in open habitats; **World distribution:** pantropical and extending into subtropics; **Sonoran distribution:** lowland thorn forests of Sonora.

CANDELARIA

by M. Westberg and T. H. Nash III

Candelaria A. Massal., Flora 35: 567 (1852).

Family: Candelariaceae; Type: *Candelaria vulgaris* A. Massal. (= *C. concolor* (Dicks.) B. Stein.); No. species: *c.* seven world-wide; Selected lit.: Hillmann (1936), Jørgensen and Galloway (1992), Poelt (1974), Almborn (1966), and Westberg (in prep.).

Life habit: lichenized; **Thallus:** small foliose, circular to irregular in outline, often forming rosettes, sometimes irregularly coalescing and spreading over its substrate, loosely adnate to adnate, lobate; **lobes:** usually flat to convex but sometimes subterete, discrete, often loosely imbricate, elongate; apices: horizontal, sometimes ascending or semierect to erect, eciliate; **upper surface:** lemon yellow to mustard yellow but in shade paling to yellow-green, dull to somewhat shiny, with or without pruina, with or without isidia or soredia; **upper cortex:** paraplectenchymatous; **medulla:** white, reticulate; **photobiont:** primary one a chlorococcoid alga, secondary photobiont absent; **lower cortex:** paraplectenchymatous, sometimes lacking; **lower surface:** white to yellow, smooth to somewhat wrinkled, often rhizinate but sometimes with hapters; rhizines: simple or or sparingly branched; **Ascomata:** apothecial, lecanorine, laminal, sessile; margin: concolorous with the thallus, persistent, smooth or sorediate or lobulate; disc: darker yellow than the thallus; epithecium: yellow-brown, granular; hymenium: colorless below, I+ blue; paraphyses: simple or sparingly branched, cylindrical or submoniliform, sometimes anastomosing below, septate; hypothecium: colorless to pale brown; **asci:** clavate, *Candelaria*-type (apical dome I+ blue only in the lower part), 8-64+-spored; **ascospores:** usually ellipsoid, simple to thinly 1-septate, uni- or biguttulate or with numerous oil-droplets, colorless; **Conidiomata:** pycnidial, more or less globular, concolorous with the thallus or darker (walls pale), usually appearing as raised warts on thallus surface; **conidia:** ellipsoid to narrowly ellipsoid, simple, colorless; **Secondary metabolites:** pulvinic acid derivatives present in colored parts;

Geography: world-wide; **Substrate:** common on rocks or bark, rarely on soil or mosses.

Key to the species of ***Candelaria*** from the Sonoran region:

1. Thallus not sorediate ..... ***C. fibrosa***
1. Thallus sorediate 2

2. Not sorediate on the lower side, lower cortex present, spores numerous ..... ***C. concolor***
2. Sorediate on the lower side which usually lacks a cortex, spores eight ..... ***C. "pacifica"***

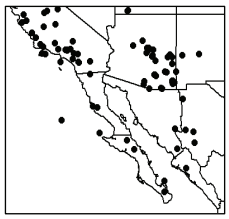
The Species

Candelaria concolor (Dicks.) B. Stein., Krypt. Fl. Schlesien 2: 84 (1879).

Basionym: *Lichen concolor* Dicks., Fasc. Pl. cryptog. Brit. 3: 18 (1793); Synonyms: see Almborn (1966 note: *C. quintanilhae* Tavares = *C. crawfordii* (Müll. Arg) P. M. Jørg & D. J. Galloway) and Nimis (1993); Illustrations: Brodo et al. (2001), p. 206; Swinscow and Krog (1988) plate 7A; Wirth (1995), p. 241; McCune and Geiser (1997), p. 44.

Thallus: small foliose, up to 1 cm wide or coalescing to form extensive colonies, tightly adnate to adnate, lobate; **lobes:** dorsiventral to subterete, loosely imbricate, narrow, 0.1-0.5 (-1.2) mm wide; **upper surface:** lemon yellow to mustard yellow, paling to yellow green in shade, smooth to somewhat coarse, sorediate; **soredia:** granular, blastidious, marginal to submarginal or at lobe tips; **upper cortex:** *c.* 10-30 µm thick; **medulla:** white, very thin; **lower cortex:** *c.* 20 µm thick; **lower surface:** white to pinkish, somewhat shiny; rhizines: simple, white; **Apothecia:** rare, laminal or appearing terminal, sessile, up to c. 1 mm diam.; margin: smooth but often sorediate or lobulate; disc: darker yellow than the thallus; epithecium: *c.* 5-10 µm thick; hymenium: *c.* 60-90 µm tall; paraphyses: simple, cylindrical to submoniliform with up to 5 µm wide tips; hypothecium: *c.* 50 µm thick; **asci:** clavate, >30-spored; **ascospores:** uni- or biguttulate, colorless, 7-10 x 4-6 µm; **Pycnidia:** common, appearing as raised warts on the thallus surface, concolorous with upper surface or darker; **conidia:** ellipsoid to narrowly ellipsoid, 2-3 x 1,5 µm; **Spot tests:** upper surface K- (or + deeper yellow), C-, KC-, P-; medulla K-, C-, KC-, P-; **Secondary metabolites:** calycin (major) and pulvinic dilactone (minor).

Habitat and ecology: on rock or bark, often in relatively eutrophicated habitats; **World distribution:** pan-arctic and southwards into north temperate regions, extending farther south in maritime areas; also occurring in subantarctic regions and Australasia; **Sonoran distribution:** one of the most common of small foliose lichens throughout the region from coastal regions to at least 3000 m in Arizona, southern California, Chihuahua, Sinaloa, Sonora, Baja California and Baja California Sur.



Notes: In var. *effusa* the thallus is very rudimentary. Most material collected in California and previously identified as *C. concolor* belongs to *Candelaria* sp.

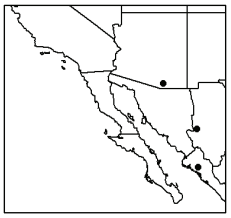
Candelaria fibrosa (Fr.) Müll. Arg., Flora, Jena 70: 319 (1887).

Basionym: *Parmelia fibrosa* Fr., Syst. Orb. 1: 284 (1825); Synonyms: *Candelaria kenyensis* Dodge and see Almborn (1966) and Swinscow and Krog (1988); Illustrations: Brodo et al. (2001), p. 206; Swinscow and Krog (1988), p. 31.

Thallus: small foliose, up to 4 cm wide, adnate, lobate; **lobes:** dorsiventral, imbricate, *c.* 0.5-2 mm wide, often with secondary lobes, margin ± crenulate; **upper surface:** lemon yellow to mustard yellow, smooth to somewhat wrinkled; soredia and isidia: absent; **upper cortex:** *c.* 5-20 µm thick; **medulla:** white, thin; **lower cortex:** *c.* 10-35 µm thick; **lower surface:** white to pinkish, white; rhizines: abundant, simple; **Apothecia:** common, laminal, sessile, up 2 mm diam.; margin: smooth, often with white or yellow cilia; disc: darker yellow than the thallus; epithecium: *c.* 10 µm thick; hymenium: *c.* 60-90 µm tall; paraphyses: simple or branched near the tips, cylindrical

to submoniliform with up to 5 µm wide tips; hypothecium: 30-45 µm thick; **asci:** clavate, >30-spored; **ascospores:** uni- or biguttulate, colorless, 7-11 x 4-6 µm; **Pycnidia:** common, immersed, concolorous with upper surface or slightly darker; **conidia:** ellipsoid, to narrowly ellipsoid 2-3.5 x 1.5 µm; **Spot tests:** upper surface K- (or + deeper yellow), C-, KC-, P-; medulla K-, C-, KC-, P-; **Secondary metabolites:** calycin (major) and pulvinic dilactone (minor).

Habitat and ecology: on bark, often in very humid microclimates, such as martime regions; **World distribution:** pantropical and extending into some warm temperate regions; **Sonoran distribution:** in oak forests up to at least 2000 m in southern Arizona, Chihuahua and Sinaloa.

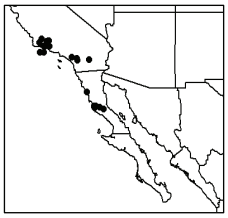


Notes: This species is characterized by the lack of soredia or isidia.

Candelaria "pacifica" Westberg, in prep.

Thallus: small foliose, up to 1 cm wide or coalescing to form extensive colonies, adnate to ascending to erect, often with a shrubby appearance; **lobes**: dorsiventral but often convex and twisted, imbricate, narrow 0.1 -0.6 mm wide; **upper surface**: lemon yellow to orange yellow, in shade paling to yellow green, smooth to somewhat coarse; **soredia**: granular, blastidious, marginal or from the lobe tips and from the lower side of the lobes; **upper cortex**: *c.* 10-45 µm thick (may reach through the whole thallus); **medulla**: white, very thin; **lower cortex**: lacking or partly lacking, *c.* 5-20 µm thick; **lower surface**: arachnoid at least in parts, white or more often greenish when algal layer is exposed, sparsely rhizinate; rhizines: short, white and simple; **Apothecia**: fairly common, laminal, sessile, up to *c.* 1 mm diam.; margin: smooth but often sorediate or lobulate; disc: concolorous with or darker yellow than thallus; epithecium: *c.* 5-10 µm thick; hymenium: *c.* 45-85 µm tall; paraphyses: simple, cylindrical or with somewhat swollen, up to 3 µm wide tips; hypothecium 50-70 µm thick; **asci:** clavate, 8-spored; **ascospores**: oblong–narrowly ellipsoid, often somewhat curved, with numerous oil-droplets, colorless, 11-16 x 4-6 µm; **Pycnidia**: common, appear as raised orange warts on the surface; **conidia**: ellipsoid, 2.5-3.5 x 1.5 µm; **Spot tests**: upper surface K- (or + deeper yellow-reddish), C-, KC-, P-; medulla K-, C-, KC-, P-; **Secondary metabolites**: not investigated but probably similar to the other *Candelaria* species (i.e. containing calycin and pulvinic dilactone).

Habitat and ecology: on bark or wood, rarely on rocks; **World distribution**: known from westernmost North America up to Washington and Idaho; **Sonoran distribution**: mainly on twigs of exposed trees and shrubs at low elevations in the desert up to at least 1500 m in open woodlands in southern California and Baja California.



Notes: *Candelaria* "*pacifica*" is apparently an undescribed species, that differs from *C. concolor* in spore number and in the production of soredia from the lower side, which mostly lacks a cortex. Its erect habit with convex and often twisted lobes, together with the contrasting greenish color of the soredia produced from the lower side, gives this undescribed species a rather characteristic appearance. The lobe morphology is, however, rather variable and the thalli may sometimes form isidiate-sorediate crusts in a similar way to *C. concolor*. *Candelaria* "*pacifica*" is used as an interim name here because material from Europe has also proved to be similar. Thus, the synonyms of *C. concolor* need further investigation before the nomenclatural status of this taxon can be resolved (Westberg, in prep.)

CANDELINA

by M. Westberg and T. H. Nash III

Candelina Poelt, Phyton 16: 194 (1974).

Family: Candelariaceae; Type: *Candelina mexicana* (de Lesd.) Poelt; No. species: three world-wide; Selected lit.: Poelt (1974).

Life habit: lichenized; **Thallus:** placodioid, clearly forming rosettes, adnate to loosely adnate, lobate peripherally; **lobes:** flat to convex, sometimes with secondary lobes formed centrally; **upper surface:** bright yellow to golden yellow to red orange, smooth to somewhat rugulose, sometimes somewhat shiny, pseudocyphellae lacking, isidia and soredia lacking; **upper cortex:** paraplectenchymatous, thin, the direction of the individual hyphae is easily observed; **medulla:** loose, either white and without granules, or yellow (at least in part) from yellow granules; **photobiont:** primary one a chlorococcoid alga, secondary photobiont absent; **lower cortex:** absent centrally or absent throughout, paraplectenchymatous, similar to the upper cortex; **lower surface:** yellow peripherally but becoming pale yellow centrally, with or without stout hapters peripherally; **Ascomata:** apothecial, lecanorine, sessile to substipitate; margin: concolorous with the thallus, persistent, smooth to somewhat crenulate; disc: darker yellow than the thallus; epithecium: yellow-brown, granular; hymenium: colorless below, I+ blue; paraphyses: simple, cylindrical or with somewhat swollen tips, sometimes anastomosing below, septate; hypothecium: colorless; **asci:** clavate, *Candelaria*-type, 8-spored; **ascospores:** simple, narrowly ellipsoid to weakly kidney-shaped, colorless; **Conidiomata:** pycnidial, concolorous with the thallus or darker yellow (walls pale), immersed or appearing as raised warts on the thallus surface; **conidia:** narrowly ellipsoid, colorless; **Secondary metabolites:** pulvinic acid derivatives present in colored parts; **Geography:** from northern South America to southern USA and Namibia in Africa; **Substrate:** on calcium-free rocks in arid regions and where arid microclimates occur.

Key to the species of ***Candelina*** from the Sonoran reigon:

1. Medulla yellow ..... ***C. mexicana***
1. Medulla white ..... ***C. submexicana***

The Species

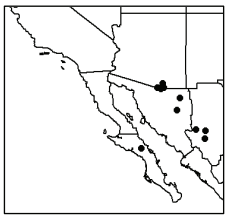
Candelina mexicana (de Lesd.) Poelt, Phyton 16: 194 (1974).

Basionym: *Placodium mexicanum* de Lesd., Lich. Mexiq. 10 (1914); Synonyms: *Caloplaca mexicana* (de Lesd.) Zahlbr., *Xanthoria costariceusis* Hillmann; Illustration: Poelt (1974), p. 190 (cortex only).

Thallus: placodioid, clearly forming rosettes, 2-3 cm wide, loosely adnate, lobate peripherally; **lobes:** convex often folded, up to 5 mm long, and 0.5-1.5 mm wide; **upper surface:** bright yellow to golden yellow, smooth to somewhat rugulose; **upper cortex:** 10-20 µm thick; **medulla:** yellow throughout, inspersed with yellow granules; **lower cortex:** 20-30 µm thick under lobes but absent centrally; **lower surface:** yellow peripherally but becoming pale yellow centrally; hapters: sometimes present, stout, peripheral; **Apothecia:** occasional, sessile, up to 1.4 mm wide; margin: smooth, becoming crenulate with age, occasionally lobulate; disc: darker yellow than the thallus; epithecium: *c.* 5 µm thick; hymenium: *c.* 50-65 µm tall; paraphyses: simple, cylindrical or with somewhat swollen, up to 3 µm wide tips; hypothecium: *c.* 70-90 µm thick; **asci:** clavate, 8-spored; **ascospores:** narrowly ellipsoid to weakly kidney-shaped, (9-) 11-16.5 x 3.5-5 µm; **Pycnidia:** frequent, spherical to broadly ellipsoid, immersed or appearing as raised warts on the thallus surface; **conidia:** narrowly ellipsoid, 2-3 x 1.5 µm; **Spot tests:** upper surface K+ reddish C-, KC-, P-; medulla K+ reddish, C-, KC-, P-; **Secondary metabolite:** calycin.

Substrate and ecology: on calcium free rocks and boulders in open montane habitats; **World distribution:** northern South America to southwestern USA; **Sonoran**

distribution: relatively rare but conspicuous, extending from 1000 m. to at least 2200 m. in the foothills and mountains of Arizona, Chihuahua, Sonora and Baja California Sur.

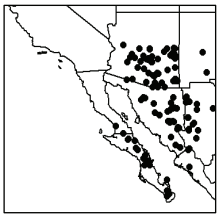


Candelina submexicana (de Lesd.) Poelt, Phyton 16: 198 (1974).

Basionym: *Placodium submexicanum* de Lesd., Lich. Mexiq. 11 (1914); Synonyms: *Candelariella submeicana* (de Lesd.); *Caloplaca submexicana* (de Lesd.) Zahlbr.; *Caloplacopsis submexicana* de Lesd; Illustrations: Brodo et al. (2001), p. 210; Hale (1979), p. 32; St. Clair (1999), p. 48.

Thallus: placodioid, clearly forming rosettes, 2-4 cm wide, tightly to loosely adnate, lobate peripherally; **lobes:** flat to convex and then sometimes folded, up to *c.* 6 mm long and 0.3-1.5 mm wide; **upper surface:** bright yellow to golden yellow to red orange, smooth to somewhat rugulose, sometimes somewhat shiny; **upper cortex**: 10-20 µm thick; **medulla**: white, not inspersed with granules; **lower cortex:** 20-30 µm thick under lobes tips but absent centrally or absent throughout; **lower surface:** yellow peripherally but becoming pale centrally; hapters: sometimes present, stout, peripheral; **Apothecia:** common, sessile to substipitate, up to 1.5 mm wide; margin: smooth, becoming crenulate with age; disc: darker yellow than the thallus, sometimes with a greenish tinge; epithecium: *c.* 5 µm thick; hymenium: *c.* 45-55 µm tall; paraphyses: simple, cylindrical or with somewhat swollen, up to 4 µm wide tips; hypothecium: *c.* 60-70 µm thick; **asci:** 8-spored; **ascospores:** narrowly ellipsoid to weakly kidney-shaped, 11-15 x 4-5 µm; **Pycnidia:** frequent, globular to broadly ellipsoid, immersed or appearing as raised warts on the thallus surface; **conidia:** narrowly ellipsoid, 2-3 x 1.5 µm; **Spot tests:** upper surface K+ reddish C- KC- P-; medulla K+ reddish, C-, KC-, P-; **Secondary metabolite:** calycin.

Substrate and ecology: on calcium free rocks and boulders in open habitats; **World distribution:** central Mexico to southwestern USA; **Sonoran distribution:** one of the more conspicuous and common lichens in the interior desert and extending up to at least 2600 m in the mountains of Arizona, Chihuahua, Sonora, Sinaloa, Baja California and Baja California Sur.



Notes: *Candelina submexicana* is morphologically very variable. The variation ranges from more or less crustose forms with flat and tightly adnate lobes to subfoliose forms with convex lobes similar to *C. mexicana*. The two species are easily separated by the color of the medulla.

CANOMACULINA

by T. H. Nash III & J.A. Elix

Canomaculina Elix & Hale, Mycotaxon 29: 239 (1987).

Family: Parmeliaceae; Type: *Canomaculina pilosa* (Stiz.) Elix & Hale; No. species: *c.* 19 world-wide; Selected lit.: Elix (1997), and Elix and Hale (1987).

Life habit: lichenized; **Thallus:** foliose, *c.* circular in outline, 5-20 cm wide, lobate: **lobes:** irregular to sublinear, elongat; apices: usually subrotund to rotund, ciliate; cilia: sparse to dense, simple or often branched, often tapered; **upper surface:** pale gray to gray, gray-green or pale green, pruinose or not towards the tips, conspicuously effigurate-maculate, becoming irregularly cracked but lacking true pseudocyphellae; **upper cortex:** pored epicortex, palisade plectenchymatous; **medulla:** white, loosely packed, cell walls containing *Cetraria*-type lichenan; **photobionts**: primary one a *Trebouxia*, secondary photobiont absent; **lower surface:** pale tan to black, plane to sometimes wrinked, attachment by simple (rarely branched),

rhizinate; rhizines: dimorphic (short ones throughout and longer ones in tufted group)s; cyphellae, pseudocyphellae and tomentum: absent; **Ascomata:** apothecial, perforate or imperforate, laminal on thallus, orbicular, cup-shaped, sessile; margin: prominent, with thalloid rim, eciliate; exciple: gray or hyaline; epithecium brown or brownish yellow; hypothecium: hyaline; **asci:** lecanoral, wall layers apex thickened, apex amyloid, with wide, axial body divergent towards apex, *c.* 8-spored; **ascospores:** simple, ellipsoid to broadly ellipsoid; 8-20 x 5-12 µm; walls: thin, hyaline; **Conidiomata:** pycnidial, laminal, immersed, punctiform; **conidia:** filiform, 9-16 x 1 µm; **Secondary metabolites:** upper cortex with atranorin and chloroatranorin or lichexanthone; medulla with some combination of orcinol or ß-orcinol depsidones and (higher) aliphatic acids; **Geography:** temperate to tropical forests and woodlands; **Substrate:** mostly bark or acidic rock.

Notes: Although the genus established in 1987, the concept of the genus was expanded by Elix (1997) to include species segregated to *Rimeliella* by Kurokawa (1991).

Key to the species of ***Canomaculina*** from the Sonoran region:

1. Thallus isidiate ..... ***C. subtinctoria***
1. Thallus sorediate 2

2. Medulla K+ yellow, turning dark red (salazinic acid major) ..... ***C. leucosemotheta***
2. Medulla K- (salazinic acid absent) ..... ***C. conferenda***

The Species

Canomaculina conferenda (Hale) Elix, Mycotaxon 65: 476 (1997).

Basionym: *Parmotrema conferendum* Hale, Mycotaxon 5: 433 (1977); Synonym: *Rimeliella conferenda* (Hale) Kurok.; Illustration: Hale (1977), p. 443 as *Parmotrema conferendum*.

Thallus: loosely adnate, foliose, 4-12 cm in diam., membranous, lobate; **lobes:** narrow, sublinear, contiguous to imbricate, elongate, plane, separate, 5-12 mm wide; apices: subrotund, ciliate; cilia: simple, up to 2 mm long; **upper surface:** pale greenish to yellowish gray, smooth but cracked with age, shiny, becoming rimose, strongly effigurate maculate, becoming rugulose; **soredia:** farinose, in linear to irregular, submarginal soralia; isidia and pustulae: absent; **medulla:** white; **lower surface:** pale brown to blackening, densely rhizinate, rhizines: black, simple; **Apothecia:** not seen; **Pycnidia:** not seen; **Spot tests:** cortex K+ yellow, C-, KC-, P+ yellow; medulla K-, C-, KC-, P-; **Secondary metabolites:** upper cortex with atranorin and chloroatranorin; medulla with norlobaridone (major).

Substrate and ecology: frequent on bark and rocks in woodlands and forests; **World distribution:** neotropics and subtropics, from Texas to Argentina; **Sonoran distribution:** rare on oaks in the foothills of the Sierra Madre Occidental in northern Sinaloa.

Canomaculina leucosemotheta (Hue) Elix, Mycotaxon 65: 477 (1997).

Basionym: *Parmelia leucosemotheta* Hue, Nouv. Arch. Mus. Paris, ser 4, 1: 192 (1899); Synonym: *Parmotrema leucosemothetum* (Hue) Hale; Illustration: Hale (1965), plate 16 as *Parmelia leucosemotheta*.

Thallus: adnate to loosely adnate, foliose, 3-20 cm in diam., lobate; **lobes:** subirregular, elongate, slightly imbricate, plane, separate, 10-15 mm wide; apices: rotund, becoming dentate-lacinate with age, ciliate; cilia: sparse, simple, up to 2.5 mm long; **upper surface:** gray with some blackened areas, smooth, shiny, sometimes white pruinose, strongly white maculate, frequently reticulately cracked with age; **soredia:** granular, common, in linear, submarginal, soralia; isidia and pustulae: absent; **medulla:** white with continuous algal layer; **lower surface:** black with brown to mottled white naked zone peripherally, centrally rhizinate, rhizines scattered, simple; **Apothecia:** very rare, substipitate, up to 6 mm in diam.; margin: sorediate; disc: imperforate; **asci:** clavate, 8-spored; **ascospores:** ellipsoid, 12-16 x 7-10 µm; **Pycnidia:** not seen; **Spot tests:** upper cortex K+ yellow, C-, KC-, P+ yellow; medulla K+ yellow turning deep red, C-, KC-, P+ orange; **Secondary metabolites:** upper cortex with atra-

norin and chloroatranorin; medulla with salazinic acid (major) and consalazinic acids (minor).

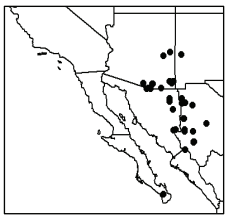
Substrate and ecology: usually on trees in open habitats, rarely on rocks; **World distribution:** neotropics from Mexico to northern Argentina and southern Africa; **Sonoran distribution:** Sinaloa, in the Sierra Madre Occidental.

Canomaculina subtinctoria (Zahlbr.) Elix, Mycotaxon 65: 477 (1997).

Basionym: *Parmelia subtinctoria* Zahlbr., Symb. Sin 3: 193 (1930); Synonyms: *Parmotrema subtinctorium* (Zahlbr.) Hale; *P. haitense* (Hale) Hale; *Rimeliella subtinctoria* (Zahlbr.) Kurok. and see Hale and Kurokawa (1964) under *Parmelia subtinctoria*; Illustrations: Brodo et al. (2001), p. 211; Elix (1994m), p. 194 as *Rimeliella subtinctoria*.

Thallus: adnate to loosely adnate, foliose, 4-15 cm in diam., membranous, lobate; **lobes:** narrow, sublinear to subirregular, contiguous to imbricate, elongate, plane, separate, 7-13 mm wide; tips: rotund, sparsely to moderately ciliate; cilia: simple, black, up to 4 mm long; **upper surface:** mineral gray (but turning buff in herbarium), smooth but cracked with age, shiny, becoming rimose, strongly effigurate maculate, becoming rugose; **isidia:** cylindrical, simple to coralloid branched, laminal, rarely ciliate apically; soredia and pustulae absent; **medulla:** white; **lower surface:** pale brown to dark brown in center, densely rhizinate, rhizines black, simple; **Apothecia:** rare, 3-8 mm diam.; margin: isidiate; disc: imperforate when young; **asci:** clavate, 8-spored; **ascospores:** ellipsoid, 8-11 x 5-8 um; **Pycnidia:** laminal, immersed; **conidia:** cylindrical-fusiform, 4-7 x 1 µm; **Spot tests:** cortex K+ yellow, C-, KC-, P+ yellow; medulla K+ yellow turning dark red, C-, KC-, P+ orange; **Secondary metabolites:** upper cortex with atranorin and chloroatranorin (both major) and usnic acid (accessory); medulla with salazinic acid (major), consalazinic acid and norlobaridone (both minor) and protolichesterinic acid (accessory).

Substrate and ecology: frequent on bark in woodlands, rare on rock; **World distribution:** pantropical and into adjacent temperate regions; North America, Europe, Asia and Australasia; **Sonoran distribution:** common on boulders and canyon walls in mid-montane habitats from SE Arizona south through the Sierra Madre Occidental in Chihuahua, Sonora and Sinaloa and in the mountains of southern Baja California Sur.



Notes: The chemistry profile basically corresponds to Hale's (1977) interpretation for the species (e.g. see discussion under *Parmotrema neotropicum*, p. 438). Earlier reports (Hale 1965) of cryptochlorophaic acid was a misidentification of norlobaridone.

CANOPARMELIA

by T. H. Nash III and J.A. Elix

Canoparmelia Elix & Hale, Mycotaxon 27: 278 (1986).

Family: Parmeliaceae; Type: *Canoparmelia texana* (Tuck.) Elix & Hale; No. species: *c.* 45 world-wide; Selected lit.: Elix (1993a & 1994b), Elix et al. (1986) and Hale (1976c).

Life habit: lichenized; **Thallus:** foliose, *c.* circular in outline, lobate, sometimes imbricate; **lobes:** usually subirregular but sometimes sublinear; apices: usually rotund, eciliate; **upper surface:** pale gray to greenish gray, plane to rugulose, sometimes reticulately ridged, smooth, shiny or dull, sometimes maculate, usually epruinose; without or with soredia, pustules or isidia; pseudocyphellae: absent; **upper cortex:** pored epicortex, palisade plectenchymatous; **medulla:** white, loosely packed; cell walls: contain-

ing isolichenan; **photobionts**: primary one a *Trebouxia*, secondary photobiont absent; **lower surface:** black, brown peripherally, plane to sometimes wrinked, attachment by simple rhizines but peripherally erhizinate; cyphellae, pseudocyphellae and tomentum absent; **Ascomata:** apothecial, imperforate, laminal on thallus, orbicular, cup-shaped, sessile; margin: prominent, with thalloid rim; exciple: gray or hyaline; epithecium brown or brownish yellow; hypothecium: hyaline, **asci:** lecanoral, wall layers apex thickened, apex amyloid, with wide axial body divergent towards apex, *c.* 8-spored; **ascospores:** simple, ellipsoid to broadly ellipsoid, 10-14 µm long, 6-8 µm wide, wall thin, hyaline; **Conidiomata:** pycnidial, laminal or rarely marginal, immersed; **conidia:** bifusiform to rarely bacilliform or fusiform, 7-10 (-15) x 1 µm; **Secondary metabolites:** upper cortex with atranorin (rarely usnic acid accessory) and chloroatranorin; medulla some combination of orcinol depsides, ß-orcinol depsides, ß-orcinol depsidones, (higher) aliphatic acids, anthraquinones, or amino acid derivatives; **Geography:** predominantly tropical and subtropical to temperate forests and woodland; **Substrate:** mostly bark or acidic rocks.

Notes: This segregate from *Parmelia s. lato* and *Pseudoparmelia* sensu Hale (1976c) is characterized by the relatively narrow, eciliate lobes, a pored epicortex, the presence of isolichenin, and simple rhizines. Superficially it is somewhat similar to *Paraparmelia*, a Southern Hemispheric genus, that is obligately saxicolous, contains *Xanthoparmelia*-type lichenin, and has smaller spores.

Key to the species of ***Canoparmelia*** from the Sonoran region:

1. Thallus isidiate ..... ***C. caroliniana***
1. Thallus sorediate. 2

2. Medulla P-; KC + pinkish or faint purple (divaricatic acid present) ..... ***C. texana***
2. Medulla P+ yellow, turning orange, KC- (divaricatic acid absent; stictic acid present) 3

3. Lobes subirregular, 3-6 mm wide ..... ***C. crozalsiana***
3. Lobes sublinear, 1-2.5 mm wide ..... ***C. carneopruinata***

The Species

Canoparmelia carneopruinata (Zahlbr.) Elix & Hale, Mycotaxon 27: 280 (1986).

Basionym: *Parmelia carneopruinata* Zahlbr., Sitz. kaiser. Akad. Wissenschaft. Math.-Naturwissenschaft. 1: 419 (1902); Synonym: *Pseudoparmelia carneopruinata* (Zahlbr.) Hale, and see Hale (1976c) under *Pseudoparmelia carneopruinata*; Illustration: Hale (1976c), p. 19 as *Pseudoparmelia carneopruinata*.

Thallus: adnate, foliose, 3-9 cm in diam., irregularly lobate; **lobes:** sublinear, elongate, plane to subconvex, separate, 1-2.5 mm wide; apices: rotund, sometimes lacinate, eciliate; **upper surface:** pale gray to greenish gray, strongly reticulate ridged, rugulose, dull, pruinose at lobe tips and emaculate; **soredia:** farinose, common, laminal, initially in orbicular soralia but becoming confluent; isidia and pustulae absent; **medulla:** white, with continuous algal layer; **lower surface:** black; rhizines: sparse, black, simple; **Apothecia:** rare, laminal, substipitate, 1-4 mm wide; disc: brown; margin: usually sorediate, often pruinose; **ascospores:** ellipsoid, 9-13 x 6-9 µm; **Pycnidia:** not seen; **Spot tests:** upper cortex K+ yellow, C-, KC-, P+ yellow; medulla K + orange, C-, KC-, P+ orange-red; **Secondary metabolites:** upper cortex with atranorin and chloroatranorin; medulla with stictic acid (major), constictic acid (minor), and cryptostictic acid (minor to trace).

Substrate and ecology: on trees in open forests; **World distribution:** neotropics from Mexico to Argentina, southern Europe; **Sonoran distribution:** only known from one locality in coastal plain of southern Sonora.

Note: As noted by Hale (1976c) *C. carneopruinata* and *C. crozalsiana* tend to intergrade and thus large specimens of the former may not be readily distinguishable from small specimens of the latter.

Canoparmelia caroliniana (Nyl.) Elix & Hale, Mycotaxon 27:28 (1986).

Basionym: *Parmelia caroliniana* Nyl., Flora 68: 614 (1885); Synonyms: *Pseudoparmelia caroliniana* (Nyl.) Hale and see Hale (1976c) under *Pseudoparmelia caroliniana*; Illustrations: Brodo et al. (2001), p. 212; Hale (1976c), p. 23 as *Pseudoparmelia caroliniana*.

Thallus: adnate, foliose, 4-10 cm in diam., irregularly lobate; **lobes:** subirregular, elongate, plane to subconvex, separate, 2-5 mm wide; apices: rotund, eciliate; **upper surface:** pale gray, smooth to rugose, dull, pruinose at lobe tips and strongly reticulately white maculate, finely cracked, isidiate; **isidia:** common, dense, laminal, cylindrical, simple to coralloid; soredia and pustulae absent; **medulla:** white with continuous algal layer; **lower surface:** black to rarely dark brown; rhizines: sparse to moderately dense (except margin), black, simple; **Apothecia:** rare, laminal on thallus, substipitate, 1-4 mm wide; disc: red brown to dark brown, margin usually isidiate; **ascospores:** ellipsoid, 13-15 x 6-8 µm; **Pycnidia:** not seen; **Spot tests:** upper cortex K+ yellow, C-, KC-, P+ yellow; medulla K-, C-, KC+ pale pink, P-; **Secondary metabolites:** upper cortex with atranorin and chloroatranorin; medulla with perlatoic acid (major) and unknown acids (trace).

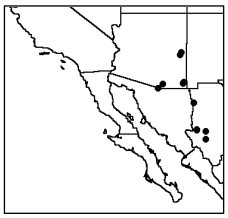
Substrate and ecology: often on pines in montane, open pine-oak woods, rarely on rocks; **World distribution:** pantropics and extending into adjacent temperate areas of SE USA and southern Europe; **Sonoran distribution:** Sinaloa, in the Sierra Madre Occidental.

Canoparmelia crozalsiana (de Lesd. *ex* Harm.) Elix & Hale, Mycotaxon 27: 278 (1986).

Basionym: *Parmelia crozalsiana* de Lesd. *ex* Harm., Lich. France 4: 555 (1909); Synonym: *Pseudoparmelia crozalziana* (de Lesd. *ex* Harm.) Hale; Illustrations: Hale (1976c), p. 26, and Hale (1979), p. 80, both as *Pseudoparmelia crozalsiana*.

Thallus: adnate, foliose, 3-10 cm in diam., irregularly lobate; **lobes:** subirregular, elongate, plane to subconvex, separate, 3-6 mm wide; apices: rotund, eciliate; **upper surface:** pale gray to greenish gray, strongly reticulately ridged, rugulose, shallowly foveate, becoming cracked with age, dull, sometimes white pruinose and maculate; **soredia:** farinose, common, initially in laminal orbicular soralia but becoming confluent; isidia and pustulae absent; **medulla:** white with continuous algal layer; **lower surface:** black centrally, brown zone peripherally; rhizines: sparse, black, sometimes pale tipped, simple; **Apothecia:** not seen; **Pycnidia:** rare, immersed; **conidia:** filiform 12-15 x 1 µm; **Spot tests:** upper cortex K+ yellow, C-, KC-, P+ yellow; medulla K + orange, C-, KC-, P+ orange-red; **Secondary metabolites:** upper cortex with atranorin and chloroatranorin; medulla with stictic acid (major), constictic acid (minor), and cryptostictic acid (minor to trace).

Substrate and ecology: on hardwood trees and rocks in moist, montane canyons at mid-elevations; **World distribution:** SW Europe, southern U.S.A., Mexico, South America, Africa, India, Australia; **Sonoran distribution:** SE and E Arizona southwards through the Sierra Madre Occidental in Chihuahua and Durango.



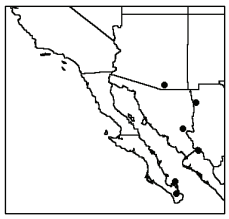
Canoparmelia texana (Tuck.) Elix & Hale, Mycotaxon 27: 279 (1986).

Basionym: *Parmelia texana* Tuck., Amer. J. Sci. Arts, ser. 2, 32: 424 (1858); Synonym: *Pseudoparmelia texana* (Tuck.) Hale and see also Hale (1976c) under *Pseudoparmelia texana*; Illustrations: Brodo et al. (2001), p. 212; Hale (1976c), p. 51 as *Pseudoparmelia texana*.

Thallus: adnate, foliose, 4-12 cm in diam., irregularly lobate; **lobes:** sublinear to subirregular, elongate, plane to subconvex, separate, 3-5 mm wide; apices: rotund, crenate to deeply incised, eciliate; **upper surface:** pale gray to ashy white, smooth to rugose, dull, maculate, sorediate; **soredia:** coarse, granular, whitish, laminal, initially in pustulae that develop into orbicular, capitate soralia; soralia usually not confluent; isidia absent; **medulla:** white with continuous algal layer; **lower surface:** black with a brown bare zone marginally; rhizines: sparse to moderately dense (except margin), black, simple; **Apothecia:** rare, laminal on thallus, 2-5 mm wide; disc: red-

brown to dark brown; margin: usually sorediate; **ascospores:** ellipsoid, 8-11 x 5-7; **Pycnidia:** rare, immersed; **conidia:** weakly bifusiform 6-8 x 1 µm; **Spot tests:** upper cortex K+ yellow, C-, KC-, P+ yellow, medulla K-, C-, KC- [or + pale pink], P-; **Secondary metabolites:** upper cortex with atranorin and chloroatranorin; medulla with divaricatic acid (major), nordivaricatic and stenosporic acids (trace).

Subtrate and ecology: on pines and hardwoods in dry open woods or along roads in lower to mid-elevation montane areas; **World distribution:** pantropical and some adjacent temperate areas of North and South America, Asia and Australasia; **Sonoran distribution:** SE Arizona southwards through the Sierra Madre Occidental of Chihuahua, Sonora and Sinaloa and in the southern mountains of Baja California Sur.



CATAPYRENIUM

by O. Breuss

Catapyrenium Flot., Botan. Zeitung 8: 361 (1850).

Family: Verrucariaceae; Type: *Catapyrenium cinereum* (Pers.) Körb.; No. species: eight world-wide; Selected lit.: Breuss (1990, 1993 & 1996).

Life Habit: lichenized; **Thallus:** squamulose, composed of irregularly arranged squamules or rosulate; attached by a rhizohyphal weft, tufts of rhizohyphae, rhizines, or basal ends of squamules; **squamules:** dispersed, rounded, contiguous or imbricate, loosely or closely adnate; margins: sometimes ascending, lobed, and/or incised; **upper surface:** brownish or greenish gray or brown, dull, smooth or minutely scabrose, often whitish pruinose; isidia and soredia: absent (but isidia-like lobules present in one species); **upper cortex:** paraplectenchymatous, thin (10-30 µm thick), composed of rounded-subangular cells 5-8 µm in diam., poorly delimited from algal layer, with or without an amorphous epinecral layer; **medulla:** white, of intricately interwoven hyphae, filamentous or with many spherical cells to subparaplectenchymatous; **photobiont:** primary one a chlorococcoid alga, secondary photobiont absent; algal cells: 5-12 µm in diam.; algal layer: usually 50-100 µm high, horizontally continuous, unevenly delimited above and below; **lower cortex:** paraplectenchymatous or composed of more densely packed, globular medullary cells, or lacking; rhizohyphae (if present at all): colorless or brown; **lower surface:** pale to black, bare or with loose to dense rhizohyphal weft, hyphal tufts or true rhizines; **Ascomata:** perithecial, laminal, immersed, subglobose or broadly pyriform, without involucrellum; exciple: hyaline, brownish or brown-black; interascal filaments: absent; hymenial gel: amyloid (I+ orange-red or blue, always blue after pretreatment with K); ostiolar filaments (periphyses): present, simple or sparsely branched; **asci:** clavate, thin-walled, wall non-amyloid, apically not or slightly thickened, without ocular chamber, 8-spored; **ascospores:** biseriately arranged, ellipsoid, ovoid to clavate or subfusiform, simple, hyaline, thin-walled, smooth, without halo; **Conidiomata:** pycnidial (known only from one species), immersed, of *Dermatocarpon*-type; **conidia:** short cylindrical; **Secondary metabolites:** none detected; **Geography:** arid, semi-arid or arctic-alpine regions of the world and wherever arid microclimates are found; **Substrate:** soil, detritus, mosses and bark.

Key to the species of ***Catapyrenium*** from the Sonoran region:

1. Squamules with dactyloid, inflated outgrowths ..... ***C. dactylinum***
1. Squamules without outgrowths 2
   2. Squamules ascending, olive- or brownish green, epruinose, thin, with finely crenate margins, attached by tufts of rhizohyphae ..... ***C. squamellum***

2. Squamules loosely adnate, patchily pruinose, thick, lobate, attached by a dense rhizohyphal weft or true rhizines 3

3. Squamules with a dark brown, rhizohyphal weft gradually emerging from the medullary tissue; lower cortex lacking; medulla with many spherical cells .... ***C. psoromoides***

3. Squamules rhizinate (lacking rhizohyphae); with a thin cellular lower cortex; medulla filamentous ***C. simulans***

The Species

Catapyrenium dactylinum Breuss, Linzer Biol. Beitr. 32 (2): 1054 (2000).

Illustration: Breuss (2000b), p. 1055. and Fig. 41 below.

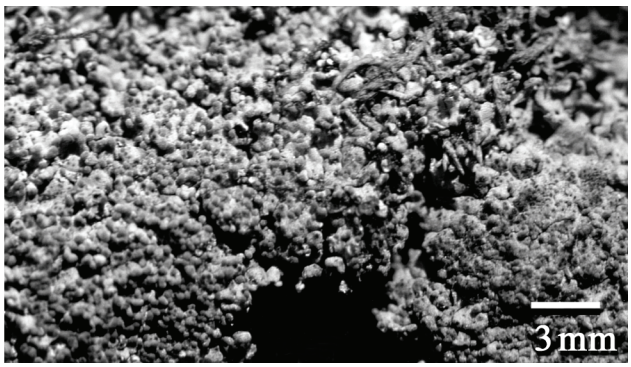


Fig. 41. *Catapyrenium dactylinum*, photo by O. Breuss.

Thallus: squamulose, irregularly rosulate; **squamules:** densely aggregated to form orbicular, flattened cushions up to 30 mm across; individual squamules: 1.5 - 2.5 mm wide, 0.25-0.35 mm thick, slightly convex and undulate or flattened, the outer squamules: somewhat enlarged and weakly concave; central squamules: irregularly divided into erect, nodular or slightly elongated, inflated lobes or lobules up to 0.35 mm wide; **upper surface:** brownish gray, dull, densely covered by granular pruina (lobules less densely pruinose, their extreme tips often epruinose and brown); **medulla:** composed of intricated filamentous hyphae without spherical cells; hyphae: 2.5-3 µm in diam.; medulla of lobules: more loosely organized to almost arachnoid; algal layer: 30-50 µm thick, algal cells 5-8 µm in diam.; **lower cortex:** thin, composed of 1-3 layers of brownish, roundish-angular cells (8-12 µm in diam.); rhizohyphae: lacking; **lower surface:** brown centrally, pale marginally, dull, naked, attached by their elongated basal ends; **Perithecia:** subglobose, up to 0.25 mm broad; exciple: colorless or yellowish; **asci:** narrowly clavate, 50-55 x 12-16 µm, 8-spored; **ascospores** narrowly ellipsoid, 14-17 x 5-6 µm; **Pycnidia:** immersed in the apices of erect lobules; **conidia:** shortly cylindrical, 3.5-4 x 1 µm; **Spot tests:** all negative; **Secondary metabolites:** none detected.

Substrate and ecology: on mosses over acidic rock; **World** and **Sonoran distribution:** known only from the type locality in Chihuahua.

Notes: The formation of nodular or finger-like lobules with a loosely filamentous medulla is distinctive. The species is the only member of the genus known to have pycnidia.

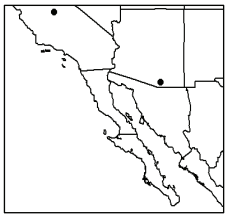
Catapyrenium psoromoides (Borrer) R. Sant., Lichenologist 12: 106 (1980).

Basionym: *Verrucaria psoromoides* Borrer, in Hooker & Sowerby, Engl. Bot., Suppl. 1, tab. 2612, fig. 1 (1831); Synonyms: *Dermatocarpon psoromoides* (Borrer) DT. & Sarnth., *D. daedaleum* var. *corticola* H. Magn.; Illustrations: Swinscow and Krog (1988), p. 34; Harada (1993), pp. 126 & 128 as *Endocarpon psoromoides*.

Thallus: squamulose; **squamules:** dispersed or slightly overlapping to imbricate, loosely attached, divided; **upper surface:** grayish or greenish brown, often with spotty pruina (mostly on distal parts of the lobes); **medulla:** composed of ± loose hyphae with many spherical cells and distinct interhyphal spaces; **lower cortex:** lacking; **surface:** with medullary hyphae merging into the blackish-brown rhizohyphal web; **Perithecia:** pyriform; walls: hyaline or pale yellowish-brown except for the dark ostiole; periphyses: rather short (up to 30 µm long), often with somewhat swollen (-5 µm in diam.) apical cells; **asci:** clavate, 55-65 x 13-16 µm, 8-spored; **ascospores:** elongate ellipsoid to subfusiform, *c.* 12-18 x 5-7 µm; **Spot**

tests: all negative; **Secondary metabolites:** none detected.

Substrate and ecology: mostly on bark and mosses in warm temperate sites; **World distribution:** temperate Europe, East Africa, New Zealand, Japan, southwestern North America; **Sonoran distribution:** known from several sites in central California, on oak (*Quercus douglasii* and *Q. lobata*) and from one site in southern Arizona on a mossy boulder and an oak.



Notes: This species is the only bark-inhabiting species of *Catapyrenium* s.str. It is closely related to the terricolous and mainly arctic-alpine *C. daedaleum* (not known from the Sonoran area).

Catapyrenium simulans Breuss, **sp. nov.**

Diagnosis: *Similis Catapyrenio psoromoide a quo differt medulla prosoplectechymatica, cortice inferiore paraplectenchymatico, e cellulis subanguloso-rotundatis 10-13 µm latis composito, rhizohyphis nullis. Squamae solum rhizinis nigrescentibus in substrato affixae.*

Type: MEXICO, Chihuahua: along route 16, *c.* 28 km W of Basaseachic, riparian area with scattered boulders, on soil among mosses, 28°20'50"N, 108°15'45"W, 1720 m, 25 July 1994, T. H. Nash 37882 (ASU - holotype).

Thallus: squamulose; **squamules:** loosely attached by long and slender rhizines, irregularly lobate; lobes: mostly linear, 1.5-2.5 mm long and *c.* 1 mm broad, 0.20-0.35 mm thick; **upper surface:** pale grayish brown, scantily whitish pruinose; pruina: ± punctiform; **medulla:** composed of intricated filamentous hyphae (2.5-3.5 µm in diam.), without spherical cells; algal layer: *c.* 50-80 µm thick, algal cells: 7-12 µm in diam.; **lower cortex:** cellular, brownish, composed of 2-3 layers of roundish-angular cells (10-13 µm in diam.); **lower surface:** brown, paler marginally, dull, without a rhizohyphal weft, rhizinate; rhizines: several per squamule, brown or blackening, up to 0.15 mm thick and several mm long; **Perithecia:** broadly pyriform, up to 0.30 mm wide; exciple: colorless; **asci:** clavate, 50-60 x 13-17 µm, 8-spored; **ascospores:** narrowly ellipsoid to subfusiform, 13-17 x 5-6 µm; **Spot tests:** all negative; **Secondary metabolites:** none detected.

Substrate and ecology: on soil among mosses; **World** and **Sonoran distribution:** known only from the type collection from Chihuahua.

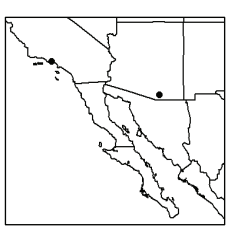
Notes: Externally the species resembles small specimens of *Catapyrenium psoromoides*, from which it is easily separable anatomically. It approaches the European *Catapyrenium alvarense* which differs in having rhizohyphae and shorter ascospores.

Catapyrenium squamellum (Nyl.) J. W. Thomson, Bryologist 90: 36 (1987).

Basionym: *Verrucaria squamella* Nyl., in Hasse, Bull. Torrey Bot. Club 21: 449 (1897); Synonym: *Dermatocarpon squamellum* (Nyl.) Herre; Illustration: Thomson (1987), p. 30.

Thallus: squamulose; **squamules:** small, 1-2 mm wide, 200-300 µm thick, loosely aggregated, ascending, with finely divided margins; **upper surface:** olive- or brownish green; **medulla:** subparaplectenchymatous (hyphae divided into many globular cells of 5-8 µm diam.); algal layer: throughout most of the thallus; algal cells: 6-10 µm diam.; **lower cortex:** lacking; **lower surface:** pale to brownish; rhizohyphae: hyaline or pale brownish, mostly aggregated to form hapter-like or almost rhizine-like bundles; **Perithecia:** pyriform, up to 0.25 mm diam., with colorless walls; **asci:** clavate, 50-60 x 13-15 µm, 8-spored; **ascospores:** narrowly ellipsoidal, 15-22 x 5-6 µm; **Spot tests:** all negative; **Secondary metabolites:** none detected.

Substrate and ecology: over soil or acidic rocks and among mosses; **World distribution:** known only from SW North America and the West Indies; **Sonoran distribution:** Santa Monica Range in



southern California and southern Arizona.

CETRARIA

by I. Kärnefelt

Cetraria Ach., Meth. Lich. 292 (1803).

Family: Parmeliaceae; Type: *Cetraria islandica* (L.) Ach.; No. species: 15 world-wide; Selected lit.: Kärnefelt et al. (1992 & 1993), Kärnefelt (1979), and McCune and Geiser (1997).

Life habit: lichenized; **Thallus:** fruticose; **lobes:** more or less canaliculate, subtubular or terete, rather broad to narrow, *c* 0.5-20.0 mm wide; lobe tips: occasionally becoming expanded, rounded to fusiform; margins: with scattered, branched or unbranched projections; **surface:** dark brown to paler brown, occasionally reddish at base, rather smooth to rough, occasionally markedly foveolate or wrinkled, rather shiny or dull; without soralia, dactyls or lobules; pseudocyphellae: rather abundant on margins; **upper cortex:** with non-pored epicortex, strongly white, composed of external pachydermatous paraplectenchymatous hyphae overlying prosoplectenchymatous hyphae, **medulla:** white, loosely packed; **photobionts:** primary one a *Trebouxia*, secondary photobiont absent; **lower cortex:** composed of external pachydermatous paraplectenchymatous hyphae overlying prosoplectenchymatous hyphae; pseudocyphellae rather abundant; **Ascomata** apothecial, frequent, marginal to laminal, at first concave, later becoming convex, pedicellate; margin: prominent, thalloid; disc: imperforate, dark brown; exciple: hyaline, epithecium: brown or brownish yellow; hypothecium: hyaline; **asci:** lecanoral, *Cetraria*-type, with thickened wall layers; apex: amyloid, thickened, with a narrow axial body surrounded by a distinct, strongly amyloid ring structure, 8-spored; **ascospores:** simple, ellipsoid to broadly ellipsoid; walls: thin, hyaline, not amyloid; **Conidiomata:** pycnidial, abundant on marginal projections; **conidia:** citriform, 5-7 x 1 µm; **Secondary metabolites:** aliphatic acids and/or β-orcinol depsidones; **Geography:** occurring in temperate/ boreal regions of the Northern Hemisphere, from low altitudes to alpine areas, and also in a few scattered locations in the Southern Hemisphere; **Substrate:** terricolous or rarely on bark or wood.

Notes: Thirteen segregates of *Cetraria s. l.* concerning the North American flora has been proposed: *Allocetraria, Arctocetraria, Asahinea, Cetrariella, Cetrelia, Esslingeriana, Flavocetraria, Kaernefeltia, Masonhalea, Platismatia, Tuckermannopsis, Tuckneraria* and *Vulpicida* (Randlane et al. 1997). The published and unpublished molecular data reveal that *Cetrariella* and *Vulpicida* are the most closely related genera. *Cetraria s. str.* differs from these two segregates in having oblong citriform conidia, asci of *Cetraria*-type and a different secondary chemistry (Kärnefelt et al. 1993, Kärnefelt and Thell 2000).

The Species

Cetraria ericetorum Opiz subsp. **reticulata** (Räsänen) Kärnef., Opera Botanica 46: 82 (1979).

Illustrations: Brodo et al. (2001), p. 216; Thomson (1984), p. 79.

Thallus: fruticose; **lobes:** ± canaliculate, subtubular or terete, *c.* 0.5-8.0 mm broad; lobe tips: occasionally becoming expanded, rounded to fusiform; margins: with scattered, branched or unbranched projections; **upper surface:** dark brown to paler brown, occasionally reddish at base, rather smooth to rough, occasionally markedly foveolate or wrinkled, rather shiny or dull; soredia: absent; pseudocyphellae: rather abundant on the margins; **medulla:** white, loosely packed; **lower surface:** dull, medium brown to light brown with pale reddish basal parts or with dark brown upper parts and grayish or pale brown middle parts; usually with prominent reticulate ridges;

pseudocyphellae: confined to the margins; **Apothecia** rather frequent, often on expanded lobe portions; disc: imperforate, dark olivaceous brown; exciple: hyaline; epithecium: brown or brownish yellow; hypothecium: hyaline; **asci:** clavate, *c.* 8-spored; **ascospores:** simple, hyaline, ellipsoid to broadly ellipsoid, 5-9 x 2.5-4 µm; **Pycnidia:** laminal or marginal, immersed or emergent sessile; **conidia:** citriform, 6-7.5 x 1 µm; **Spot tests:** cortex and medulla K-, C-, KC- and P-; **Secondary metabolites:** lichesterinic and protolichesterinic acids.

Substrate: on soil and moss, or rarely on bark or wood; **World distribution:** occurring in temperate/boreal areas of western North America from low altitudes to alpine areas and at high altitudes; **Sonoran distribution:** limited to upper subapline and alpine areas of Arizona.

Notes: *Cetraria ericetorum* is distinguished from *C. islandica* (incorrectly reported from Arizona by Imshaug, [1957] and Nash and Johnson [1975]) by having a consistently P- medulla, and by the pseudocyphellae being strictly marginal and sometimes indistinct or absent. *Cetraria ericetorum* ssp. *reticulata* belongs within the *C. ericetorum* complex comprising three mainly geographical races. Subspecies. *reticulata* basically comprises the subspecies occurring in North America. The closest allied species to *C. ericetorum* is presumably *C. arenaria*, centered around the Great Lakes and extending towards northeastern North America, from which it differs in more narrow lobes, more blunt marginal projections and having a more alpine habitat ecology.

CETRELIA

by B. D. Ryan and T. H. Nash III

Cetrelia W. L. Culb. & C. F. Culb., Contrib. U.S. Nat. Herb. 34: 490 (1968).

Family: Parmeliaceae; Type: *Cetrelia cetrarioides* (Del. *ex* Duby) W. L. Culb. & C. F. Culb.; No. species: 15 world-wide; Selected lit.: Culberson and Culberson (1968).

Life habit: lichenised; **Thallus:** foliose, dorsiventral, heteromerous, large (5-25 cm diam.), spreading, loosely attached; **lobes:** subirregular, 0.5-2.5 cm broad, rounded; without marginal cilia; **upper surface:** ashy white to gray or tan, with small, punctiform pseudocyphellae, isidiate or sorediate; **upper cortex:** prosoplectenchymatous [paraplectenchymatous according to Elix (1993)], with a non-pored epicortex, 10-30 µm thick; **medulla:** white, loose; cell walls: containing isolichenan, I-; **photobiont:** primary one a *Trebouxia*, secondary photobiont absent; **lower surface:** black, shiny, corticate, sometimes punctate, rhizinate; rhizines: simple; **Ascomata:** apothecial, laminal, occasionally marginal, 0.5-4 mm diam., round, stipitate, submarginal, usually perforate; thalline exciple: persistent; hymenium: colorless; paraphyses: unbranched or little branched; hypothecium: hyaline; **asci:** cylindrical, *Parmelia*-type, unitunicate, thick-walled, I+ blue, tholus I+ blue, 8-spored; **ascospores:** ellipsoid, simple, hyaline, 11-22 (-25) x 6-12 µm; **Pycnidia:** marginal, immersed; **conidia:** simple, colorless, 5 x 1 µm; **Secondary metabolites:** upper cortex with atranorin and chloroatranorin, medulla with a range of orcinol depsides and depsidones; **Geography:** temperate to tropical; one species boreal-arctic; **Substrate:** on bark or wood, less frequently rocks.

Notes: It is characterized by punctiform pseudocyphellae on upper surface, perforate apothecia with large, ellipsoid spores, and bifusiform conidia. It is closely related to *Platismatia*; distinguished from that genus (at least from *P. glauca*) by having distinct pseudocyphellae, ± continuously rounded margins, the I- medulla and distinctive medullary chemistry. It may also be mistaken for *Parmotrema* species, but they lack pseudocyphellae.

The Species

Cetrelia olivetorum (Nyl.) W. L Culb. & C. F. Culb., Contrib. U.S. Nat. Herb. 34: 515 (1968).

Basionym: *Parmelia olivetorum* Nyl., Not. Sällsk Fauna Fl. Fenn. Förhandl. 5: 180 (1866); Synonyms: see Culberson and Culberson (1968); Illustrations: Brodo et al. (2001), p. 221; Culberson and Culberson (1968), plate 52; Hale (1979), p. 57.

Thallus: loosely attached, 6-20 cm broad, forming wavy, wide-spreading patches; **lobes:** broad and rotund, 0.5-1 (-2) cm wide; margins wavy, crisped, raised; **upper surface:** greenish mineral gray (glaucous gray, sometimes tinged brown), pseudocyphellate with small pores (up to 0.5 mm wide); **soredia:** farinose, primarily along margins of lobes; without isidia; **lower surface:** black, often with brown, rhizine-free zone towards the margin, somewhat wrinkled; rhizines: scattered, simple, black; **Apothecia:** rare, 1-7 mm in diam.; hymenium: 60-110 µm tall; **ascospores:** ellipsoid, 12-15 x 7-10 µm; **Pycnidia:** unknown; **Spot tests:** upper cortex K+ yellow, C-, KC- and P+ yellow; medulla K-, C+ red, KC+ red, P-, UV+ white; **Secondary metabolites:** upper cortex with atranorin and chloroatranorin; medulla with olivetoric acid.

Substrate and ecology: amongst mosses on broad-leaved trees, or less frequently rocks, in well-lit, but moist or boggy, sheltered, often long-established, woodlands and *Salix*; **World distribution:** temperate and montane forests of the Northern Hemisphere, particularly in eastern North America, western Europe and eastern Asia; **Sonoran distribution:** only reported for southern California [Hasse (1913), as *Parmelia olivetorum* determined by Nylander].

Notes: The species may be extinct now as it was not found by Ross (1982) and was not recognized by Culberson and Culberson (1968) as occurring in southern California. The spot test reactions given by Hasse do, however, fit the species.

CHROMATOCHLAMYS

by H. Mayrhofer

Chromatochlamys Trevis., Conspectus Verrucarinarum 7 (1860).

Family: Thelenellaceae; Type: *Chromatochlamys muscicola* (Ach. *ex* Nyl.) Trevis. = *Chromatochlamys muscorum* (Fr.) H. Mayrhofer & Poelt; No. species: two worldwide; Selected lit.: Mayrhofer and Poelt (1985), Mayrhofer (1987a) and Harris (1995).

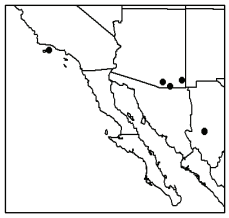
Life habit: lichenized; **Thallus:** crustose, verrucose, attached by the whole lower surface; **upper surface:** dirty whitish or pale gray to pale brownish, membranous to cracked; soredia and isidia absent; **photobiont:** primary one a chlorococcoid alga, secondary photobiont absent; **Ascomata:** perithecial, ± immersed, thick walled, pale to brownish; exciple: globose, colorless to brown; hamathecium: composed of persistent paraphyses, delicate, branched and/or anastomosed, especially towards the base and at the apices; conglutinate periphysoids towards the inner side of the ostiole; **asci:** bitunicate with fissitunicate dehiscence, thick-walled, with non-amyloid tholus; apex rounded with an obvious ocular chamber, 2 (-8)-spored; **ascospores:** submuriform to strongly muriform, cylindrical-ellipsoid or fusiform-elongate, the outer wall scarcely thicker than the septa, colorless to pale brownish; **Conidiomata**: not seen; **Secondary metabolites:** none detected; **Geography:** predominately (sub)mediterranean to cool temperate and boreal; **Substrate:** encrusting mosses or on non-calciferous rocks.

The Species

Chromatochlamys muscorum (Fr.) H. Mayrhofer & Poelt, Herzogia 7: 28 (1985) var. **muscorum**

Basionym: *Verrucaria muscorum* Fr., Systema 287 (18 25); Synonyms: *Chromatochlamys muscicola* (Ach. *ex* Nyl.) Trevis., *Microglena muscicola* Lönnr., *Microglaena leucothelioides* (Vain.) Zahlbr., *Microglaena lesdainii* (Harm.) Zahlbr.; Illustrations: Mayrhofer and Poelt (1985), pp. 32 & 77; Mayrhofer (1987a), p. 71.

Thallus: effuse, often mixed with scattered pale granules; **upper surface:** whitish or pale brown, membranous; **prothallus**: absent; **Perithecia:** immersed, amongst moss leaves and stems with only ostioles obvious, dispersed, rounded to broadly pyriform; exciple: colorless becoming brownish above, pale or colorless below, 50-70 µm thick; **asci:** cylindrical, 2- to 4-spored; **ascospores:** colorless, becoming straw-colored or brownish when old, muriform, elongate-ellipsoid or subcylindrical, 60-110 x 20-27 µm; **Pycnidia:** not seen; **Spot tests:** all negative; **Secondary metabolites:** none detected.



Substrate and ecology: encrusting mosses in montane habitats; **World distribution:** Europe, northern Africa, Canary Islands and North America; **Sonoran distribution:** Arizona, southern California and Chihuahua.

Notes: This species is characterized by its thin thallus, its very thick-walled asci with an ocular chamber and fissitunicate dehiscence, its muriform ascospores, its persistent, branched-anastomosed paraphysoids and the presence of periphysoids.

CLADONIA

by T. Ahti and S. Hammer

Cladonia P. Browne, Civ. Nat. Hist. Jamaica 81 (1756), nom. cons.

Family: Cladoniaceae; Type: *Cladonia subulata* (L.) F.H. Wigg.; No. species: *c.* 450 species world-wide, 42 in the study area; Selected lit.: Ahti (1993 & 2000), Goward (1999), Hammer (1995), Thomson (1967 & 1984), Vainio (1887, 1894 & 1897).

Life habit: lichenized; **Thallus:** composed of primary (basal, horizontal) and secondary (erect) parts; **cortex:** dense, composed of ± vertically-oriented hyphae; **medulla:** usually 2-layered; the outer layer: white, composed of ± loose hyphae, containing algal glomerules; the inner layer: hyaline or white, cartilaginous, with conglutinate hyphae surrounding the central canal; **Primary thallus:** composed of basal squamules, closely adpressed to the substrate, or ascending to erect, rounded to elongate, entire or variously indented, sorediate or esorediate, sometimes persistent, occasionally dominant; **upper surface:** corticated; **lower surface:** composed of ecorticate layer of hyphae, hyphae roughly parallel-oriented, radiating in a flabelliform pattern from the basal portio, which is generally attached to the substrate; **Secondary thallus:** consisting of hollow to rarely solid podetia, growing from upper surface or margins of primary thallus, blunt, pointed, or cup-forming, simple or branched; branch axils: closed or perforate; perforations: occasionally enlarging (forming funnel-like structures often called “open cups”) and deforming; **surface:** variably corticate to ecorticate, generally composed of some combination of continuous cortex, cortical granules, verruculae, soredia, and squamules; **photobiont:** primary one a *Trebouxia*, secondary photobiont absent; **Ascomata:** lecideine apothecia, borne at apices of podetia, on cup rims, at branch apices, or rarely sessile on basal squamules; discs: red, pale or dark brown, darkening with age and sometimes blackening; **asci:** cylindrical to elongate-clavate; apex: *Porpidia* type, with strongly amyloid (I+ blue) apical dome, including very narrow weakly amyloid central zone surrounded by a tube-like, strongly amyloid zone; wall: nonamyloid except for outer layer; 8-spored; **ascospores:** biseriate, ellipsoid to oblong-ellipsoid, simple to rarely one-septate, hyaline, oblong or ovoid, 6-16 (-24) x 2-6 µm; **Conidiomata:** pycnidial, borne at apices of podetia, on cup rims, at branch apices, or on basal squamules, in-

frequently arising laterally on podetia, red, brown or carbonaceous to blue-black, cylindrical to urn-like (ampullaceous), short-stalked or sessile, often constricted at base; containing hyaline or red gelatin; **conidia:** sickle-shaped, rarely straight, hyaline, 3-10 (-14) x 0.5-1 µm; **Secondary metabolites**: depsides, depsidones, dibenzofurans and derivatives (incl. usnic acids), terpenoids, aliphatic acids, and quinone pigments; **Geography:** arctic regions to Antarctica, tundra to tropical forests but widely absent from arid regions; **Substrate:** on soil, especially acidic humus and sand, rotting wood, tree bases and trunks, mossy or bare rocks.

Notes: Lichens of the genus *Cladonia* occur on a variety of terricolous substrata in periodically damp, semi-exposed habitats. They are relatively common in most temperate ecosystems, while in the Sonoran Desert region they are restricted to habitats that provide adequate moisture and protection from extreme exposure. In general, *Cladonia* lichens require an organic substrate in order to establish. One challenge with *Cladonia* is that the morphology of most of the species is quite variable. Therefore characters of secondary chemistry are often useful, but even then many species are difficult to identify and the taxonomy of several groups is still problematic. The Mexican species were generally included in the monograph of Neotropical species by Ahti (2000), but several additions to the Mexican flora are made here. Some of them were indicated before in a supplement in Ahti (2000: 348) or in Ryan et al. (2000). Most of the species of California and Arizona are also keyed and discussed in treatments by Hale and Cole (1988), Hammer (1991, 1995 & 1996), McCune and Goward (1995), McCune and Geiser (1997), and Goward (1999).

In the descriptions below only the major secondary metabolites are listed. For instance, with fumarprotocetraric acid there are always (in *Cladonia*) trace amounts of protocetraric and confumarprotocetraric acids, and often convirensic acid as well as other satellite compounds, which may be visible in TLC analyses but are not indicated here. Similarly, barbatic acid is accompanied with 4-*O*-demethylbarbatic acid, thamnolic acid with decarboxythamnolic acid, and psoromic acid with 2'-*O*-demethylpsoromic acid. In addition to the species treated herein, there is an unidentified, apparently undescribed species of *Cladonia* collected in the state of Sonora, Mexico (the only species known from Sonora!), but due to insufficient material (in MIN; only large primary squamules, veined below) it is not treated.

Key to the species of ***Cladonia*** from the Sonoran region:

1. Thallus P+ red or yellow; containing fumarprotocetraric, norstictic, psoromic or thamnolic acids 13
1. Thallus P-; no reactive acids 2

2. Podetia cup-forming; always yellowish (contains pigment usnic acid) 3
2. Podetia not cup-forming (or with cup-like funnels); gray, green or brown, rarely yellow 8

3. Apothecia, if present, pale brown; podetia totally sorediate, cups broad (see also *C. bacilliformis*, which may rarely form narrow cups) ..... ***C. carneola***
3. Apothecia, if present, red 4

4. Podetia UV+ white (at least when scratched) ..... ***C. sulphurina***
4. Podetia UV- 5

5. Podetia esorediate, short (to 15 mm); containing barbatic acid or zeorin 6
5. Podetia sorediate in upper parts, often tall (over 15 mm); containing zeorin (needle-shaped crystals deposited on surface) 7

6. Containing barbatic acid (no needle crystals on surface); cortex with flat, smooth areolae, rather continuous towards the base ..... ***C. borealis***
6. Containing zeorin (in older specimens needle crystals deposited on surface); surface rough, with bullate-granulose areolae ..... ***C. coccifera***

7. Podetia 15-60 mm tall; soredia farinose ..... ***C. deformis***
7. Podetia 5-20 mm tall; soredia granulose .... ***C. pleurota***

8. Podetia sorediate 9
8. Podetia esorediate 11

9. Podetia UV-; unbranched or axils closed 10
9. Podetia UV+ white; axils perforated ..... ***C. cenotea***

10. Podetia white to gray (no usnic acid); apothecia, if present, red ***C. macilenta*** (barbatic acid chemotype)
10. Podetia yellowish (with usnic acid); apothecia, if present, pale brown ..... ***C. bacilliformis***

11. Podetia with abundant squamules 12
11. Podetia esquamose or barely squamulose 27

12. Podetia tiny, to 10 mm tall; with red apothecia; squamules very small, in part granulose; UV- (barbatic acid) ..... ***C. didyma***
12. Podetia taller, 20-80 mm; with brown apothecia; squamules to 5 mm long; UV+ white (squamatic acid) ..... ***C. squamosa***

13. P+ orange-yellow (thamnolic acid), slowly red (norstictic acid) or deep golden yellow (psoromic acid) 14
13. P+ instantly orange red to brick red (fumarprotocetraric acid) 19

14. Podetia at least partially sorediate 15
14. Podetia esorediate (if richly squamulose, go to couplet 11 – as thamnolic acid chemotype of *C. squamosa*) 16

15. Podetia farinose sorediate; apothecia red; P+ yellow ... . ***C. macilenta*** (thamnolic acid chemotype)
15. Podetia granulose sorediate; apothecia brown; P+ slowly red (norstictic acid) ..... ***C. acuminata***

16. Podetia with "shredded" appearance, i.e., longitudinally cracked, glaucous to pale gray; apothecia brown, constantly present on podetia 17
16. Podetia without "shredded" appearance; not glaucous; apothecia red or brown, not constantly present 18

17. Primary squamules small (to 4 mm long); podetia slender; slightly branched; cortex checkered; P- or pale yellow or reddish ..... ***C. cariosa***
17. Primary squamules large (to 10 mm); podetia stout, almost unbranched; cortex not checkered; P+ deep yellow (psoromic acid) ..... ***C. symphycarpia***

18. Podetia 10-20 mm tall, mostly corticate; primary squamules 1-2 mm long, esorediate; apothecia red, usually present; usually on soil ..... ***C. jaliscana***
18. Podetia 1-8 mm tall, mostly ecorticate; primary squamules tiny, granulose sorediate; apothecia rarely present, brown; on wood ..... ***C. parasitica***

19. Podetia almost completely corticate, without soredia or granules 20
19. Podetia corticate or not, sorediate or granulose 27

20. Podetia not cup-forming 21
20. Podetia cup-forming 23

21. Podetia short (to 10 mm), furrowed and verruculose; unbranched or with short apical branchlets; always with apothecia ..... ***C. peziziformis***
21. Podetia tall (to 100 mm), smooth; with long branches; often sterile 22

22. Cross-section of apical branchlets round; never cup-bearing; coastal ..... ***C. furcata***
22. Cross-section of apical branchlets flattened; often with some cups; inland areas ..... ***C. multiformis***

23. Cups with tiers of proliferations arising along margin, central proliferations very rare 24
23. Cups with tiers of proliferations from center of cup, marginal proliferations rare 25

24. Sieve-like perforations present in interiors of cups .. .. ***C. multiformis***
24. Cups not perforated ..... ***C. gracilis*** subsp. ***turbinata***

25. Primary squamules persistent, large (to 20 mm long), glaucous gray; K+ yellow (atranorin present) 26
25. Primary squamules persistent or evanescent, smaller (to 10 mm), hardly glaucous gray; K- (atranorin normally absent) ..... ***C. cervicornis*** subsp. ***cervicornis***

26. Primary squamules with conspicuous raised bumps on upper surface ..... ***C. macrophyllodes*** (compare to *C. symphycarpia*, which never has a rapid P+ red reaction)
26. Primary squamules without conspicuous bumps .... ***C. firma***

27. Podetia corticate, verruculose to granulose but hardly clearly finely sorediate 28
27. Podetia clearly finely sorediate, at least in part 39

28. Podetia stout, short, cup width generally equal to or greater than height of supporting stalk 29
28. Podetia slender, cups (if present) generally narrower than height of supporting stalk 34

29. Primary thallus thick, adnate, glossy, forming continuous cover over substrate; inside and below chalky white; podetia often scarce ..... ***C. pocillum***
29. Primary thallus usually ascending, squamules thinner, hardly glossy; rarely chalky white inside and below 30

30. Cortex of podetia primarily areolate-corticate or somewhat granulose and schizidiate 31
30. Cortex of podetia primarily granulose (especially in cups and on outer surface of cups), easily disintegrating 32

31. Apothecia on short stalks at cup margins; podetia usually brownish in part ..... ***C. pyxidata***
31. Apothecia on long (to 20 mm), longitudinally fissured proliferations from cup margins; podetia whitish gray ..... ***C. dimorpha***

32. Cortex granulose, not abundantly schizidiate; podetia usually brownish, somewhat elongated; usually in mountains ..... ***C. chlorophaea***
32. Cortex usually densely granulose to schizidiate, schizidia often pillow-like; podetia shortish, pale green to gray; coastal 33

33. Primary squamules to 4 mm long; cups subregular, margins shortly dentate; surface densely granulose to schizidiate, smoothly corticate at very base; containing fumarprotocetraric acid only; common in S. California ..... ***C. hammeri***
33. Primary squamules large, to 12 mm long; cups usually irregular, much proliferating from margins; surface schizidiate but not densely (except in cups), with little cortex at base; containing atranorin, bourgeanic acid and fumarprotocetraric acid; not common ***C. pulvinella***

34. Podetia never cup-forming; inner medulla very hard cartilaginous 35
34. Podetia cup-forming, at least in part; medulla not very hard 36

35. Podetia 20-80 mm tall; branched; mostly corticate, granulose and ecorticate at apical parts, otherwise densely squamulose ..... ***C. scabriuscula***
35. Podetia 5-15 mm tall; almost unbranched; mostly ecorticate, granulose, scarcely squamulose ..... ***C. cartilaginea***

36. Podetia forming wide (to 15 mm) cups (very rarely some podetia cupless) ..... ***C. subsquamosa***
36. Podetia cupless or cups narrow (to 3 mm) 37

37. Podetia tall (to 120 mm); cups usually present, with occasional central proliferations; outer surface granulose and verruculose ..... ***C. verruculosa***
37. Podetia shorter (to 50 mm); often cupless, without central proliferations; outer surface clearly sorediate to granulose 38

38. Podetia thin; finely sorediate, with isidioid soredia toward the base; ecorticate areas exposing translucent outer medulla; K- (no atranorin) ..... ***C. subradiata***
38. Podetia stoutish; coarsely granulose; ecorticate areas exposing arachnoid, opaque medulla; K+ yellow (atranorin) ..... ***C. mexicana***

39. Podetia stout; cup width generally equal to or greater than height of supporting stalk 40
39. Podetia slender; cups (if present) generally narrower than height of supporting stalk 42

40. Podetia brownish; primary thallus evanescent; rangiformic or lichesterinic acid complexes present in addition to fumarprotocetraric acid ..... ***C. asahinae***
40. Podetia gray; primary squamules abundant, persistent; without rangiformic and lichesterinic acids . 41

41. Basal surface of podetia smoothly corticate, sometimes up to the rim of cups; upper part, at least the interior of cups, very finely sorediate; containing fumarprotocetraric acid and additionally either atranorin or bourgeanic acid ..... ***C. humilis***
41. Basal surface of podetia essentially ecorticate; almost totally sorediate, soredia coarser; containing only fumarprotocetraric acid ..... ***C. nashii***

42. Podetia brownish; constantly with broad cups; soredia coarsely farinose; with rangiformic or lichesterinic acid complex in addition to fumarprotocetraric acid ..... ***C. asahinae***
42. Podetia never brownish; cups present or absent, often narrow; soredia mostly finely farinose; with fumarprotocetraric acid only 43

43. Cups present, at least in some podetia 44
43. Cups absent, tips of podetia subulate 48

44. Podetia stoutish; cups wide (to 6 mm), constant, finely sorediate; stalks usually mostly ecorticate, sorediate ..... ***C. fimbriata***
44. Podetia slender; cups narrow (to 3 mm), often absent; bases of podetia corticate or not 45

45. Podetia basally corticate up to 1/3 of their length; higher up sorediate, with corticate patches, even in interior of cups (if present) ..... ***C. ochrochlora***
45. Stalks of podetia ecorticate or very shortly corticate; cortex not in patches higher up 46

46. Podetia essentially sorediate, ecorticate throughout, occasionally with corticoid areas near base; often with some lateral branchlets ..... ***C. subulata***
46. Podetia with a short corticate sheath at base, otherwise sorediate; no lateral branchlets 47

47. Podetia whitish; cups usually present, to 2.8 mm wide; soredia with some granular bodies; almost no cortex at base; growing on soil ..... ***C. subfimbriata***
47. Podetia green to gray; cups rarely present, to 1 mm; soredia without granules; usually some cortex at base; usually on wood, especially coniferous ***C. coniocraea***

48. Podetia ecorticate, totally sorediate (or occasionally slightly corticate near base), usually with some lateral branchlets ..... ***C. subulata***
48. Podetia with distinct corticate sheath at base, distal part sorediate, not branching 49

49. Cortical sheath extending up to 1/3 or more of podetial length, patches of cortex present even higher up; podetia somewhat robust, appearing whitish-gray ..... ***C. ochrochlora***
49. Cortical sheath very short, no cortical patches higher up; podetia thin, appearing greenish-gray ..... ***C. coniocraea***

The Species

Cladonia acuminata (Ach.) Nyl., in Norrlin and Nylander, Herb. Lich. Fenniae No. 57a (1875).

Basionym: *Cenomyce pityrea* f. *acuminata* Ach., Syn. Lich. 254 (1814); Synonyms: *Cladonia norrlinii* Vain., nom. illeg.; Illustrations: Thomson (1967), pl. 8: 43-44 and Thomson (1984), pp. 105 & 152 (as *Cladonia norrlinii*).

Primary thallus: squamulose, persistent, sinuate to crenate-edged, narrowly lobed, becoming involute-concave, ascending; squmules: 2-5 mm long and 0.3-2 mm wide, esorediate or sparsely granulose-sorediate on the margins and underside; **podetia:** simple or fastigiately branched toward apices; sterile branches: blunt; fertile branches: ± dilated, 15-45 mm tall, up to 3 mm wide, cupless; **surface:** basally verruculose, areolate to squamulose; podetial squamules: similar to primary squamules, narrowly lobed; upper surface of podetia: decorticate and subfarinose to granular sorediate; **Apothecia:** dark brown to reddish-brown, up to 3 mm diam, perforate, lobate, or conglomerate, bulging over edge of the podetia; **ascospores:** oblong, 10-16 x 3 µm; **Pycnidia**: on basal squamules or at tips of podetia, urn-shaped to ovoid, constricted at base, containing hyaline gelatin; **conidia:** 5-8 x 0.5 µm; **Spot tests:** K+ yellow, C-, KC-, P+ orange, UV-; **Secondary metabolites:** atranorin, norstictic acid (major), connorstictic acid (minor or accessory); elsewhere chemistry more variable (Ahti 2000), often including psoromic acid.

Habitat and ecology: on mineral to humus-rich soil, preferably calcareous, and on thin soil over rocks; **World distribution:** Asia, Europe, North America and South America, mainly in the boreal forest region; **Sonoran distribution:** central Arizona (Gila Co.).

Notes: This species is expected to occur on base-rich soils in higher elevations in the mountains.

Cladonia asahinae J. W. Thomson, J. Jap. Bot. 51: 361 (1976 ['1977']).

Illustrations: Brodo et al. (2001), p. 238; Thomson (1976), p. 361; Krog et al. (1994), p. 147.

Primary thallus: squamulose, persistent or disappearing, glaucescent green or glaucescent blue-green to olivaceous or brown above, often pruinose along margins; squamules: 2-3 mm long, 1-2 mm wide, esorediate or with granular soredia beneath margins; **podetia:** produced from upper side of primary squamules, borne singly or with several podetia emerging from one squamule, cup-forming, 5-35 mm tall; cups: 3-8 mm wide, flaring abruptly; **surface:** farinose to granularly sorediate; soredia: giving rise to isidioid-flattened squamules toward bases; **Apothecia:** on margins of cups, 1-4 mm wide,

brown; **ascospores:** not observed; **Pycnidia:** at cup margins, pyriform, constricted at base, with hyaline gelatin; **conidia:** not observed; **Spot tests:** K- or K+ dingy yellowish, changing to brownish, C-, KC-, P+ red, UV-; **Secondary metabolites**: fumarprotocetraric, rangiformic and/or norrangiformic acids (north of the Sonoran area chemotypes with lichesterinic and/or protolichesterinic acid or fumarprotocetraric acid alone are also known).

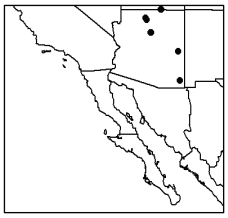
Habitat and ecology: on twigs, rotting stumps, tree bases, thin soil, and sometimes over sand dunes, generally at lower elevations, mainly occurring in temperate, oceanic habitats; **World distribution:** Asia (Ural Mountains), Europe, North America (west) and South America (southern portion) and Antarctica; **Sonoran distribution:** southern California; reported from Los Angeles and Santa Barbara Counties by Hammer (1995).

Notes: *Cladonia asahinae* is generally included in the so-called *C. chlorophaea* complex and is characterized by presence of aliphatic acids (rangiformic or lichesterinic acid complexes, both identified with TLC if concentrations are sufficient [Culberson et al. 1986; Hennings 1983; Holien and Tønsberg 1985]). The lichesterinic acid chemotype is more frequent in California (Hammer 1995). Brodo and Ahti (1997) included some material without these acids, relying on morphology alone. Hennings (1983) and Hammer (1995) suggested that the chemotypes may sometimes be distinguishable by morphology or thallus color. This species is very common on the coast of Pacific Northwest, where one can learn to recognize it with some difficulty by its brownish, broadly cupped podetia, that are finely to coarsely sorediate or granulose and that tend to have toothed cup rims. However, *C. asahinae* is still a very poorly known and much overlooked species.

Cladonia bacilliformis (Nyl.) Glück, Verh. Naturhist.-Med. Vereins Heidelberg, ser. 2, 6:97 (1899).

Basionym: *Cladonia carneola* var. *bacilliformis* Nyl., Syn. Meth. Lich. 1: 201 (1860); Illustrations: Thomson (1967), pl. 5: 28 and Thomson (1984), p. 112.

Primary thallus: squamulose, persistent; squamules: 0.2-0.3 mm wide, up to 3 mm long, entire to crenate-lobate, yellowish above, sorediate; **podetia:** up to 20 (-25) mm tall, usually shorter, conspicuously yellow-green, unbranched, without cups or with age forming very narrow cups, occasionally with proliferations arising from cup margins; **surface:** sorediate; soredia: farinose, at base only slightly corticate; **Apothecia:** infrequent, 0.5-1 mm wide, pale brown; **ascospores:** fusiform, 9-12 x 2.5-4 µm; **Pycnidia:** on primary squamules or at tips of podetia, ovoid to cylindrical, containing hyaline gelatin; **conidia:** 5-6 x 0.5 µm**; Spot tests:** K-, C-, KC+ yellow P-, UV-; **Secondary metabolites:** usnic and barbatic acid.



Habitat and ecology: on rotting pine wood in open woodlands, mainly in boreal habitats; **World distribution:** Asia, Europe, North America and southern South America; **Sonoran distribution:** Arizona.

Notes: This is species is similar to *C. coniocraea* and *C. macilenta* in structure but has a bright yellow green color (usnic acid is abundant) and the soredia are plentiful down to the base of podetia.

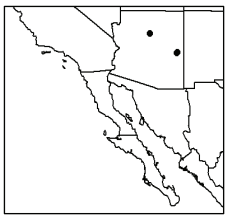
Cladonia borealis S. Stenroos, Ann. Bot. Fenn. 26: 160 (1989).

Illustrations: Brodo et al. (2001), p. 241; Kershaw et al. (1998), p. 350; Vitt et al. (1988), p. 201 (as *C. coccifera*); Wirth (1995), p. 299.

Primary thallus: squamulose, persistent; squamules: 4-5 mm long, 2-3 mm wide, crenate-lobate, upturned or involute, with dying bases ochraceous; **podetia:** 10-40 mm tall, yellowish green, cup-bearing; cups: up to 1 cm wide, regular to slightly asymmetrical; margins: entire; **surface:** mostly corticate, esorediate, not granulose but occasionally squamulose; **cortex:** continuous to chinky-areolate, often appearing as rough scales on the podetia; **Apothecia:** common, up to 6 mm wide, red; **ascospores:** fusiform, 9-10 x 3 µm; **Pycnidia:** common, on cup margins, ovoid to conical, at base constricted or not, with red gelatin; **co-**

nidia: 6-8 x 1 µm; **Spot tests:** K-, KC+ yellow, P-, UV- (or UV+ weak bluish-white); **Secondary metabolites:** thallus with barbatic and usnic acids; apothecial discs with rhodocladonic acid as a red pigment.

Habitat and ecology: on mossy boulders and rocks (including lava) and thin acidic soils in well-lighted habitats at high elevations, mainly arctic to boreal; **World distribution:** Antarctica, Asia, Europe, North America and South America; **Sonoran distribution:** Arizona at high elevations.



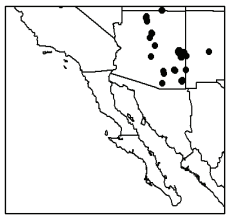
Notes: Stenroos (1989a & b) segregated *C. borealis* from *C. coccifera* on the basis of secondary chemistry and subtle morphological differences. The primary squamules of the material studied here were evanescent rather than persistent, and the podetia were shorter than in Stenroos's description. Some specimens with the chemistry of *C. borealis* (barbatic and usnic acids) approach *C. coccifera* (zeorin and usnic acid), which is very rare in the Sonoran region. The podetia of *C. borealis* are esorediate, unbranched, cup-forming, with scarlet apothecia on the margins of the cups. Partially corticate specimens of *C. pleurota* may be confused with *C. borealis*, but *C. pleurota* is always sorediate.

Cladonia cariosa (Ach.) Spreng., Syst. Veg. 4(1): 272 (1827).

Basionym: *Lichen cariosus* Ach., Lichenogr. Suec. Prodr. 198. (1799, ['1798']); Illustrations: Brodo et al. (2001), p. 243; Corbridge and Weber (1998), p. 13; Kershaw et al. (1998), p. 348; McCune and Geiser (1997), p. 79; St. Clair (1999), p. 57.

Primary thallus: squamulose, persistent; squamules: 1-4 mm long, 1-2 mm wide, crenulately lobate along margins, greenish-gray with bluish tinge, sometimes with pruina toward lobe tips; **podetia:** 5-35 mm tall, up to 8 mm wide, branched, twisted from the base upward, fissured longitudinally along the length; branches: anastomosing, without cups; **surface:** mostly corticated; cortex: continuous or breaking up and disappearing in places, esorediate; **Apothecia:** constantly present from early stages, chestnut brown to darker, larger than podetial support, solitary; **ascospores:** ellipsoid, 10.5-18 x 3.5-5.5 µm; **Pycnidia:** uncommon, on primary squamules or on tiny appressed podetial squamules, obconical, with hyaline jelly; **conidia:** 0.5-1 x 3-4 µm; **Spot tests:** K+ yellowish changing to dingy brown or K+ persistent yellow, C-, KC-, P+ deep yellow, rarely changing to red, or P-, UV-; **Secondary metabolites:** atranorin only or with additional fumarprotocetraric acid (as minor substance).

Habitat and ecology: on thin soil and roadcuts, usually in damp microhabitats; **World distribution:** Asia, Europe, North America and South America (south), mainly temperate, western North America; **Sonoran distribution:** common in Arizona at mid to high elevations.



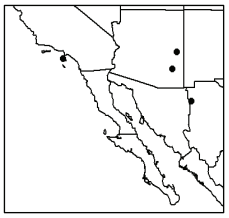
Notes: *Cladonia cariosa* is easily recognized by its fertile, gray, slender, cupless podetia and smallish squamules. When the squamules are larger, it can be difficult to distinguish from *C. symphycarpia*.

Cladonia carneola (Fr.) Fr., Lichenogr. Eur. Reform. 233 (1831).

Basionym: *Cenomyce carneola* Fr., Sched. Crit. Fl. Suec. 1-4: 23 (1825); Illustrations: Brodo et al. (2001), p. 244; McCune and Geiser (1997), p. 80; Thomson (1984), p. 117; Vitt et al. (1988), p. 200.

Primary thallus: squamulose, persistent or evanescent; squamules: 2-3 mm long, 0.5-1 mm wide, deeply, irregularly laciniate; **podetia:** (3-) 5-20 (-50) mm tall, 2-4 mm wide, pale yellow, cup-bearing; cups: 2-9 mm wide, flaring abruptly; margins: dentate; **surface:** corticate at the very base, otherwise farinose sorediate, granulose below cups or on inner surfaces of cups; **Apothecia:** fairly common, 0.5-5 mm wide, pale brown; **ascospores:** fusiform, 12-16.5 x 3.5-5 µm; **Pycnidia:** very common, dark brown to black, conical to cylindrical, blunt to somewhat pointed, with hyaline gelatin; **conidia:** 3-4 x 0.5-1 µm; **Spot tests:** K-, C- (unless barbaric present), KC+

yellow, P-, UV-; **Secondary metabolites:** usnic acid with accessory barbatic and isousnic acids and zeorin.



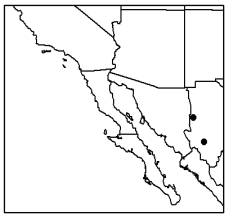
Habitat and ecology: on rotten conifer wood and acidic humus in moist habitats; **World distribution:** Antarctica, Asia, Europe, North America; South America (south), mainly boreal; **Sonoran distribution:** Arizona, Chihuahua and Channel Islands.

Notes: *Cladonia carneola* is widespread in the western United States. The pale yellow color and P- reaction of *C. carneola* distinguish it from other sorediate, cup-bearing species. However, specimens with low concentrations of usnic acid appear greenish rather than pale yellow and may be confused with *C. pleurota*. The pale brown or beige apothecia in *C. carneola* distinguish it from similar species, but the color may be confused with the darker brown apothecia of species such as *C. fimbriata*. One useful, but often overlooked character in *C. carneola* is the regular arrangement of small, usually pointed, black pycnidia along the cup margins. These pycnidia sometimes resemble a corona around the edge of the cup.

Cladonia cartilaginea Müll. Arg., Flora 63: 260 (1880).

Illustration: Ahti (2000), p. 241.

Primary thallus: squamulose, persistent or evanescent; squamules: 1.5-9 mm x 0.5-2 mm, ± laciniate, esorediate; **podetia:** up to 2. 5 cm tall, 0.3-2 mm wide, whitish gray, without cups, unbranched to sparsely dichotomously branched, occasionally richly branched at apices, tips blunt to acute, branches flexuose or recurved; **surface:** decorticate or cortex sparsely verruculose-granulose, or sorediate, occasionally microsquamulose, somewhat striate, very hard inner medulla usually exposed; **Apothecia** rather frequent, 0.3-1.5 mm wide, red brown; **spores:** oblong, 7-13 x 2.5-3.5 µm; **pycnidia**: on primary squamules or at tips of podetia, with hyaline gelatin; **conidia:** 4-8 x 0.5 µm; **Spot tests:** K-, KC-, C- and P+ red; **Secondary metabolites:** fumarprotocetraric acid (chemistry more variable in other areas; Ahti 2000).



Habitat and ecology: on bare mineral soil, especially trail banks, collected at 1340-1800 m in Chihuahua; **World distribution:** North America (Mexico), West Indies and South America, mainly tropical; **Sonoran distribution:** Chihuahua.

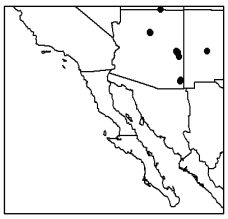
Notes: *Cladonia cartilaginea* is a widespread farther south in Mexico, where it is a short-lived pioneer species of disturbed habitats. It is easily overlooked, or confused with a more common species with simple podetia, *C. subradiata,* in Mexico. It can be recognized by its very hard inner medulla (difficult to cut with a razor blade!), its poor development of soredioid bodies, and the absence of cups.

Cladonia cenotea (Ach.) Schaer., Lich. Helv. Spic. 35 (1823).

Basionym: *Baeomyces cenoteus* Ach., Methodus 345 (1803); Illustrations: Brodo et al. (2001), p. 245; Kershaw et al. (1998), p. 351; McCune and Geiser (1997), p. 81; Thomson (1984), p. 118; Vitt et al. (1988), p. 205; Wirth (1995), pp. 301 & 319.

Primary thallus: squamulose, persistent; squamules: 1-10 mm long, 1-2 mm wide, palmate-lobate, laciniate, with accessory isidioid lobules reiterating and resembling the original squamules; esorediate or granular sorediate beneath margins, sometimes disintegrating into a soredial mass; **podetia:** 13-65 (-80) mm tall, gray to green, irregularly tubular, sparingly to much branched from margins of funnel-like openings, which may give rise to one or more proliferations from margins; **surface:** ecorticate, sorediate from base to apices, with soredia toward base growing into elongate (1-2 mm) sinuate-edged squamules, soredia above these squamules granular to farinose; **Apothecia:** infrequent, 1-3 mm diam, dark brown; **ascospores:** oblong to ellipsoid, (5-) 7-17 x 3-5 µm; **Pycnidia:** at margins of funnel-like openings, cylindrical to

conical, with red gelatin; **conidia:** 3-8 x 0.5-1 µm; **Spot tests:** K-, C-, KC-, P-, UV+ ice blue; **Secondary metabolites:** thallus with squamatic acid (in other regions also thamnolic acid chemotype [P+ yellow] present); apothecia with barbatic acid.



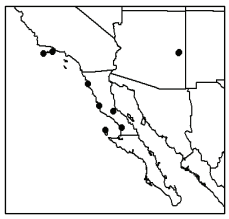
Habitat and ecology: growing in deep shade on rotting stumps or partially buried, rotting wood, usually in north-facing situations; **World distribution:** Africa, Asia, Europe, North America and South America (southern part); **Sonoran distribution:** rare in Arizona.

Notes: This species is distinguishable by the abundant farinose soredia and open axils. The Arizona material is atypical, as it scarcely forms funnel-like axils.

Cladonia cervicornis (Ach.) Flot. subsp. **cervicornis**, Jahresber. Schles. Ges. Vaterl. Cult. 27: 105 (1849).

Basionym: *Lichen cervicornis* Ach., Lichenogr. Suec. Prodr. 184 (1799 ['1798']); Illustration: McCune and Geiser (1997), p. 82 (*Cladonia cervicorrnis* s. lat.).

Primary thallus: squamulose, persistent, forming large cushions; squamules: 3-6 mm long, 2-5 mm wide, entire to irregularly crenate-lobed to irregularly digitate lobed; **podetia:** scarce to common, 14-55 mm tall, greenish gray, cup-bearing; cups: 2-9 mm wide, entire or with blunt to finger-like proliferations along margins, often simple and without proliferations but infrequently bearing one to three tiers of proliferations from center; **surface:** smoothly corticate, squamulose or esquamulose, esorediate, slightly arachnoid in young parts; **Apothecia:** uncommon, up to 3.5 mm diam, dark brown; **ascospores:** narrowly fusiform, 10-16 x 2-3 µm; **Pycnidia:** common, at cup margins, subglobose to ovoid, with hyaline gelatin; **conidia:** 3-4 x 0.5-1 µm; **Spot tests:** K- or K+ dingy yellow changing to brownish, C-, KC-, P+ brick red, UV-; **Secondary metabolites:** fumarprotocetraric acid, occasionally with atranorin.



Habitat and ecology: on soil or over duff; **World distribution:** northern Africa, Asia, Europe and North America; mainly Mediterranean to temperate; **Sonoran distribution:** eastern Arizona, Baja California, and southern California.

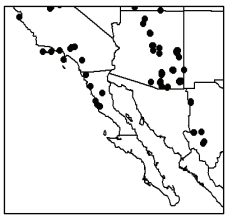
Notes: Persistent primary squamules and usually poorly developed, short podetia distinguish this subspecies from subsp. *verticillata*, which is present further north in western North America (Hammer 1995). Specimens of *C. cervicornis* from California containing atranorin (in Santa Barbara and Amador Counties) were discussed in Hammer and Ahti (1990); their taxonomic status is still uncertain. *Cladonia cervicornis* probably includes more than two taxa in western North America, and is in need of further study. Here *C. cervicornis* is reported as new to Mexico.

Cladonia chlorophaea (Flörke *ex* Sommerf.) Sprengel., Syst. Veg. 4: 273 (1827).

Basionym: *Cenomyce chlorophaea* Flörke *ex* Sommerf., Suppl. Fl. Lapp. 130 (1826); Illustrations: Ahti (2000), p. 101; St. Clair (1999), p. 58; Thomson (1984), p. 119; Vitt et al. (1988), p. 202; Wirth (1995), p. 307 (upper fig.).

Primary thallus: squamulose, persistent or disappearing; squamules: 3-6 mm long, 2-4 mm wide, irregularly crenate-lobate; **podetia:** 2-15 (-45) mm tall, brownish green to gray, stout to more or less slender, cup-bearing; cups: 2-6 mm wide; **surface:** ecorticate, granulose to sorediate, largely bare on old podetia; soredia: coarse, intergrading with granules and isidioid structures, sometimes forming podetial squamules; **Apothecia:** uncommon, 2-4 mm in diam., brown; **ascospores:** oblong, 9-17 x 3.5-4.5 µm; **Pycnidia**: common, ovoid to turbinate, often constricted at base, with hyaline gelatin; **conidia:** 5-9 x 1 µm; **Spot tests:** K- or K+ dingy yellowish-brownish, C-, KC-, P+ red, UV-; **Secondary metabolite:** fumarprotocetraric acid.

Habitat and ecology: on rotten wood, tree trunks, mineral soil or humus; **World distribution:** all continents, mainly temperate to boreal; **Sonoran distribution:** Arizona, southern California, Baja California and Chihuahua.



Notes: This species is very similar to *C. pyxidata*, and especially juvenile or senescent specimens can be impossible to identify with certainty. Some authors are inclined to unite *C. chlorophaea* and *C. pyxidata*, because it is difficult to make a clear-cut distinction between them, even though the presence or absence of "soredia" (actually granules) should distinguish the two. The chem.-ically more variable "*Cladonia grayi* complex " (not present in the Sonoran region) and the "*C. humilis* complex" should be recognized as distinct in any case.

Cladonia coccifera (L.) Willd., Fl. Berol. Prodr. 361 (1787).

Basionym: *Lichen cocciferus* L., Sp. Pl. 1151 (1753); Illustration: Stenroos (1989a), p. 161.

Primary thallus: squamulose, persistent; squamules: 3-10 mm long, 2-5 mm wide, sparsely divided into roundish lobes, glaucescent green above, white or towards the base orange below; margins: esorediate; **podetia:** 7-35 mm tall, stalk 1-2 mm thick, greenish, yellowish or whitish gray, cup-bearing; cups: 4-7 (-15) mm wide, generally symmetrical base, usually single, occasionally prolixferating from the margins (or rarely centers) to form another cup; **surface:** areolate-corticate at the base; fertile podetia: with a fairly continuous cortex that may extend to the cup margins; sterile podetia: with the upper part of podetium densely covered by bullate granules (also inside the cups) and irregular scaly plates (elevated areolae), often in part squamulose, esorediate; surface structures: disintegrating and exposing the medulla; **Apothecia:** infrequent, red, up to 4 mm wide; **ascospores:** fusiform to oblong, 6-12 x 2.5-3.4 µm; **Pycnidia:** on cup margins, common, broadly pyriform, constricted at base, black to red, with red gelatin; **conidia:** 3 x 0.5 µm; **Spot tests:** K-, C- & KC+ yellow, P-, UV-; **Secondary metabolites:** thallus with usnic acid, zeorin (visible as tiny needle crystals on surface of older herbarium specimens), accessory isousnic acid and porphyrilic acid, plus unidentified aliphatic acids; apothecia and pycnidia with rhodocladonic acid.

Habitat and ecology: on humus-rich soils, occasionally on wood, in mountain woodlands; **World distribution:** arctic to temperate regions in Asia, Europe, North and South America (along the Andes); **Sonoran distribution:** Sinaloa/Durango border, very rare.

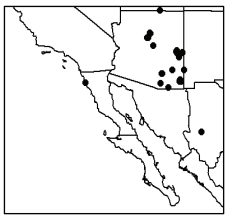
Notes: This species is very similar to *C. pleurota* in morphology and chemistry, but *C. pleurota* is clearly (coarsely) sorediate rather than merely granulose. Fertile specimens of both species may be corticate so that they may be difficult to distinguish. Highly squamulose specimens are also difficult to interpret. See also the discussions under *C. borealis* and *C. pleurota*.

Cladonia coniocraea (Flörke) Spreng., Syst. Veg. 4 (1): 272 (1827).

Basionym: *Cenomyce coniocraea* Flörke, Deutsche Lich. 7: 14. (1821), nom. cons. prop. (ined.); Illustrations: Brodo et al. (2001), p. 247; St. Clair (1999), p. 59; Wirth (1995), p. 303.

Primary thallus: squamulose, persistent; squamules: 3-9 mm long, 2-5 mm wide, deeply laciniate to palmately lobed, sparingly to abundantly sorediate along margins of underside; **podetia:** 8-45 mm tall, 1-2 mm wide, green to gray-green, unbranched or sparingly branched; apices: subulate or bearing very small (up to 2 mm wide), shallow cups; **surface:** ecorticate and sorediate above, lower portions corticate; cortex: thinning or almost lacking, not reaching high up on podetia or to cup interiors; soredia: farinose; **Apothecia:** rare, up to 1.5 mm diam, brown; **ascospores:** ellipsoid, 10-16 x 3-5 µm; **Pycnidia:** inferquent, on tips of podetia, ovoid, with hyaline gelatin; **conidia:** 4-8 x 0.5-1.5 µm; **Spot tests:** K- or K+ dingy yellow to brownish, KC-, C-, P+ orange to brick red, UV-; **Secondary metabolites:** fumarprotocetraric acid complex (the minor satellite convirensic acid probably less frequent than in *C. ochrochlora*).

Habitat and ecology: on rotting wood and tree bases, rarely on bare soil; **World distribution:** Asia, Europe and North America; temperate-boreal; **Sonoran distribution:** Arizona, Baja California, and Chihuahua.



Notes: *Cladonia coniocraea* and *C. ochrochlora* are morphologically very similar, and some authors are inclined to unite them. The present treatment is provisional. The squamules of *C. coniocraea* are always deeply incised, whereas the margins of the squamules of *C. ochrochlora* can be nearly entire. *Cladonia coniocraea* is usually found without cups, but *C. ochrochlora* rarely lacks them completely. The base of the podetium in *C. coniocraea* is only thinly corticate, while the cortex of *C. ochrochlora* is thick, extends beyond the immediate base, and is often longitudinally rugose. The soredia of the present taxon are usually farinose, rarely occurring in small, diffuse soralia; soredia in *C. ochrochlora* are variable, but are usually larger than those of *C. coniocraea*, and often largely occur in well defined, erumpent soralia. The podetia of *C. coniocraea* are greenish rather than gray, fairly slender, usually not more than 1.5 mm diam., and are usually straight. The podetia of *C. ochrochlora* have a grayish tint, are generally thicker, and are often somewhat branched and twisted (Hammer 1993). The nomenclatural status of the names *C. coniocraea* and *C. ochrochlora* is open; their retention requires conservation. Other species easily confused with *C. coniocraea* include *C. norvegica*, *C. bacilliformis*, and *C. macilenta* (barbatic acid chemotype), but they all react P- rather than red. The thamnolic acid chemotype of *C. macilenta* is distingished by a P+ yellow reaction. See also notes under *C. subulata*.

Cladonia deformis (L.) Hoffm., Deutschl. Fl. 2: 120 (1796).

Basionym: *Lichen deformis* L., Sp. Pl. 1152 (1753); Illustrations: Brodo et al. (2001), p. 251; Flenniken (1999), pl. 6 I; Thomson (1984), p. 129; Wirth (1995), p. 301.

Primary thallus: squamulose, persistent; squamules: up to 5 mm long and 3 mm wide, crenulate to crenate-lobate, esorediate, yellowish brown at base; **podetia:** 15-40 mm tall and up to 4 mm wide, yellowish green to gray, dying base orange brown, cup-bearing; cups: 2-4 mm wide, rarely flaring; margin: entire or regularly dentate, sometimes with proliferations; **surface:** with a persistent cortex a quarter to half the length of the podetium, longitudinally rugose to chinky-areolate; cortex: intermixed with soredia and upper 1/3 to 2/3 of podetium totally covered by soredia; soredia: farinose; **Apothecia:** infrequent, up to 5 mm diam, red; **ascospores:** fusiform, 8-10 x 2.5-3.5 µm; **Pycnidia:** scarce, at cup margins, ovoid, with red gelatin; **conidia:** 8-11 x 1 µm; **Spot tests:** K-, C-, KC+ yellow, P-, UV-; **Secondary metabolites:** thallus with usnic acid, isousnic acid and zeorin (visible as needle crystals on old herbarium specimens); apothecial discs with rhodocladonic acid as a red pigment.

Habitat and ecology: on humus or rotting wood; **World distribution:** Antarctica, Australasia, Europe, North America and southern South America; **Sonoran distribution:** upper elevations of eastern Arizona (Apache Co.).

Notes: See discussion under the more frequent *Cladonia sulphurina*, which can be very similar to *C. deformis*.

Cladonia didyma (Fée) Vain., Acta Soc. Fauna Fl. Fenn. 4: 137 (1887).

Basionym: *Scyphophorus didymus* Fée, Essai Crypt. Ecorc. cxviii, ci (1825 [‘1824’]); Synonyms: *Cladonia vulcanica* Zoll. & Moritzi, *Cladonia didyma* var. *vulcanica* (Zoll. & Moritzi) Vain.; Illustrations: Brodo et al. (2001), p. 252; Flenniken (1999), pl. 6J; Ulloa and Herrera (1994), front cover (as *Cladonia ‘crystatella’*).

Primary thallus: squamulose, persistent; squamules: 1-2 x 1-1.5 (4) mm, crenate to irregularly crenulate to lobulate-laciniate, esorediate, with shiny upper side; **podetia:** up to 5 cm tall (usually much shorter), 1.0-1.5 mm wide, green to glaucescent, or brownish, subulate, without cups, unbranched to sparingly branched; **surface:** ecorticate to slightly corticate at base, esorediate (but sometimes granulose in part), microsquamulose; microsquamules: fragile, projecting downward, inner stereome translucent, pale to dark brown; **Apothecia:** fairly common, 0.5-4 mm wide,

red; **ascospores:** fusiform, 10-13 x 5µm; **Pycnidia:** common, turbinate, short-stalked, with red gelatin; **conidia:** falciform, 5-7 x 1 µm; **Spot tests:** K- or K+ yellow, C- & KC- (or C+ & KC+ yellow if barbatic acid present), P- or P+ yellow, UV-; **Secondary metabolites:** thallus with two major chemotypes: (1) didymic and barbatic acids (rarely only one of them) or (2) didymic and thamnolic acids (rarely with accessory barbatic acid) with only the first one known in the Sonoran area; apothecial discs with rhodocladonic acid as a red pigment.

Habitat and ecology: on tree trunks, rotting wood and earth banks, mainly tropical to warm-temperate regions; **World distribution:** Africa, Asia, Australasia, North America and South America; **Sonoran distribution:** only known from one location in the Sierra Madre Occidental region of Sinaloa.

Notes: This species is common further south in Mexico. It is very similar to *C. macilenta* (they may grow together!) but the latter species has farinose soredia, while *C. didyma* has rough microsquamules or granules and is not clearly sorediate. The thamnolic acid chemotype, which is the more frequent one in Mexico (see maps in Ahti [2000], pp. 196-197), was commonly recognized earlier as a distinct species (e.g., Thomson 1967, usually under the name *C. vulcanica.* For more data on the chemical variability of this species see Ahti (2000), p. 195.

Cladonia dimorpha S. Hammer, Mycotaxon 37: 339 (1990).

Illustrations: Ahti (2000), p. 113; Hammer and Ahti (19 90), p. 340.

Primary thallus: squamulose, persistent; squamules: 2-4 x 1-3 mm, subentire to lobed; **podetia:** 5-35 mm tall, ashy white to glaucescent green, cup-forming; cups: 4-10 mm wide, with long (up to 2 cm), slender, branching and anastomosing proliferations from margins; **surface:** mostly smoothly corticate, esorediate, or in part verruculose or squamulose; **Apothecia:** rare, at tips of proliferations, 0.3-3.2 mm diam, dark brown; **ascospores:** oblong to fusiform, 10-16 x 4-5 µm; **Pycnidia:** common, on cup margins, pyriform, constricted at base, short-stalked, with hyaline gelatin; **conidia:** 3-8 x 0.5-1µm; **Spot tests:** K-, C-, KC-, P+ red, UV-; **Secondary metabolite:** fumarprotocetraric acid.

Habitat and ecology: on soil on roadcuts and in sandy areas near coast; **World distribution:** western North America and the West Indies; **Sonoran distribution:** southern California (Santa Barbara Co.).

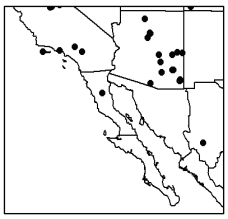
Notes: *Cladonia dimorpha* is similar in habit to *C. pyxidata*, but the cup margins produce long, fissured proliferations that are similar to those of *C. furcata*. When the proliferations are not developed (in juvenile podetia), the species are difficult to separate. However, in the Sonoran region the ranges of the two species probably do not overlap.

Cladonia fimbriata (L.) Fr., Lichenogr. Eur. Reform. 222 (1831).

Basionym: *Lichen fimbriatus* L., Sp. Pl. 1152. (1753); Illustrations: Brodo et al. (2001), p. 254; McCune and Geiser (1997), p. 87; Vitt et al. (1988), p. 202; Wirth (1995), p. 326.

Primary thallus: squamulose, persistent; squamules: up to 6 mm long and 4 mm wide, unevenly dentate to crenate-lobate or sinuate, coarsely sorediate (especially under margins), sometimes breaking into masses of soredia; **podetia:** 6-30 (-40) mm tall, 1-2 mm wide, green to whitish gray, unbranched, with trumpet-shaped cups forming at apices; cups: 2-6 mm wide; margins: entire or minutely dentate; **surface:** ecorticate or persistently corticated at the base (sometimes cortex extending up to cup bases); soredia: abundant, farinose, sometimes enlarging, later disintegrating and exposing the white medulla; **Apothecia:** uncommon, brown, up to 1.5 mm diam; **ascospores:** oblong, 8-14 x 3-4.4 µm; **Pycnidia:** at cup margins, subglobose, with hyaline gelatin; **conidia:** 7-8 x 1.5-2.5 µm; **Spot tests:** K- or K+ dingy yellow to dingy brown, C-, KC-, P+ brick red, UV-; **Secondary metabolite:** fumarprotocetraric acid.

Habitat and ecology: on wood, tree trunks, soil or mosses over rocks, usually in deep shade; mainly temperate-boreal; **World distribution:** on all continents; **Sonoran distribution:** Arizona, southern California, Baja California and Chihuahua.



Notes: This species is widespread in Arizona but rare elsewhere in the Sonoran Region. Earlier reports from southern California belong either to *Cladonia subfimbriata*, which has narrower, dentate cups (sometimes cups are missing) and more elongate, whitish podetia, or *C. nashii*, which has very short podetia with wide cups, like those in *C. humilis* (see discussion under that species). *Cladonia fimbriata* is characterized by the green (grayish when exposed so sun), thick, persistent layer of very fine soredia on podetia. The cups are generally symmetrical and often bear fimbriate proliferations on the margin.

Cladonia firma (Nyl.) Nyl., Bot. Zeitung (Berlin) 19: 352 (1861).

Basionym: *Cladonia alcicornis* var. *firma* Nyl., Syn. Meth. Lich. 1: 191 (1860); Synonym: *Cladonia nylanderi* Cout., nom. illeg. Illustration: Clauzade and Roux (1985), p. 333.

Primary thallus: squamulose, persistent, conspicuous; squamules: up to 25 mm long and 10 mm wide, glaucescent green to olivaceous above, bluish gray below (lobe tips: often white!), clearly thick (about 400 µm), irregularly crenate-lobate; lobe ends: strongly incurved; **podetia:** very rare, up to 15 mm tall, cup-forming; cups: 2-4 mm wide, rarely proliferating from center; **surface:** smoothly corticate to verruculose, esorediate, rarely squamulose, sometimes bearing abundant squamules along cup margins; **Apothecia:** rare, 1-2.5 mm wide, dark brown; **ascospores:** oblong-ellipsoid, 14-17 x 2-4 µm; **Pycnidia** and **conidia:** rare, not observed; **Spot tests:** K+ yellow, C-, KC-, P+ red, UV-; **Secondary metabolites:** atranorin and fumarprotocetraric acid.

Habitat and ecology: on soil, primarily in Mediterranean regions; **World distribution:** Africa, Asia and Europe, western North America; **Sonoran distribution:** not known from the area but occurring in adjacent California.

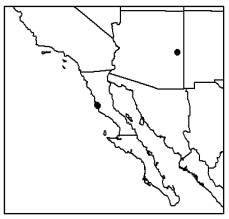
Notes: *Cladonia firma* was discussed and first reported from North America in Hammer (1991). It is restricted to a few localities in San Luis Obispo Co., southern California, where it is locally abundant. It is expected to be more widespread because it is easily overlooked due to its poor production of podetia. It is distinguished by its large, thick squamules, which are green above, bluish below and contain atranorin (K+ yellow). The taxonomic status of the North American *C. firma* is somewhat uncertain.

Cladonia furcata (Huds.) Schrad., Spic. Fl. Germ. 107 (1794).

Basionym: *Lichen furcatus* Hudson, Fl. Angl. 458 (1762); Synonym: *Cladonia herrei* J. Hedrick; Illustrations: Brodo et al. (2001), p. 256; Flenniken (1999), pl. 7 F; McCune and Geiser (1997), p. 88.

Primary thallus: squamulose, usually disappearing; squamules: up to 4 mm long and 3 mm wide, irregularly lobate to crenate-lobate; **podetia:** (8-) 15-80 (-95) mm tall, 0.5-5 mm wide, pale or bluish gray to dark brown, subulate, without cups or, occasionally, forming cup-like axils, dichotomously branched; branches: with longitudinal fissures; axils: open or closed; **surface:** smoothly corticated; cortex: chinky, areolate; squamules: present or absent, up to 3 mm long, esorediate; **Apothecia:** frequent, brown, up to 1.5 mm diam, subglobose, usually clustered at tips of branches; **ascospores:** fusiform to oblong, 5-15 x 3-5 µm; **Pycnidia:** common, at tips of podetia, urn-like, constricted at base, with hyaline gelatin; **conidia:** 3-8 x 0.5-1 µm; **Spot tests:** K- or K+ dingy yellow to dingy brown, C-, KC-, P+ red (test medulla!), UV-; **Secondary metabolites:** fumarprotocetraric acid (in other areas, like in the eastern United States and Hidalgo, Mexico, atranorin may additionally be locally frequent).

Habitat and ecology: on soil or among mosses, or rarely on rotting wood, mainly temperate; **World distribution:** all continents except Antarctica; **Sonoran distribution:** eastern Arizona (high elevation) and Baja California (coastal).



Notes: *Cladonia furcata* in western North America is generally comparable to, but does not exactly match specimens from Europe, eastern North America or South America. Although it is quite variable in the region, specimens of *C. furcata* here more closely resemble specimens from New Zealand (Hammer, pers. obs.). *Cladonia furcata* is distinguished by branched, brownish to bluish gray, corticate podetia. The morphologically similar *C. scabriuscula* resembles *C. furcata*, but the apices of *C. scabriuscula* are granulose and microsquamulose and even slightly sorediate.

Cladonia gracilis (L.) Willd. subsp. **turbinata** (Ach.) Ahti, Ann. Bot. Fenn. 17: 212 (1980).

Basionym: *Lichen turbinatus* Ach., Lichenogr. Suec. Prodr. 192 (1799 [‘1798’]); Synonym: *Cladonia gracilis* var. *turbinata* (Ach.) Schaer.; Illustrations: Ahti (1980), pp. 10-12; Flenniken (1999), pl. 7 G; Thomson (1984), p. 136; Vitt et al. (1988), p. 206.

Primary thallus: squamulose, persistent, entire to crenate lobate; squamules: 1-3 mm wide, 1-5 mm long, esorediate; **podetia:** green to brownish-green, 35-80 mm tall, cup-bearing; cups: 4-8 mm wide, flaring rapidly from podetial support, proliferating from margins, occasionally with proliferations from center; **surface:** corticate, esorediate, occasionally shiny, cortex smooth, continuous to subcontinuous; **Apothecia:** common, up to 7 mm wide, dark brown; **ascospores:** narrowly ovoid, 10-15 x 3-4.5 µm; **Pycnidia**: common, on cup margins, ovoid, usually not constricted at base, with hyaline gelatin; **conidia:** 6-7 x 0.5-1 µm; **Spot tests:** K-, C-, KC-, P+ red, UV-; **Secondary metabolite:** fumarprotocetraric acid.

Habitat and ecology: on rotting wood and acidic forest floor at high elevations, mainly boreal; **World distribution:** Asia, Europe and North America; **Sonoran distribution:** only known from one location in the Chiricahua Mountains of SE Arizona.

Notes: This is a common species of the Canadian boreal forest with a southern outlier in mountains of Arizona. It is distinguished by the constant presence of brownish green, esorediate podetia that are rather large and have wide cups.

Cladonia hammeri Ahti, **sp. nov.**

Diagnosis: *Podetia curta ut in Cladonia humili sed granulosa, non sorediosa. Acidum fumarprotocetraricum continens.*

Type: U.S.A.: California, Los Angeles Co., Santa Catalina Island, Parsons Landing, 20 m, T. H. Nash 32201 (ASU).

Illustration: Fig. 42 below.

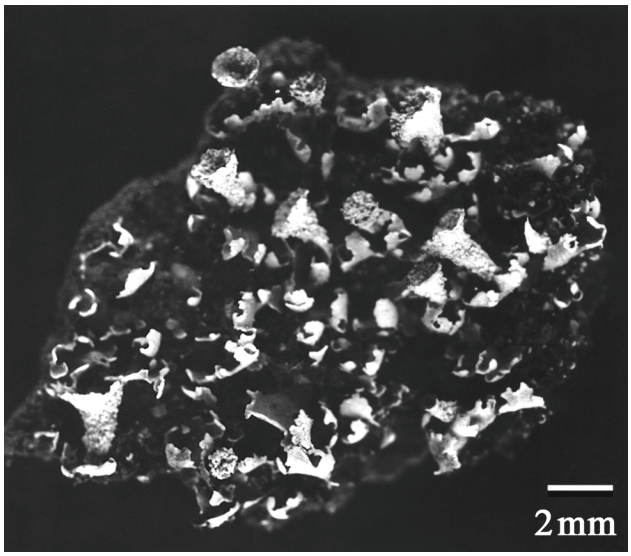
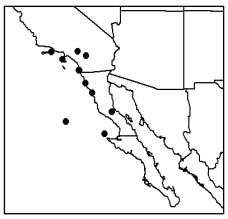


Fig. 42. *Cladonia hammeri.* California, 1893, Hasse (DS 682591). photo by T. Ahti.

Other specimens examined: MEXICO: Baja California, Isla Guadalupe, narrow E-W canyon into the southern peak on the east side, 800 m, Nash 38545b (ASU); Isla

Cedros, W of Cerro Redondo, 1000 m, Nash 34524 (ASU); Cabo Punta Banda, SW of Ensenada, 60 m, Nash 38583 (ASU); 1 km N of Cataviña, northern Vicaiño Region, 560 m, Nash 26294 (ASU); 2 km SE of Colonet, 200 m, Nash 40158 (ASU). USA: California, Los Angeles Co., Santa Monica, 1893, Hasse (DS); Riverside County, Potrero San Jacinto, near San Gorgonio Pass, Parish 1003 (DS); Agua Tibia Wilderness, 1.5 km S of Dripping Springs Campground, 550 m, Ryan 26008 (ASU); Santa Catalina Island, S of Avalon, McGregor 28, 31 (PH); San Bernardino County, N of San Bernardino, 1893, Parish 2621 (DS); San Bernardino Mts., 390 m, 1893, Parish 2617 (DS); San Diego County, 1895, Alderson 828, 901, 917, 945 (DS), San Diego, 1911, Orcutt (DS); Ventura County, W end of West Anacapa Island, 100 m, Nash 37066 (ASU); West Anacapa Island, W side of summit, 250 m, Nash 37107 (ASU).

Primary thallus: squamulose, persistent; squamules: 2-4 mm wide, ascendent; **podetia:** 4-10 mm tall, whitish-gray, cup-forming; cups: 2-5 mm wide; margin: subentire, not proliferating in sterile state; **surface:** esorediate, densely granulose (to schizidiose), corticate at base; **Apothecia:** rare, dark brown; **ascospores:** not seen; **Pycnidia:** scarce, on cup margins; **conidia:** not seen; **Spot tests:** K-, C-, KC-, P+ red, UV-; **Secondary metabolites:** fumarprotocetraric acid, trace amounts of protocetraric and confumarprotocetraric acids, traces of three unknown substances.



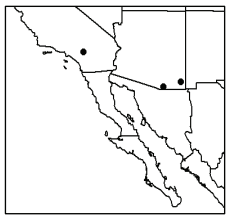
Habitat and ecology: on earthen banks in arid lowland regions; **World distribution:** western North America; **Sonoran distribution:** Baja California and southern California.

Notes: *Cladonia hammeri* resembles *C. humilis*, but it is not sorediate and not as distinctly corticate. We initially placed it in *C. kurokawae* Ahti & S. Stenroos, a similar granulose species with atranorin, which is known from Japan and China. However, a well-developed cortex is found on the podetia of *C. kurokawae*, and it extends higher up. *Cladonia kurokawae* is frequently fertile, with many proliferations arising from the cup margins. *Cladonia pulvinella*, another similar species, contains atranorin and bourgeanic acid and the cup margins are irregularly dentate and proliferating.

Cladonia humilis (With.) J. R. Laundon, Lichenologist 16: 220 (1984).

Basionym: *Lichen humilis* With., Bot. Arr. Veg. Gr. Brit. 721 (1776); Synonyms: *Cladonia conista* Robbins *ex* A. Evans, *C. humilis* var. *bourgeanica* A. W. Archer; Illustrations: Flenniken (1999), pl. 7I; Hale (1979), p. 178 (as *Cladonia conista*).

Primary thallus: squamulose, persistent; squamules: 3-10 mm long, 1-3 mm wide; margins: entire or irregularly lobate; **podetia:** 5-12 (35) mm tall, pale gray to glaucescent green, cup-forming; cups: 2-8 mm wide, gradually flaring, short-stalked (stalk may be shorter than cup); **surface:** cortex: continuous at base and persistent half the length of podetium, giving way abruptly to farinose soredia; margins: entire to irregularly dentate, proliferations absent; **Apothecia:** very rare, long-stalked, brown; **ascospores:** not observed; **Pycnidia:** rare, at cup margins, subglobose; **conidia:** not observed; **Spot tests:** K+ yellow, changing to dingy yellow, C-, KC-, P+ brick red, UV-; **Secondary metabolites:** two chemotypes: (1) atranorin and fumarprotocetraric acid, (2) bourgeanic acid and fumarprotocetraric acid.



Habitat and ecology: on thin soil in exposed localities; **World distribution:** Africa, Asia, Australasia, Europe, North America and South America; **Sonoran distribution:** SE Arizona and southern California.

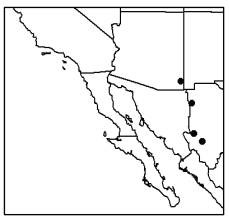
Notes: *Cladonia humilis* is comparable to *C. asahinae*, *C. chlorophaea*, *C. fimbriata* and *C. nashii,* but it is different in several respects. The podetial cortex is persistent, gray and smooth, and may continue past the flaring base of the cup. The podetia of *C. humilis* are characteristically stout, with relatively wide cups. The characteristic presence of atranorin or bourgeanic acid distinguishes *C. humilis* from species other than *C. nashii*, which has hardly any cortex on the podetial stalk. The bourgeanic acid chemotype is

sometimes recognized as a distinct species (*C. conista*), but at least in the Sonoran area it does not seem to be distinguishable morphologically, and it is therefore included in *C. humilis*. The atranorin chemotype seems to be more frequent in the Sonoran region, but in Arizona only the bourgeanic acid chemotype was recorded.

Cladonia jaliscana Ahti & Guzm.-Dáv. in Glenn et al., Lichenographia Thomsoniana 21 (1998).

Illustrations: Ahti (2000), p. 207; Ahti and Guzmán-Dávalos (1998), p. 23.

Primary thallus: squamulose, persistent, forming depressed mats; squamules: 2-3 mm lone x 0.1-1 mm wide, dense, crenulate to much-dissected, esorediate or slightly sorediate; **podetia:** yellow-green to glaucous green, unbranched to rarely sparingly branched at tips, 4-10 mm tall, clavate, broadening toward tips, without cups; **surface:** corticate, esorediate; cortex: continuous to areolate-peltate or verruculose, occasionally squamulose; **Apothecia** constantly present, red, 1-2 mm wide; **ascospores:** oblong, 9-12 x 3.5-4 µm; **pycnidia**: abundant, on primary squamules, spherical to urn-shaped, constricted at base or not, with red gelatin; **conidia:** 3-5 x 0.5 µm; **Spot tests:** K+ yellow, C-, KC-, K+ yellow, P+ yellow, UV-; **Secondary metabolites:** thallus with thamnolic and didymic acids (majors), usnic acid (accessory); apothecial discs with rhodocladonic acid as a red pigment.



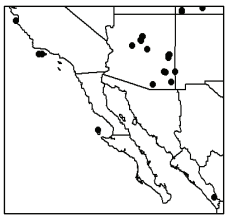
Habitat and ecology: on soil and humus in oak and pine forests; **World distribution:** North America (Mexico and Arizona); **Sonoran distribution:** SE Arizona (Chiricahua Mts.) and along the Sierra Madre Occidental of Chihuahua.

Notes: In Arzona it is an extension of its main range in Mexico. It is characterized by conspicuous wide colonies on soil and the presence of red apothecia on somewhat sturdy, short podetia.

Cladonia macilenta Hoffm., Deutschl. Fl. 2: 126 (1796), nom. cons. prop. (ined.).

Synonyms: *Cladonia bacillaris* Genth, nom. illeg.; *C. macilenta* var. *bacillaris* ("Genth") Schaer.; Illustrations: Brodo et al. (2001), p. 259; Flenniken (1999), pl. 7 K; Hale (1979), p. 185; Vitt et al. (1988), p. 199 (as *C. bacillaris*); Wirth (1995), p. 331.

Primary thallus: squamulose, persistent; squamules: 1-6 mm long, 2-5 mm wide, sometimes with granular soredia; **podetia:** 2-30 mm tall, 1-4 mm wide, grayish to whitish green, unbranched to sparingly branched, subulate or blunt, not cup-forming; **surface:** sorediate, with disappearing cortex on upper portions, but basally thickly corticate (also below apothecia); soredia: coarse at base, sometimes intergrading with isidioid structures; **Apothecia:** scarce, 0.5-3 mm wide, red; **ascospores:** oblong, 8-13 x 3-4 µm; **Pycnidia:** common, on primary squamules or tips of podetia, ovoid to cylindrical, with red gelatin; **conidia:** 3-8 x 0.5-1 µm; **Spot tests:** K+ bright yellow, persistent, or K-, C+ & KC+ canary yellow, or C- & KC-, P+ orange, or P-, UV-; **Secondary metabolites:** thallus with two major chemotypes: (1) thamnolic, barbatic (inconstant), and didymic (accessory) acids; (2) barbatic acid, didymic acid (accessory); many minor accessory metabolites also present (Ahti 2000); apothecial discs with rhodocladonic acid as a red pigment.



Habitat and ecology: on dead wood, tree bases, or sometimes over soil or rocks; **World distribution:** all continents (Antarctica uncertain); mainly temperate to boreal; **Sonoran distribution:** Arizona, southern California, Baja CalIfornia, and Sinaloa.

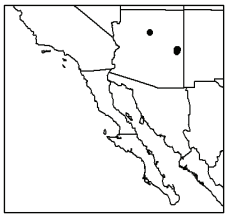
Notes: *Cladonia macilenta* is often divided into two species, called *C. macilenta* and *C. bacillaris* (the nomenclature is in need of clarification) based on the presence or absence of thamnolic acid (revealed by K and P reactions). They are here regarded as chemotypes, following Christensen (1987) and Ahti (2000), although some authors claim that they have subtle morphological differences. The barbatic acid chemotype seems to be the

only one in inland areas of the Sonoran region, while the thamnolic chemotype is more frequent in the coastal lowlands.

Cladonia macrophyllodes Nyl., Flora 58: 447 (1875).

Illustrations: Brodo et al. (2001), p. 260; Corbridge and Weber (1998), p. 14 (as *C cervicornis* var. *verticillata*); McCune and Geiser (1997), p. 89.

Primary thallus: squamulose, persistent; squamules: 8-15 mm long, 2-8 mm wide, crenate-lobate; upper surface: with waxy-appearing bumps several mm diam; **podetia:** infrequent, 9-25 (-30) mm tall, glaucous gray, senescent parts strongly blackening, cup-forming; cups: up to 7 mm wide, bearing one or more tiers of proliferations from center; **surface:** corticated, thickly verruculose to continuous-chinky, medullary layer emerging among chinks sometimes with a pinkish tinge; **Apothecia:** infrequent, up to 1.5 mm diam, brown; **ascospores:** fusiform, 9-15 x 2.5-3.5 µm; **Pycnidia:** on basal squamules or on cup margins, pyriform, not restricted at the base, ostiole not apparent, with hyaline gelatin; **conidia:** 7-8 x 1 µm; **Spot tests:** K+ yellow to dingy yellow, changing to brownish, C-, KC-, P+ red, UV-; **Secondary metabolites:** atranorin and fumarprotocetraric acid.



Habitat and ecology: on soil and in rock crevices in acidic habitats; locally abundant at high elevations; **World distribution:** Europe, Asia, North America and South America; **Sonoran distribution:** eastern and northern Arizona.

Notes: *Cladonia macrophyllodes* typically grows in acidic, high-mountain habitats and can be recognized by its large, gray squamules. The podetia are usually sparse or poorly developed, but when well developed the cups are wider than in any other species in the Sonoran region. It may be very similar to *C. symphycarpia*, which usually contains norstictic or psoromic acids besides atranorin. The latter species prefers base-rich habitats.

Cladonia mexicana Vain., Acta Soc. Fauna Fl. Fenn. 4: 452 (1887).

Illustration: Ahti (2000), p. 172 (atypical, old, fertile morphology).

Primary thallus: squamulose, evanescent, entire to sublobate; squamules: *c.* 1 mm wide and up to 3 mm long, not granulose; **podetia:** 1-5 cm tall, 1-2 (-7) mm wide, whitish gray or glaucescent to brownish, blackened at base, sparingly branched, subulate to narrowly scyphose; cups: absent or developing with age, 1-2 mm wide, closed or with secondary openings; **surface:** areolate-corticate, with arachnoid interspaces (fertile podetia more continuously corticate), pruinose near tips, becoming granulose, schizidiate, phyllidiate to microsquamulose; **Apothecia** infrequent, 0.2-0.7 mm wide, brown; **ascospores:** not observed; **Pycnidia**: on cup margins, pyriform, stalked; gelatin not observed; **Conidia:** not seen. **Spot tests:** K+ yellow, C-, KC-, P+ orange, UV-; **Secondary metabolites:** atranorin and fumarprotocetraric acid, and unknown minor compounds (accessory).

Habitat and ecology: on soil at high elevations (*c.* 2000 m); **World distribution:** North America (Mexico), the West Indies, Central and South America (Andes), especially in the páramos; **Sonoran distribution:** only known from the Basaseachic region of western Chihuahua.

Notes: This species is widespread on Mexican mountains south of the Sonoran region. It is recognized by its whitish color and granulose, arachnoid podetia.

Cladonia multiformis G. Merr., Bryologist 12: 1 (1909).

Illustrations: Brodo et al. (2001), p. 262; Thomson (19 67), pl. 18; Thomson (1984), p. 149.

Primary thallus: squamulose, evanescent; squamules: 1-4 mm long, up to 0.5 mm wide, digitately lobed, esorediate; **podetia:** glaucescent to usually more or less brown, 30-70 mm tall, 1-2 mm wide, occasionally bearing many cups; cups: successsively proliferating from cup

margins to produce new cups, with sieve-like perforations in the interiors; fertile podetia: more richly branching and without cups but producing many flattened branchlets with lateral slits; **surface:** smoothly corticate to slightly areolate, often somewhat shiny, esorediate, somewhat squamulose; **Apothecia:** common, numerous but small (up to 1 mm) at ends of the long, apical proliferations, dark brown; **ascospores:** not observed; **Pycnidia:** mainly produced on short teeth at cup margins, conical to subspherical, often somewhat constricted at base, with hyaline gelatin; **conidia:** not observed; **Spot tests:** K- or K+ yellowish changing to dingy brown, C-, KC-, P+ red, UV-; **Secondary metabolites:** fumarprotocetraric acid and occasionally accessory ursolic acid.

Habitat and ecology: on mossy, preferably base-rich, soils in sheltered, mesic mountain forests; **World distribution:** North America, mainly eastern, extending along Rocky Mountains south to Coahuila, Mexico, but not to the west coast, essentially boreal; **Sonoran distribution:** rare, in spruce-fir forest in eastern Arizona.

Notes: This species is easily recognized by its unique sieve-like cups. However, it is often only seen in fertile state, when no cups are present, and then it is extremely similar to some morphs of *Cladonia furcata*. The main axes of fertile *C. multiformis* are largely flattened in cross-section, while in *C. furcata* they are invariably round. The ranges of the two species hardly overlap in western North America.

Cladonia nashii Ahti, **sp. nov.**

Illustration: Fig. 43 to right. (*Cladonia nashii* + some *C. hammeri* on the right hand side). Part of holotype (ASU).

Diagnosis: *Podetia curta (4-10 mm), simplicia, ut in Cladonia humili sed toto sorediosa, basi fere non corticata. Atranorinam et acidum fumarprotocetraricum continens.*

Type: U.S.A.: California, Santa Barbara County, Santa Rosa Island, Twin Faults Area 0.5 km W of Lobos Canyon, 140 m, 1994, J. Marsh 6850 (ASU; isotype, H).

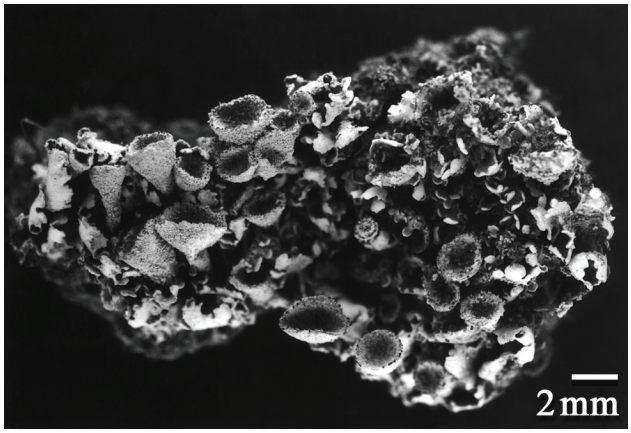
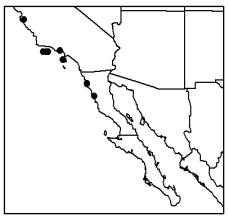


Fig. 43. *Cladonia nashii*, photo by T. Ahti.

Other specimens examined: MEXICO: Baja California, 2 km S of Colonet, 50 m, Guzmán Dávalos 4650 (H, IBUG); U.S.A.: Los Angeles County, Santa Monica Range, 1913, Hasse in Plitt: Lich. Exs. Herb. Hasse Rel. No. 33 (ASU, DS); Santa Catalina Island, Nash 32148 (ASU).

Primary thallus: squamulose, persistent; squamules: 1-4 mm wide, ascendent or adnate; **podetia:** 4-10 mm tall, whitish-gray, simple, cup-forming; cups: 2-4 mm wide; **surface:** clearly sorediate almost throughout (but in part disintegrating with age); soredia: fine to somewhat coarse; cortex: absent or very scarce at base; **Pycnidia:** along margins of cup, spherical, blackish; **Apothecia** and **ascospores:** not seen; **Pycnidia:** common, on cup margins, subglobose, with hyaline gelatin; **conidia:** not observed; **Spot tests:** K+ yellow, C-, KC-, P+ red, UV-; **Secondary metabolites:** atranorin and fumarprotocetraric acid (with traces of protocetraric and confumarprotocetraric acids).



Habitat and ecology: on earthen banks, mainly on mineral soil, arid lowland regions; **World distribution:** North America (California and Mexico); **Sonoran distribution:** Baja California and southern California, especially the Channel Islands.

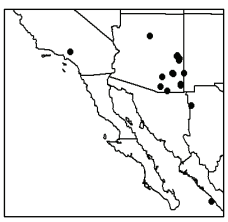
Notes: *Cladonia nashii* resembles the atranorin chemotype of *C. humilis*, but it lacks the smooth cortex found on the podetia of *C. humilis*, and its soredia are slightly coarser. It is also similar to *C. hammeri*, which has a granular surface but which lacks distinct soredia. *Cladonia hammeri* also lacks atranorin. All three of these species can occur sympatrically in southern California.

Cladonia ochrochlora Flörke, De Cladon. 75 (1828), nom. cons. prop. (ined.).

Illustrations: Brodo et al. (2001), p. 262; Flenniken (19 99), pl. 8 C; McCune and Geiser (1997), p. 90.

Primary thallus: squamulose, persistent; squamules: 5-10 mm long, 2-5 mm wide, irregularly, crenate-lobate, esorediate or granularly sorediate; **podetia:** 15-52 mm tall, up to 4 mm wide, greenish gray, unbranched or sparingly dichotomously branched, subulate, developing cups at the apices; cups: shallow, irregular, 1-3 mm wide, corticated interiorly; **surface:** corticated below, usually completely sorediate in the upper half of their length; cortex: smooth, continuous from basal portions upwards, thinning above, becoming chinky-areolate and giving rise in places to discrete soralia; soralia: 0.5-1 mm diam., soredia: farinose to granular, but corticate patches and squamules (up to 5 mm long) sometimes occurring among soredia; **Apothecia:** infrequent, on cup margins, pale to dark brown; **ascospores:** ellipsoid to oblong, (8-) 14-16.5 x 2.5-6 µm; **Pycnidia:** frequent, on cup margins, ovoid, sometimes slightly constricted at base, with hyaline gelatin; **conidia:** 3-8 x 0.5-1 µm; **Spot tests:** K- or K+ dingy yellow to dingy brown, C-, KC-, P+ red, UV-; **Secondary metabolites:** fumarprotocetraric acid and accessory convirensic acid.

Habitat and ecology: on old wood or thin soil over rotting wood, also on moss covered rocks, particularly at damp sites; **World distribution:** all continents except Antarctica; **Sonoran distribution:** Arizona, southern California, Chihuahua and Sinaloa.



Notes: See discussion under *C. coniocraea*. In western North America *C. ochrochlora* varies from the type and may represent an undescribed taxon.

Cladonia parasitica (Hoffm.) Hoffm., Deutschl. Fl. 2: 127 (1796).

Basionym: *Lichen parasiticus* Hoffm., Enum. Lich.: 39 (1784); Synonym: *Cladonia delicata* (Ehrh. ex Ach.) Flörke; Illustrations: Brodo et al. (2001), p. 263; Flenniken (1999), pl. 8 D.

Primary thallus: squamulose, persistent; squamules: up to 2.5 mm long and 1 mm wide, ascending, flat to involute, laciniate to irregularly incised, forming crust-like mats, abundantly granular sorediate or coarsely coralloid-lobulate; **podetia:** fairly common but often sparse, 3-15 mm tall, usually dark brown, occasionally gray, without cups, unbranched or very sparingly branched from blunt apices; tips and axils: usually open; **surface:** usually granularly sorediate to squamulose, rugose, sometimes totally or partly corticated; **Apothecia:** fairly common on tips of podetia, rarely sessile on primary squamules, aggregated to form up to 1.5 mm wide glomerules, dark brown; **ascospores:** oblong to fusiform, 7-14 x 2.5-3.5 µm; **Pycnidia:** common, on primary or podetial squamules, or at tips of podetia, barrel-formed, constricted at base, with hyaline gelatin; **conidia:** 5-9 x 1 µm; **Spot tests:** K+ deep yellow, C & KC- (but + yellow where barbatic acid present), P+ deep yellow, UV-; **Secondary metabolites:** thamnolic acid and (restricted to apothecia) barbatic acid.

Habitat and ecology: on rotting pine or oak wood; **World distribution:** Asia, Europe, North America (mainly in the East) and the West Indies; **Sonoran distribution:** Arizona, rare.

Notes: This is probably the first correct report of *Cladonia parasitica* from western North America (although it is common on the east coast of North America). It is easily overlooked because it is commonly without podetia, but it can be recognized by its very dense colonies of tiny, sorediate, finely dissected squamules that react P+ yellow. It grows on old pine or oak logs.

Cladonia peziziformis (With.) J. R. Laundon, Lichenologist 16: 223 (1984).

Basionym: *Lichen peziziformis* With., Bot. Arr. Veg. Gr. Brit. 720 (1776); Synonyms: *Cladonia capitata* (Michx.) Spreng., *Cladonia leptophylla* (Ach.) Flörke, *Cladonia mitrula* Tuck. *ex* Michener; Illustrations: Brodo et al. (2001), p. 264; Thomson (1967), fig. 32 (as *C. capitata*).

Primary thallus: squamulose, evanescent or occasionally persistent; squamules: very small (0.5-2 x 0.5-1 mm), undivided to somewhat laciniate, forming flat crusts; **podetia:** often abundant, 5-15 (22) mm tall, 0.5-1.5 mm thick, pale gray, usually unbranched or with some apical branchlets, in part flattened; **surface:** longitudinally grooved and cracked, almost continuously areolate-corticate and verruculose, esorediate, often slightly squamulose at the base; **Apothecia:** constantly present, 1-3 mm wide, dark brown to pale ochraceous; **ascospores:** oblong, 7-13 x 2-2.5 µm; **Pycnidia:** common, on primary squamules, ampullaceous to ovoid, constricted at base, with hyaline gelatin; **conidia:** 7-8 x 1 µm; **Spot tests:** K- or K+ dingy brown, C-, KC-, P+ red, UV-; **Secondary metabolite:** fumarprotocetraric acid.

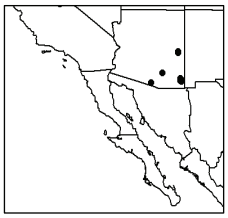
Habitat and ecology: on bare soil banks; collected at 1700 m; **World distribution:** Asia, Australasia, Europe, North America and South America; **Sonoran distribution:** only known from the Barranca del Cobre (Copper Canyon) region of western Chihuahua.

Notes: This species can be recognized by its constantly fertile, small and slender, continuously corticate podetia and its tiny primary squamules. It is common in the eastern United States, but largely absent from the West. The Chihuahua record is an extension of its range to the Mexican mountains in the south.

Cladonia pleurota (Flörke) Schaer., Enum. Crit. Lich. Eur. 186 (1850).

Basionym: *Capitularia pleurota* Flörke, Ges. Naturf. Freunde Berlin Mag. Neuesten Entdeck. Gesammten Naturk. 2: 217 (1808); Synonym: *Cladonia coccifera* var. *pleurota* (Flörke) Schaer.; Illustrations: Brodo et al. (2001), p. 265; Flenniken (1999), p. 8 I; Krog et al. (1994), p. 92; Thomson (1984), p. 154.

Primary thallus: squamulose, evanescent or rarely persistent; squamules: 1-5 mm long, 0.5-4 mm wide, on lower side ochraceous toward bases; **podetia:** greenish to whitish yellow, sometimes with bluish tint, up to 2.5 cm tall, cup-bearing; cups: up to 10 mm wide; margins: usually subentire, more rarely with teeth or proliferations; **surface:** with a thick cortex, sometimes rugose (especially toward base), variably sorediate; soredia: usually in upper portions of podetia including cup interiors, granular or in part farinose; **Apothecia:** infrequent, red, borne on cup margins; **ascospores:** oblong, 8-12 x 2.5-3 µm; **Pycnidia:** common, on cup margins (rarely on primary squamules), ovoid, with red gelatin; **conidia:** 6-8 x 1 µm; **Spot tests:** K-, C-, KC+ faintly yellow, P-, UV- or faintly whitish; **Secondary metabolites:** thallus with usnic and isousnic acids, zeorin (present as abundant, very tiny needle crystals over surface in older herbarium specimens), occasionally porphyrilic acid (UV+); apothecial discs with rhodocladonic acid as a red pigment.



Habitat and ecology: on rotting wood, soil or duff, largely temperate-boreal; **World distribution:** all continents; **Sonoran distribution:** Arizona.

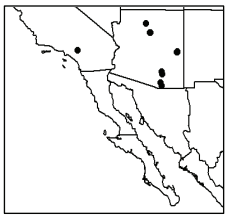
Notes: *Cladonia pleurota* is mostly restricted to inland localities at intermediate to high elevations. It is sometimes confused with *C. carneola*, which is brighter yellow and has abundant, very fine soredia down to the base of podetium, denticulate cup margins, and ochraceous apothecia. This species should be compared with *C. coccifera*, which has the same chemistry but is not sorediate (Stenroos 1989a & 1989b). See also the discussion under *C. borealis*.

Cladonia pocillum (Ach.) Grognot, Pl. Crypt. Saône-et-Loire 82 (1863).

Basionym: *Baeomyces pocillum* Ach., Methodus 336 (1803); Synonyms: *Cladonia pyxidata* var. *pocillum*

(Ach.) Flot.; *Cladonia pyxidata* subsp. *pocillum* (Ach.) Fink; Illustrations: Ahti (2000), p. 144; Brodo et al. (2001), p. 266; St. Clair (1999), p. 62; Thomson (1984), p. 156.

Primary thallus: squamulose to subfoliose, mat-forming, 1-4 cm wide, persistent; squamules: flattened, adnate on the substrate, upturned around edges, comparatively thick (300-1000 µm); lobes: 2-5 mm wide, margins subentire to crenate-lobate, fused, esorediate; upper side: greenish to olivaceous to copper to castaneous, often glossy and cracked; medulla: conspicuously white, with chalk-like structure (use razor blade!); lower side: cottony-fibrillose; **podetia:** common but sometimes scarce even on well-developed thalli, dark brown to greenish brown, 0.5-1.5 cm tall, cup-forming; cups: 3-6 mm wide; **surface:** corticate, areolate, verruculose, esorediate, microsquamulose (forming phyllidia with age) toward the base and also inside the cups; **Apothecia:** fairly common on the podetia, up to 3 mm wide, brown; **ascospores**: not observed; **Pycnidia** common on cup margins, pyriform, with hyaline gelatin; **conidia:** 6-7 x 1 µm; **Spot tests:** K- or K+ dingy yellowish, changing to brownish, C-, KC-, P+ red, UV-; **Secondary metabolite:** fumarprotocetraric acid.



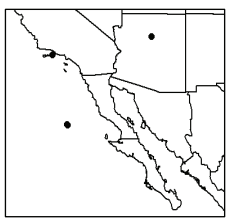
Habitat and ecology: on thin soil or duff, sometimes over pebbles or muscicolous; calciphilous, mostly cold to temperate arid regions; **World distribution:** on all continents; **Sonoran distribution:** Arizona and Chihuahua.

Notes: *Cladonia pocillum* is distinguished by thick, glossy, brown primary squamules, which are fused together, almost resembling a foliose lichen. The lower surface of the squamules is cottony. The short (< 1 cm) podetia with numerous peltate squamules on the insides of the cups also characterize this species. It is difficult to distinguish *C. pocillum* from depauperate collections of *C. pyxidata*. In montane localities *C. chlorophaea* may develop characters that resemble *C. pocillum*, particularly where the soredia have become corticate or where they have been shed. Specimens of *C. fimbriata* and *C. chlorophaea* from montane localities often consist of squamules only, which further confuses their identity. The specific status of *C. pocillum* is actually in doubt, because it is suspected to be only a sturdy morph of the *C. pyxidata* complex, that grows on base-rich soils and accumulates calcium oxalate. It may be an ecotype.

Cladonia pulvinella S. Hammer, Mycotaxon 40: 192 (1991).

Illustration: Hammer (1991), p. 193.

Primary thallus: squamulose, persistent; squamules: 7-12 mm long, 3-8 mm wide, entire to irregulary crenate-lobate to shallow subdigitately lobate; esorediate or with granular, soredia-like structures forming beneath margins; veins: appearing toward base on the lower side; **podetia:** 3-10 (20) mm tall, whitish green to gray, cup-forming; cups: 1-8 mm wide, **surface:** lacking a cortex, or with immediate basal area corticate, granulose, soft-appearing, with pillow-like schizidia (80-200 µm diam) occurring immediately above base giving rise to small peltate squamules and isidioid structures, rarely enlarging to form podetial squamules, abundantly covered with granulose soredia and peltate squamules; margins: producing numerous (5-23) blunt, digitate proliferations, or proliferations expanding to form cups, rarely giving rise to further proliferations; **Apothecia:** rare, borne singly along cup margins or at tips of proliferations, dark reddish brown; **ascospores:** not seen; **Pycnidia** and **conidia:** rare, not seen; **Spot tests:** K+ yellow, C-, KC-, P+ orange, changing to red, UV-; **Secondary metabolites:** atranorin, bourgeanic acid, fumarprotocetraric acid, but according to Ahti (2000) atranorin sometimes absent (and bourgeanic acid may be difficult to identify due to low concentration).



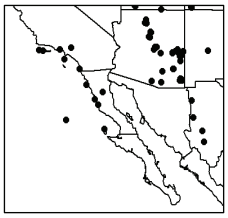
Habitat and ecology: on bare soil banks; **World distribution:** Europe and North America; probably also West Indies and South America; **Sonoran distribution:** Arizona and southern California, and Baja California (Guadalupe Island).

Notes: *Cladonia pulvinella* possesses large (to 200 µm), loosely corticate structures that fill the cup interiors and which resemble soredia. Although *C. hammeri* has similar granules on its surface, it lacks bourgeanic acid. The presence of *C. pulvinella* in the study area is somewhat uncertain, although it was reported from Los Angeles Co., California by Hammer (1995) and Baja California by Ahti (2000); the records from Arizona and Baja California are based on Ahti's identification based on morphology. Because of the recognition of *C. hammeri* in this treatment, all material needs to be re-examined and analyzed with chromatography to identify the simultaneous presence of bourgeanic acid and atranorin, which is diagnostic of *C. pulvinella*, even though (Ahti 2000) included material without atranorin. In any case, *C. pulvinella* is found further north in California (see Hammer 1991 & 1995) and is expected to occur in the Sonoran Region. See further the discussion under *C. hammeri*.

Cladonia pyxidata (L.) Hoffm., Deutschl. Fl. 2: 121 (1796).

Basionym: *Lichen pyxidatus* L., Sp. Pl. 1151 (1753); Illustrations: Brodo et al. (2001), p. 268; Corbridge and Weber (1998), p. 15; McCune and Geiser (1997), p. 92; St. Clair (1999), p. 63; Wirth (1995), p. 307 (lower fig.).

Primary thallus: squamulose, persistent; squamules: 2-5 mm long, 1-3 mm wide, entire or irregularly crenate-lobate; lobes: mostly ascending, lower side brownish white; medulla: fairly thin (less than 250 µm); **podetia:** 3-20 mm tall, greenish gray to brown, cup-bearing; cups: 8-12 mm wide, usually simple; margins: entire or with short proliferations; **surface:** corticate or ecorticate, dull, cortex verruculose, breaking into granules or giving rise to isidioid, schizidioid or phyllidioid structures (also occurring in the cup interiors, appearing as appressed squamules); **Apothecia:** common, up to 8 mm wide, on *c.* 3 mm long stalks on cup margins, reddish brown to darker; **ascospores:** oblong-ellipsoid, 12-16.5 x 3.5-4.5 µm; **Pycnidia:** very common, on cup margins, ovoid, constricted or not at base, with hyaline gelatin; **conidia:** 3.5-9 x 0.5-1.5 µm; **Spot tests:** K- or K+ dingy yellowish changing to dingy brown, C-, KC-, P+ red, UV-; **Secondary metabolite:** fumarprotocetraric acid.



Habitat and ecology: on soil, especially acidic mineral soil and thin soil over rocks, more rarely over wood, mainly arctic to temperate; **World distribution:** on all continents; **Sonoran distribution:** Arizona, southern California, Baja California, Baja California Sur and Chihuahua.

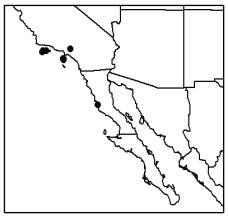
Notes: *Cladonia pyxidata* is comparable to *C. pocillum*, but its primary squamules are thinner, more ascending and almost dull, and the lower side is not clearly pure white. The almost stalkless cup of *C. pyxidata*, which widens gradually from the base, is a diagnostic character. The peltate squamules in the cup interiors of *C.* pyxidata may also occur in mature specimens of *C. chlorophaea*, *C. dimorpha*, *C. hammeri* and *C. pulvinella*. However, they are characteristic even in young specimens of *C. pyxidata*. See also the discussion under *C. chlorophaea*.

Cladonia scabriuscula (Delise) Nyl., Compt. Rend. Hebd. Séances Acad. Sci. Paris 83: 88 (1876).

Basionym: *Cenomyce scabriuscula* Delise in Duby, Bot. Gall. 623. 1830; Illustrations: Brodo et al. (2001), p. 270; Vitt et al. (1988), p. 208.

Primary thallus: squamulose, soon disappearing; squamules: 7-10 mm long, 5-7 mm wide, irregularly lobed to deeply laciniate; **podetia:** (9-) 14-32 (-60) mm tall, 1-2 mm thick, glaucous gray to brown, dichotomously branched; axils: open, more rarely closed; tips: subulate, never cup-forming; **surface:** corticate, cortex thinning above base, scattered areolate to slightly raised-verruculate, giving rise to podetial squamules; squamules: abundant, 2-5 mm long, bearing granular material beneath, at apices granular-sorediate; **Apothecia:** infrequent, 0.5-2.0 mm wide, brown; **ascospores:** oblong to ellipsoid, 11-17 x 4-6 µm; **Pycnidia:** common, at tips of podetia, urn-shaped, constricted at base, with hyaline gelatin; **conidia:** 5-8 x 1-1.5 µm; **Spot tests:** K- or K+ dingy yellow to dingy

brown, C-, KC-, P+ red, UV-; **Secondary metabolite:** fumarprotocetraric acid.



Habitat and ecology: on thin soil on road cuts and among mosses, usually terricolous, not seen on wood, in mainly coastal and oceanic habitats; **World distribution:** Asia, Australasia, Europe, North America, South America and sub-Antarctica; **Sonoran distribution:** Baja California and southern California.

Notes: *Cladonia scabriuscula* is morphologically similar to *C. furcata*. The podetia of *C. scabriuscula* can have sorediate tips, but intermediate forms may have scurfy to verruculose tips, and these characteristics may intergrade. Most of specimens from western North America are characterized by scurfy, non-squamule-forming bits of cortex at the apices. *Cladonia scabriuscula* is more frequent than *C. furcata* in the area, but has been overlooked in the past. In some populations these species are almost impossible to distinguish, but the details of their total distributions in the world are poorly known.

Cladonia squamosa Hoffm., Deutschl. Fl. 2: 125 (1796).

Synonym: *Cladonia squamosa* var. *subsquamosa* (Nyl. *ex* Leight.) Vain., *Cladonia subsquamosa* (Nyl. *ex* Leight.) Cromb, nom. illeg. (non Kremp.); Illustrations: Ahti (2000), p. 310; Brodo et al. (2001), p. 271; McCune and Geiser (1997), p. 93; Wirth (1995), p. 309.

Primary thallus: squamulose, persistent; squamules: 2-6 mm long, 1-3 mm wide, deeply incised, narrow-lobed to coralloid; upper surface: light grayish-green; lower surface: white, esorediate, involute or flattened; **podetia** (4-) 20-70 mm tall, greenish gray to dark brown, unbranched to much-branched; apices and axils: perforated; **surface:** esorediate; cortex: at base rarely continuous, breaking up above base and giving rise to abundant podetial squamules; squamules: subdigitately lobed, up to 6 mm long, upturned, imbricate, obscuring apical openings, sometimes appearing granulose; **Apothecia:** uncommon, pruinose, later brown, in groups around margins of openings, 2-3 mm diam; **ascospores:** oblong to ellipsoid, (5-) 7-17 x 3-5 µm; **Pycnidia:** on tips of podetia (rarely on basal squamules), barrel-shaped, slightly constricted at base, with pale red or hyaline gelatin; **conidia:** 3-8 x 0.5-1 µm; **Spot tests:** K- or K+ yellow, C-, KC- or KC+ yellow, P- or P+ yellow, UV+ ice blue or UV-; **Secondary metabolites:** two major chemotypes known: (1) squamatic acid (K-, P-) and (2) thamnolic acid (K and P+ yellow); both contain additional barbatic acid in apothecia, only the second is recorded in our region but the first is also expected.

Habitat and ecology: on mossy rocks, rotting wood or tree bases, primarily in temperate regions; **World distribution:** on all continents; **Sonoran distribution:** Chihuahua (Parque Recreativo El Creel).

Notes: This species is frequent further south in Mexico (Ahti 2000) and also further north (Hammer 1995). More records are expected from the moister parts of the mountain forests in the Sonoran region. *Cladonia squamosa* is distinguished by its highly squamulose, brown to gray podetia. The thamnolic acid chemotype was previously identified as *C. subsquamosa* (e.g. Thomson 1967), but the name is illegitimate (see below under *C. subsquamosa* Kremp.). There seems to be no morphological character to support its distinction as a species, although its geographic distribution is somewhat different from *C. squamosa s. str.*

Cladonia subfimbriata Ahti, **sp. nov.**

Illustration: Fig. 44. *Cladonia subfimbriata*. Part of holotype (DUKE).

Diagnosis: *Podetia ut in Cladonia subulata sed humiliora (4-15 mm alta), non ramosa, mox scyphosa et superficie magis granulosa. Acidum fumarprotocetraricum continens.*

Type: MEXICO: Guanajuato, Cerro Zamorano, near border of Querétaro, wet fir-oak woods, with mosses on bank, 16 December 1978, W. L. Culberson & C. F. Culberson 17580 (DUKE; isotypes, H, MEXU).

Other specimens examined: (selected) MEXICO: Baja California, Punta Banda W of Ensenada, 60 m, Wetmore 75967 (MIN); Coahuila, top of Sierra de la Madera above Hacienda Canyon, 2610 m, Nash 14239 (ASU); Distrito Federal, Parque Nac. Desierto de los Leones, 1944, Ruiz Oronoz (MEXU); Estado México, Barranca de Ameyalco on rd. Amecameca-Tlamacas, 3000 m, (ENCB, H); Querétaro, 2 km SW of San Joaquín, Campo Alegre, 2400 m, Valenzuela 5079 (ENCB, H); Tamaulipas, 6 km N of Villa Aldama, 150 m, Pursell 5204 (US); Veracruz, Tlacuacinita, 800 m, Purpus 121 (US). USA: Arizona, Gila County, Mogollon Rim, 2125 m, 1987, Gebauer (ASU); Yavapai County, 7 mi. NW of Prescott, Granite Basin Recreation Area, 1740 m, Nash 12699 (ASU); California, Los Angeles County, Santa Monica Range, 1914, Hasse in Plitt: Lich. Exs. Herb. Hasse Rel. No. 32 (ASU, DS), 57 (ASU, DS, OULU); Santa Monica Mountains, Espanoza Canyon, 400 m, Ryan 11272 (ASU), San Gabriel Wilderness, 525-550 m, Ryan 26369 (ASU); Santa Catalina Island, 400 m, Wetmore 73253 (MIN); Santa Catalina Island, Avalon, McGregor 16 (PH).

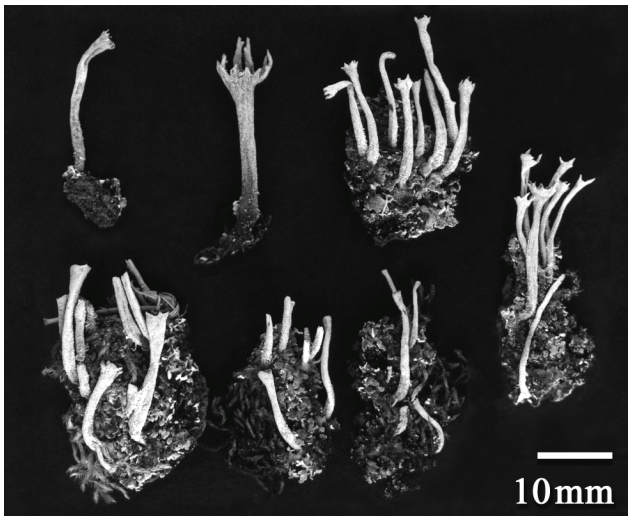
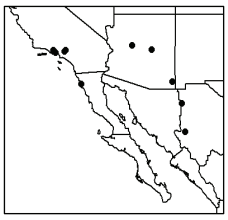


Fig. 44. *Cladonia subfimbriata*, photo by T. Ahti.

Primary thallus: squamulose, persistent; squamules: 1-5 mm long, 0.5-3.5 mm wide, gray, pruinose (occasionally strongly pruinose), with occasional granules and phyllidia on upper surface; margin: crenulate to lobulate; underside: white, softly cottony, occasionally slightly veined toward base, sometimes sorediate along the margins, dying base not blackened; **podetia:** whitish-gray, 4-15 mm tall, 1-2 mm wide, simple, straight to curved, sturdy, subulate to obtuse when young but soon forming narrow cups; cups: 1-2.8 mm wide, shallow, inner surface phyllidiate, occasionally split but generally without marginal proliferations; **surface:** totally ecorticate or corticated basally (up to 1 mm high), sorediate with distinct farinose soredia (0.1-0.2 mm diam), usually mixed with spherical, corticate granules (0.2-0.5 mm wide), with phyllidia, microsquamules or (at base) macrosquamules giving the surface a rough appearance (although podetial tips remaining farinose); medulla: white, exposed in places, **Apothecia:** rare, sometimes compound; disc: up to 2 mm wide, dark brown; **ascospores:** not observed; **Pycnidia:** rare, borne on cup margins, spherical, brown, sessile or slightly stalked, 0.5 mm wide, ascogonial primordia also brown; **conidia:** not observed; **Spot tests:** K+ reddish-brown, C-, KC-, P+ red, UV-; **Secondary metabolites:** fumarprotocetraric acid and trace amounts of protocetraric and confumarprotocetraric acids, occasionally with traces of convirensic acid or unknown secondary products.

Habitat and ecology: primarily on bare mineral soil on road banks and crevices of rock outcrops, but also on rotten wood, mainly in forested areas from 60 to 3000 m; **World distribution:** North America (central Mexico to SW USA); **Sonoran distribution:** Arizona, southern California, Baja California and Chihuahua.



Notes: *Cladonia subfimbriata* has often been identified as *C. fimbriata* because of its simple, sorediate podetia. It differs from *C. fimbriata* by producing subulate podetia at a young stage, having narrow cups and podetia (that therefore appear elongated). The soredia of *C. subfimbriata* are also rougher. *Cladonia subfimbriata* may actually be closer to *C. subulata*, as it resembles that species in surface structure and color. However, *C. subfimbriata* is smaller, unbranched, and commonly produces narrow cups, which do not bear proliferations. Young and short morphotypes of *C. subulata* may be difficult to distinguish from this species. The widespread occurrence of *C. subfimbriata* in Mexico in areas where *C. subulata* is

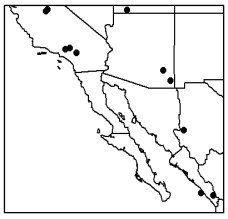
absent confirms that the two species are distinct. More field work is required to define the limits between *C. subfimbriata*, *C. fimbriata*, and *C. subulata*.

Cladonia subradiata (Vain.) Sandst., Abh. Natur wiss. Verein Bremen 25: 230 (1922).

Basionym: *Cladonia fimbriata* [var.] *chondroidea* [subvar.] *subradiata* Vain., Acta. Soc. Fauna Fl. Fenn. 10: 338 (1894); *Cladonia balfourii* Cromb., s. auct. Illustrations: Ahti (2000), p. 161; Brodo et al. (2001), p. 273.

Primary thallus: squamulose, persistent to evanescent; squamules: 2-4 x 1-2 mm, crenulate to laciniate, esorediate to granular below and at margins; **podetia:** whitish gray, 0.8-3 cm long, 0.4-1 mm thick, unbranched or sparingly branched; tips: blunt to acute in young podetia, mature podetia forming cups; cups: 0.6-3 (-4) mm wide, shallow, producing hymenium-tipped prolixferations along margins, occasionally deformed and laterally flattened; **surface:** thinly corticate at base, sorediate (but mostly covered by soredioid or isidioid structures) inside cups and below hymenial discs, also with slightly elongated, tiny (or larger) microsquamules (0.1-0.2 mm long) and granules towards base; **Apothecia:** uncommon, dark brown (but the more frequent primordia pale brown), 2-3 mm wide; **ascospores:** fusiform, 10-12 x 2 µm; **Pycnidia**: common, either on young basal squamules or at tips of podetia, bell-shaped to pyriform, strongly constricted at base, with hyaline gelatin; **conidia:** 7-10 x 1 µm; **Spot tests:** K-, C-, KC-, P+ red, UV-; **Secondary metabolites:** fumarprotocetraric acid and accessory convirensic acid.

Habitat and ecology: on rotten wood and earth banks, in tropical to warm-temperate regions; **World distribution:** Africa, Asia, Australasia, North America and South America; **Sonoran distribution:** Chihuahua and Sinaloa.



Notes: *Cladonia subradiata* is one of the most widespread species of *Cladonia* in the American tropics and subtropics (Ahti 2000), and it is common in Mexico south of the study area. The northern limit is not well known and the specimens from California could not be identified with certainty. It is very similar to *C. coniocraea* but is whitish and the soredia are loosely attached, isidioid, especially on the basal parts of the podetia.

Cladonia subsquamosa Kremp. in Warming, Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 5: 366 (1873).

Illustration: Ahti (2000), p. 161.

Primary thallus: squamulose, persistent or evanescent; squamules: 1-3 x 1-2 mm, soft, fragile, convex to imbricate, fluffy below but sometimes granular or sorediate; **podetia:** 1-3 (-4.5) cm tall, 0.3-1 (-1.5) mm wide, grayish green, producing cups (rarely subulate); cups: 3-7 (-15) mm wide; margins: entire to dentate, thin, erect or slightly recurved; **surface:** ecorticate or at base corticate, finely to coarsely sorediate, also with minute isidioid phyllidia and with globose, corticate granules or microsquamules; soredial layer: thinning and revealing grooved, white to brownish stereome; **Apothecia:** rather common, 1-5 mm wide, light to dark brown, on long (4-7 mm) stalks; **ascospores:** fusiform, 8.5-12.5 x 2-3.5 µm; **pycnidia**: infrequent, semiglobose to pyriform, with hyaline gelatin; **conidia:** not observed; **Spot tests:** K-, C-, KC-, P+ red, UV-; **Secondary metabolites:** fumarprotocetraric acid and accessory convirensic acid.

Habitat and ecology: on rotting wood , tree bases and earth banks, in tropical and subtropical habitats; **World distribution:** Africa, Asia, Australasia, North America and South America; **Sonoran distribution:** Chihuahua and Sinaloa.

Notes: *Cladonia subsquamosa* is a widespread, tropical counterpart of *C. chlorophaea* and was recently recognized as distinct (e.g., Ahti 2000). It is common in Mexico south of the study area and also extends to Florida. It contrast, *C. fimbriata* produces a persistent, thick cover of farinose soredia (although the stalk of the podetium is sometimes corticate). In *C. subsquamosa* the soredia are more loosely attached, even become isidioid, and easily disintegrate; its outer medulla is very thin and is not con-

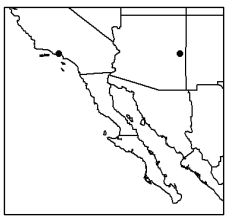
spicuously white. This species is distinguished from *C. chlorophaea* by having sorediate podetia that lack a distinct cortex on its stalks. Chemically *C. subsquamosa* differs by constantly producing rather high amounts of convirensic acid, which is scarce or absent in the other species. The name of the present species should not be confused with the much used *C. subsquamosa* (Nyl. *ex* Vain.) Cromb., which is a synonym of *C. squamosa* (see above).

Cladonia subulata (L.) F. H. Wigg., Prim. Fl. Holsat. 90 (1780).

Basionym: *Lichen subulatus* L., Sp. Pl. 1153 (1753); Synonym: *Cladonia cornutoradiata* (Leight.) Sandst.; Illustrations: Brodo et al. (2001), p. 273; Thomson (1984), p. 168; Wirth (1995), p. 303.

Primary thallus: squamulose, soon disappearing; squamules: 1-4 (-9) mm long, 1-6 mm wide, esorediate or barely sorediate beneath margins; **podetia:** abundant, 15-50 (-100) mm tall, 1.5-4 mm thick, unbranched to sparingly branched, branching angle often wide (to 90°), pale gray or grayish green, subulate but finally cup-forming; cups: 1-3.5 mm wide, often with long, subulate proliferations formed from cup margins; **surface:** mostly ecorticate, farinose sorediate but isidioid structures or small podetial squamules occurring towards the base; **Apothecia** infrequent, at cup margins, stalked, dark brown; **ascospores:** not observed; **Pycnidia:** at tips of subulate podetia or cup margins, ovoid to conical, slightly constricted at base, gelatin hyaline; **conidia:** 5-8 x 1 µm; **Spot tests:** K- or K+ dingy yellow to dingy brownish, C-, KC-, P+ red, UV-; **Secondary metabolite:** fumarprotocetraric acid.

Habitat and ecology: on bare soil over earth banks, rarely on wood, mainly in cool temperate regions; **World distribution:** all continents; **Sonoran distribution:** in upper elevations of eastern Arizona (Apache Co.) and southern California.



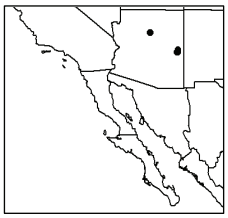
Notes: *Cladonia subulata* is variable and sometimes difficult to distinguish from *C. fimbriata*. Both species are covered with farinose to (occasionally) granular soredia. The cups of *C. fimbriata* are wider and shallower than those of *C. subulata*. Although in most populations its tall, slender, subulate podetia dominate, specimens of *C. subulata* from northern and interior localities in western North America are abundantly cupped, often with wide cups and relatively short podetia. See also the discussion under *C. subfimbriata*.

Cladonia sulphurina (Michx.) Fr., Lichenogr. Eur. Reform. 237 (1831).

Basionym: *Scyphophorus sulphurinus* Michx., Fl. Bor.-Amer. 2: 328 (1803); Synonym: *Cladonia gonecha* (Ach.) Asah.; Illustrations: Corbridge and Weber (1998), p. 14 (as *C. deformis*); Brodo et al. (2001), p. 274; McCune and Geiser (1997), p. 94; St. Clair (1999), p. 64; Thomson (1984), p. 169; Wirth (1995), p. 301.

Primary thallus: squamulose, persistent; squamules: up to 2 cm long and 1 cm wide, subentire to broadly crenate-lobate, occasionally accessory lobules along margins, edges upturned; undersides: whitish to ochraceous yellow at base, esorediate but lobules occasionally sorediate; **podetia:** 30-120 mm tall, usually unbranched, greenish yellow, some tips subulate or throughly split (longitudinal slits on podetial walls), most tips cup-bearing; cups: 1-8 mm wide, with radiating openings interiorally and many short, blunt proliferations from margins; **surface:** with corticate base in young podetia but almost entirely farinose sorediate or with a few patches of verruculae or numerous squamules (some of which approach the size of primary squamules) in older podetia; **Apothecia:** infrequent, up to 3 mm wide, red; **ascospores:** oblong, 8-10 x 2.5-3.5 mm; **Pycnidia:** common, at cup margins, with red gelatin; **conidia:** 8-11 x 1 µm; **Spot tests:** K-, C-, KC- or yellowish, P-, UV+; **Secondary metabolites:** thallus with usnic and squamatic acids, accessory bellidiflorin; apothecial discs with rhodocladonic acid as a red pigment.

Habitat and ecology: on rotting wood or acid humus in timberline woods, mainly in cold temperate regions; **World distribution:** Antarctica, Asia, Europe, North America and South America (southern portion); **Sonoran distribution:** eastern and northern Arizona.



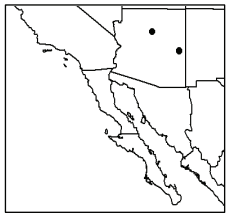
Notes: *Cladonia sulphurina* is morphologically similar to *C. deformis* in that both have yellowish, elongate, sorediate, cup-bearing podetia. But *C. sulphurina* contains squamatic acid (UV+, no crystals on surface), while *C. deformis* contains zeorin (UV-, needle crystals on surface). In most cases *C. sulphurina* is easily distinguished by its brighter yellow color, the presence of uncupped podetia and irregular, split cups and podetia. *Cladonia deformis* is actually less "deformed" than *C. sulphurina* (e.g., Goward 1999).

Cladonia symphycarpia (Flörke) Fr., Sched. Crit. Lich. Suec. 8-9: 20 (1826).

Basionym: *Capitularia symphycarpia* Flörke, Beitr. Naturk. 2: 281. 1810; Synonyms: *Cladonia dahliana* Kristinsson, *Cladonia cariosa* var. *corticata* Vain.; Illustrations: Brodo et al. (2001), p. 275; Flenniken (1999), pl. 9I; Wirth (1995), p. 341.

Primary thallus: squamulose, persistent; squamules: 3-10 mm long, 1-5 mm wide, lead-gray above, conspicuously white below; surface: papillate and maculate, often somewhat pruinose; **podetia:** rare, 5-25 mm tall, 1-4 mm thick, gray, stoutish, club-like or slightly branched at tips, without cups; **surface:** areolate-corticate, pruinose, esorediate, verruculose, grooved; **Apothecia:** common on podetia, 2-4 mm wide, dark brown, pruinose; **ascospores:** not observed; **Pycnidia:** frequent, on primary squamules, globose to broadly conical, large (to 400 µm thick), constricted at base, with hyaline gelatin; **conidia:** not observed; **Spot tests:** K+ pale yellow to golden yellow, or slowly red, C-, KC-, P+ yellow, or slowly red, UV-; **Secondary metabolites:** having several chemotypes but in our area only one with atranorin and psoromic acid known; other chemotypes (Huovinen et al. 1989) are expected.

Habitat and ecology: on calcareous or otherwise base-rich soil, also on mossy, calcareous rocks; **World distribution:** Asia, Europe, North America and South America, from polar to temperate regions; **Sonoran distribution:** eastern and northern Arizona.



Notes: This species (often misspelled *C. symphycarpa",* see Ahti 2000: 266) has been overlooked and confused in North America, apparently because it is normally found in the sterile, non-podetiate stage only. It is expected to be more widespread than indicated here, particularly in limestone areas. All the Arizona material recorded (preserved in MIN) represents the psoromic acid chemotype, which is frequently (e.g., Hammer 1995) recognized as a distinct species, *C. dahliana*, but following Harris (1975b) and Huovinen and Ahti (1989), we include the material in *C. symphycarpia.* Large morphs of *C. cariosa* are difficult to distinguish from *C. symphycarpia* and *C. macrophyllodes*, both of which occur on acidic substrates and frequently lack podetia.

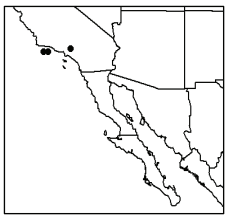
Cladonia verruculosa (Vain.) Ahti, Bryologist 81: 336 (1978).

Basionym: *Cladonia pityrea* var. *verruculosa* Vain., Acta Soc. Fauna Fl. Fenn. 10: 355 (1894); Illustrations: Ahti (1978), p. 336; Brodo et al. (2001), p. 278; McCune and Geiser (1997), p. 97.

Primary thallus: squamulose, soon disappearing; squamules: 1-3 mm long, up to 1.5 mm wide, crenate-lobate to nearly entire; **podetia:** 20-120 mm tall, up to 2 mm wide, brownish white, basal portions blackening, unbranched or sparingly dichotomously branched laterally or rarely from cup margins; branches: solid at base; tips: subulate or cup-forming; cups: 1.5-3 mm wide, irregular; margins: often with elongating proliferations, some proliferations also arising from centers of cups, although rarely in consecutive series; **surface:** rough, esorediate or spar-

ingly granulose sorediate; cortex: continuous to verruculose, scattered and disappearing in older specimens, often richly squamulose at the base; **Apothecia:** frequent, up to 3 mm wide, brown; **ascospores:** ellipsoid, 13.5-16 x 4-5 µm; **Pycnidia:** scarce, on cup margins, subglobose, with hyaline gelatin; **conidia:** 3-8 x 0.5-1 µm; **Spot tests:** K- or K+ dingy yellow changing to dingy brown, C-, KC-, P+ brick red, UV-; **Secondary metabolite:** fumarprotocetraric acid.

Habitat and ecology: on thin soil on exposed or mossy roadcuts or other soil banks, also found on stabilized sand dunes among short grasses; **World distribution:** western North America; **Sonoran distribution:** southern California.



Notes: *Cladonia verruculosa* is generally recognized by its tall, slender podetia, which are in part subulate, in part cup-bearing, and its rough surface due to granulose soredioid structures. This species is very common in Washington down to northern California, and Hammer (1995) reported it down to Santa Cruz Co., but uncertain specimens have been collected further south in California. In Mexico (Michoacán [Ahti 2000]), a very similar species, *C. aleuropoda* Vain. approaches the Sonoran area. Its cups more regularly produce central proliferations.

CLAVASCIDIUM

by O. Breuss

Clavascidium Breuss, Ann. Naturhist. Mus. Wien 98B Suppl.: 41 (1996).

Family: Verrucariaceae; Type: *Clavascidium umbrinum* (Breuss) Breuss; No. species: four world-wide; Selected lit.: Breuss (1996).

Life Habit: lichenized; **Thallus:** squamulose, attached by rhizoidal web, partly with additional rhizines of longitudinally arranged hyphae; **squamules:** dispersed or loosely aggregated, barely overlapping, adpressed or with ascending margins or ± undulate, rounded or lobed; **upper surface:** cream or pale brown to dark brown, dull, epruinose, smooth or roughened or fissured (in one sp.); **upper cortex:** paraplectenchymatous, 20-50 µm thick, composed of angular cells 6-15 µm in diam., with or without an amorphous epinecral layer deriving from dead, collapsed cortical cells; **medulla:** intricately interwoven hyphae with few to many globose cells (6-13 µm in diam.); **photobiont:** primary one a chlorococcoid alga, secondary photobiont absent; algal layer: *c.* 50-100 µm high, horizontally continuous, sharply delimited from the upper cortex, paraplectenchymatous; algal cells: 5-12 µm in diam.; **lower cortex:** weakly differentiated or lacking, if present composed of roundish-angular cells similar to those of the medulla; rhizohyphae: hyaline or brown; **lower surface:** pale or blackish; **Ascomata:** perithecial, laminally immersed in the thallus, pyriform to subglobose; exciple: colorless to yellowish brown or black, 20-35 µm thick, without involucrellum; periphyses: present, interascal filaments absent; hymenial gel I+ reddish (KI+ blue); **asci:** clavate, thin-walled, non-amyloid, 8-spored; **ascospores:** biseriate, simple, ellipsoid, hyaline, smooth, without halo; **Conidiomata:** pycnidial, laminal, of *Dermatocarpon*-type; **conidia:** oblong-ellipsoid to subcylindrical, subfusiform or bacilliform; **Secondary metabolites:** none detected; **Geography:** Europe, Japan, North and Central America; **Substrate:** on soil and detritus.

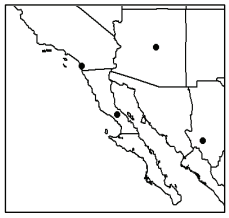
Notes: In anatomy, the genus is similar to *Placidium*, from which it differs by clavate asci with biseriately arranged ascospores and smaller algal cells.

The Species

Clavascidium umbrinum (Breuss) Breuss, Ann. Naturhist. Museum Wien 98 B Suppl.: 41 (1996).

Basionym: *Catapyrenium umbrinum* Breuss, Linzer Biol. Beitr. 22: 78 (1990).

Thallus: squamulose; **squamules:** 2-4 mm wide, 200-300 µm thick, roundish or slightly lobed, **upper surface:** medium to dark brown, dull; **upper cortex:** paraplectenchymatous, 20-50 µm thick, **medulla:** ± filamentous with hyphae divided into a varying number of spherical cells, with a conspicuous brown basal layer of more densely aggregated spherical cells, **lower cortex:** no true developed; **lower surface:** pale or blackish; rhizohyphae: brown, 4-5.5 µm in diam.; also attached with a few additional brown rhizines; **Perithecia:** broadly pyriform, up to 0.4 mm broad, with blackish brown walls; **asci:** clavate, *c.* 50-70 x 15-25 µm; **ascospores:** biseriate, ellipsoid, 13-17 x 6-8 µm; **Pycnidia:** laminal, immersed; **conidia:** oblong-ellipsoid, 3-4.5 x 1.5 µm; **Spot tests:** all negative; **Secondary metabolites:** none detected.



Substrate and ecology: on soil; **World distribution:** scattered in Europe and North America where most records are from the periphery of the Great Plains; **Sonoran distribution:** rarther rare in Arizona, California, Chihuahua and Baja California.

Notes: Characteristic features of the species are its brown basal layer (of varying thickness) and dark perithecial walls. The thallus is rather thin and fragile.

COCCOCARPIA

by L. Arvidsson and T. H. Nash III

Coccocarpia Pers., in Gaudichaud-Beaupré, C. Voyage autour du monde: 206 (1826).

Family: Coccocarpiaceae; Type: *Coccocarpia erythroxyli* (Spreng.) Swinsc. & Krog; No. species: 21 world-wide; Selected lit.: Arvidsson (1982); Swinscow and Krog (1976b).

Life habit: lichenized; **Thallus** foliose (rarely dwarf-fruticose), heteromerous, up to 0.23 mm thick, rosette-shaped, roughly circular in outline, 1-8 (-15) cm in diam., tightly to loosely adnate, lobate; **lobes:** narrow, linear and stellate-radiating or broad-lobed and flabellate or cuneate (rarely terete), contiguous to imbricate or well separated, rarely branched or strongly dichotomously branched, usually flat but in one species terete; apices: usually rotund or ± truncate; margin: often deflexed (in broad lobed species); **upper surface:** light to dark gray, slate blue, or rarely yellow or yellowish gray (non-Sonoran species), smooth but in larger species often with concentric, curved ridges, with or without pruina, isidia or laciniae; soredia and pseudocyphellae: absent; **upper cortex:** paraplectenchymatous, with periclinal hyphae running along the length of the lobes, colorless or rarely yellow; pored epicortex: usually present; **medulla:** white, pale yellow or rarely orange-red; **photobiont:** primary one a filiform cyanobacterium (*Scytonema*), secondary photobiont absent; **lower cortex:** usually present, paraplectenchymatous, composed of periclinal hyphae running in the length direction of the lobes, often merging gradually with the medulla; **lower surface:** yellowish white to pale tan to black, rhizinate; rhizines: white to gray or blue to black, simple, often projecting beyond the margin, usually dense, often forming a hypothallus, rarely sparse; **Ascomata:** apothecial, biatorine (or lecideine), gymnocarpous, adnate or sessile; margin: sometimes with white hairs; disc: carneous to reddish or blackish brown or black, usually ± convex; hymenium: hyaline, I+ deep blue; paraphyses: simple or sparsely branched, septate; **asci:** cylindrical or clavate, with apically thickened wall (I+ blue), 8-spored; **ascospores:** globose or ellipsoid to fusiform, hyaline, simple, often with two oil droplets; **Conidiomata:** pycnidial, laminal or marginal, immersed or sessile; **conidia:** rod-shaped or bacilliform, simple, colorless, 3-6 x 1-1.5 µm; **Secondary metabolites:** usually absent, but fallacinals, lichexanthones and unknowns occasionally present (non-Sonoran species); **Geography:** pantropical and subtropical, rarely extending into moist temperate

areas; **Substrate:** mostly on trees but also on rocks and soil (three species are folicolous).

Notes: *Coccocarpia* was placed in a family of its own by Henssen (1963a), based on the unique ontogeny of the ascocarps. Here apothecial primordia with upright ascogones (and often with projecting trichogynes) are formed in a paraplectenchyma of isodiametric cells. Coccocarpiaceae contain four genera, viz. *Coccocarpia, Peltularia, Spilonema* and *Steinera.* The thallus of *Degelia* species (Pannariaceae) is very similar to that of *Coccocarpia*.

Key to the species of ***Coccocarpia*** from the Sonoran region:

1. Thallus with simple or weakly branched, terete isidia (granular when young) ..... ***C. palmicola***
1. Thallus not isidiate, but sometimes with round, accessory lobules ..... ***C. erythroxyli***

The Species

Coccocarpia erythroxyli (Spreng.) Swinscow & Krog, Norw. J. Bot. 23: 256 (1976).

Basionym: *Lecidea erythroxyli* Spreng., Kungl. Vetensk.-Acad. Nya Handl I: 47 (1820); Synonyms: *Coccocarpia parmelioides* (Hook.) Tuck. and see Arvidsson (1982); Illustrations: Arvidsson (1982), pp. 2, 9, 11, 14-15, 17, 20-21, 25-267, 29, 59 & 60; Swinscow and Krog (1988), p. 63; Brodo et al. (2001), p. 280; and Fig. 45 to right.

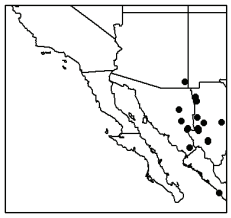
Thallus: foliose, ± orbicular, 2-8 (-15) cm wide, adnate to loosely adnate, with or without concentric rings, lobate, **lobes:** flabellate or cuneate, 1-3 (-7) mm wide, contiguous to imbricate or well separated, lobulate (especially older parts) and weakly branched; apices: rounded and deflexed, broader than interior parts of the lobes, usually incised; **upper surface:** light gray to dark bluish gray when dry, darker when wet, smooth, usually glossy, rarely scabrid, epruinose, sometimes with concentric, curved ridges; lacking isidia, but often with small rounded, laminal or marginal accessory lobules in central parts of the thallus;

Fig. 45. *Coccocarpia erythoryli*, photo by L. Arvidsson.

upper cortex: white or pale yellow, 12-20 µm thick, with an epicortex; **medulla:** white or pale yellow, loose, 30-60 µm thick; **lower cortex:** hyaline to black, 12-20 µm thick; **lower surface:** usually pale brown but sometimes deeper brown to black, glabrous, rhizinate; rhizines: white, light to dark brown or black (black in Sonoran material), scarce to numerous, sometimes forming a dense hypothallus; **Apothecia:** usually present, laminal, irregularly orbicular, 1-4 (-9) mm wide, adnate or sessile, orbicular; margin: thin, only visible in young apothecia, sometimes with white hairs (especially towards base of apothecia and hidden when viewed from above); disc: reddish brown to black (black in Sonoran material), flat to strongly convex; exciple: hyaline or light brown, up to 200 µm thick but covered by disc, epihymenium: pale brown or brownish or black, 4-8 µm thick; hymenium: colorless, 40-60 µm high; paraphyses: ± branched, septate, apically capitate;

subhymenium: pale brown to almost black, up to 100 µm thick; **asci:** narrowly clavate, 8-spored; **ascospores:** narrowly to broadly fusiform to ellipsoid, hyaline, simple, often with two oil droplets, 7-14 x 3-5 µm; **Pycnidia:** laminal or marginal, immersed or sessile, ostiole dark; **conidia:** bacilliform, 2-4 x 1 µm; **Spot tests:** all negative; **Secondary metabolites:** none detected (reports of atranorin may be in error).

Habitat and ecology: on rocks and soil among mosses in moist habitats, but also on tree trunks (*Quercus* etc.); **World distribution:** pantropical and subtropical with a few outlying temperate to arctic localities; **Sonoran distribution:** scattered locations in SE Arizona and south along the Sierra Madre Occidental in Chihuahua, Sonora and Sinaloa.



Coccocarpia palmicola (Spreng.) Arv. & D. J. Galloway, Bot. Notiser 132: 242 (1979).

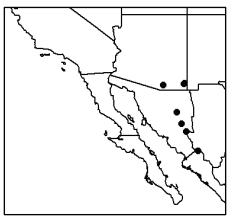
Basionym: *Lecidea palmicola* Spreng., Kungl. Vetensk.-Acad. Nya Handl I: 46 (1820); Synonyms: *Coccocarpia cronia* (Tuck.) Vainio, *Coccocarpia fuscata* Zahlbr. and see Arvidsson (1982); Illustrations: Arvidsson (1982), p. 12-13, 15, 28 & 73; Swinscow and Krog (1988), p. 64; Brodo et al. (2001), p. 280; and Fig. 46 to right.

Thallus: foliose, ± orbicular, 2-7 (-12) cm wide, tightly or loosely adnate, with or without concentric rings, lobate, **lobes:** broadly flabellate or cuneate, 1-4 (-7) mm wide, contiguous to imbricate, lobulate and branched; apices: broader than interior parts of the lobes, usually incised, rounded and deflexed; **upper surface:** usually dark lead gray when dry, bluish green to brownish black when wet, smooth, usually glossy, epruinose, sometimes with concentric, curved ridges, rarely scabrid, isidiate; **isidia:** granular initially, becoming simple and terete (rarely flattened) and sometimes coralloid branched, scarce or forming a dense mat; **upper cortex:** hyaline or pale yellow, 12-20 µm thick, with an epicortex; **medulla:** white or pale yellow, loose hyphae, 30-60 µm thick; **lower cortex:** hyaline to black, 12-20 µm thick; **lower surface:** usually pale, brown or black, glabrous, rhizinate; rhizines: white, light to dark brown or black (black in Sonoran material), scarce to numerous, sometimes forming a dense hypothallus;

Fig. 46. *Coccocarpia palmicola*, photo by L. Arvidsson.

Apothecia: infrequent, laminal, irregularly orbicular, up to 1-3 (-4.5) mm wide, adnate or sessile; margin: thin, with proper one only visible in young apothecia, sometimes with white hairs (especially towards base of apothecia and hidden when viewed from above); disc: pale brownish red to black (black in Sonoran material), flat to strongly convex; exciple: hyaline or light brown, up to 110 µm thick but covered by disc; epihymenium: pale yellow or brownish or black, 4-9 µm thick; hymenium: colorless, 40-70 µm high; paraphyses: ± branched, septate, 2-5 µm thick, apically capitate; subhymenium: pale brown to almost black, up to 100 µm thick; **asci:** narrowly clavate, 40-60 x 8-15 µm, 8-spored; **ascospores:**, narrowly to broadly fusiform to ellipsoid, hyaline, simple, often with two oil droplets, 7-14 x 3-5 µm; **Pycnidia:** usually laminal, immersed, ostiole dark; **conidia:** bacilliform, 2-4 x 1 µm; **Spot tests:** all negative; **Secondary metabolites:** none detected.

Habitat and ecology: on rocks and soil among mosses in moist habitats, but also on tree trunks (*Quercus* etc.); **World distribution:** pantropical and subtropical with a few outlying temperate to



arctic localities; **Sonoran distribution:** scattered locations in SE Arizona and south along the Sierra Madre Occidental in Sinaloa and Sonora.

COLLEMOPSIDIUM

by M. Grube and B. D. Ryan

Collemopsidium Nyl., Flora 64: 6 (1881).

Family: Dothideales *incertae sedis*; Type: *Collemopsidium iocarpum* (Nyl.) Nyl. (*Pyrenopsis iocarpa* Nyl.); No.: species *c.* 10 world-wide; Selected lit.: Coppins (1992), and Harris (1975 & 1995) [under *Pyrenocollema*].

Life habit: lichenized; **Thallus:** immersed or superficial, usually subgelatinous, the hyphae often vertically oriented; **photobiont:** primary one a cyanobacterium (*Gloeocapsa*, *Hyella*, or *Nostoc*, the cells orange or blue-green), secondary photobiont absent; **Ascomata:** perithecial, unilocular; exciple: light to dark brown; intercellular spaces in peridium normally melanized; **involucrellum:** absent or present, hyphae arranged in a textura intricata; hamathecium of sparingly to richly branched and anastomosed and often irregularly thick hyphae, septate, I-; **asci:** with two functional wall layers and an internal apical beak, fissitunicate, ovoid to subcylindrical, usually stalked, I-, usually 8-spored; **ascospores:** colorless, oblong to ovoid-fusiform, 1-septate, the upper cell usually broader than the lower, a poorly defined gelatinous perispore sometimes present; **Conidiomata:** pycnidial; conidiogenous cells ± cylindrical, phialidic; **Conidia:** bacilliform to ellipsoid; **Geography:** cosmopolitan; **Substrate:** on calcareous substrata in moist situations, on wet sand, or on calcareous to acid rocks in freshwater or marine habitats.

Notes: In recent works, *Pyrenocollema* Reinke has been used as a genus for the species treated here, but in the current concept, this is a highly heterogeneous assemblage of species. The type of the genus seems to be a parasite on *Nostoc*. It has thin, tangentially flattened cell walls at the outer layers of the peridium, which are polygonal in surface view. Another old name under consideration is *Magmopsis* Nyl., but its type species with unclear biological relation to algae or cyanobacteria has rounded cells in the peridium. The peridium of *Collemopsidium* is constructed differently; it is composed of irregularly shaped, interwoven cells (textura intricata). In contrast to the type species *C. iocarpum*, marine species usually have strongly carbonized peridia, at least at the apical parts. At a glance, marine species may be confused with the lichenicolous fungus *Stigmidium marinum* [not definitely reported from the Sonoran region, but not unlikely] which occurs on littoral *Verrucaria* species; it has perithecia 0.15-0.2 mm diam., lacks hamathecial filaments, and has the spores constricted at the septum, 10-15 x 4-6 µm.

Key to species of ***Collemopsidium*** from the Sonoran region:

1. Thallus with abundant and distinct carbonaceous ridges and punctae (jugae), rosette-forming or discontinuous and spreading ..... ***C. elegans***
1. Thallus without distinct ridges or jugae. 2

2. Thallus immersed in soft chalk (appearing whitish), limestone or shell (barnacles, limpets, etc.); perithecia up to 0.2-0.6 (-1.5) mm diam., immersed to half-immersed by erosion of the substrate, ostiole inconspicuous, involucrellum present ..... ***C. sublitoralis***
2. Thallus yellow-brown, often glossy, superficial and to nearly 100 µm thick on siliceous rocks (less commonly on calcareous substrates), dull brown, scabrid in sheltered sites; perithecia 0.2-0.25 (-0.3) mm diam., sessile on siliceous rocks, flattened, with a black ring around the ostiole and a pale base (resembling life savers, especially when wet), globose and immersed on calcareous substrata, sometimes with a distinct involucrellum ..... ***C. halodytes***

The Species

Collemopsidium elegans (R. Sant.) Grube & B. D. Ryan, **comb. nov.**

Basionym: *Pyrenocollema elegans* R. Sant., Lichenologist 24 (1): 7 (1992); Illustration: Santesson 1992: 8-10.

Thallus: superficial, thin (up to *c.* 25 µm thick); **surface:** brown, matt when dry, shiny and translucent when wet; with abundant carbonaceous ridges and punctae (jugae); jugae: convex, branched and irregularly stellate, typically 0.1 x 0.2-0.5 mm, flattening and broadening at the thallus margin to form a distinct edge; **photobiont:** a cyanobacterium, *Hyella*; cells: orange; **Perithecia:** immersed in the black ridges, 0.1-0.3 mm diam., flattened and circular, with deeply depressed ostioles, base blackened; **involucrellum:** carbonized, extending part way down over the exciple and spreading; exciple: hyaline to pale; **hamathecium:** much-branched paraphysoids, persistent; **asci:** obclavate to subcylindrical, *c.* 8-spored; **ascospores:** narrowly ovoid, hyaline, 1-septate, cells unequal in size, 11.5-18 (-20) x 3.5-7 µm; **Pycnidia** immersed in the black ridges; **conidia:** not observed; **Spot tests:** all negative; **Secondary metabolites:** none detected.

Substrate and ecology: on siliceous or ultramafic rocks in the littoral zone; **World distribution:** Europe, North and South America; **Sonoran distribution:** southern California (Santesson 1992).

Note: The species is well characterized by the superficial ridges, which often give the thallus an effigurate appearance.

Collemopsidium halodytes (Nyl.) Grube & B. D. Ryan, **comb. nov.**

Basionym: *Verrucaria halodytes* Nyl.; Synonyms: *Pyrenocollema halodytes* (Nyl.) R. C. Harris in Egan, Bryologist 90(2): 164 (1987); Illustrations: Swinscow 1965: Fig. 1-E (p. 58).

Thallus: superficial and to nearly 100 µm thick; **surface:** yellow-brown to dull brown, often glossy, scabrid in sheltered sites, subgelatinous; **photobiont:** a cyanobacterium, *Hyella*; cells: orange, small, up to 12 um in diam.; **Perithecia:** 0.2-0.25 (-0.3) mm diam., sessile on siliceous rocks, flattened, with a black ring around the ostiole (resembling life savers, especially when wet) and a pale base, globose and immersed on calcareous substrate; **involucrellum:** sometimes distinct; **asci:** ovoid to subcylindrical, *c.* 8-spored; **ascospores:** narrowly ovoid, hyaline, 1-septate, cells unequal in size, 12-20 (-27) x 5-8 (-10) µm; **Pycnidia:** 60-80 µm diam; **Conidia:** bacilliform to ellipsoid, 2.5-3.5 x 0.5-1 um; **Spot tests:** all negative; **Secondary metabolites:** none detected.

Substrate and ecology: on siliceous rocks, also superficial on limestone and shells (barnacles, limpets, etc.) in the littoral zone; **World distribution:** widespread in Northern Hemisphere; **Sonoran distribution:** coastal California [reported from central part, but likely to also occur in southern part].

Notes: This widespread, morphologically variable taxon needs further study and may include several species.

Collemopsidium sublitoralis (Leighton) Grube & B. D. Ryan, **comb. nov.**

Basionym: *Verrucaria sublitoralis* Leight., Lich. Flora Great Brit.: 435 (1871); Synonyms: *P. sublitorale* (Leighton) R. C. Harris, Lichenologist 24(4): 368 (1992); Illustrations: Purvis (2000), p. 65 (as *Pyrenocollema halodytes*); Swinscow (1965), fig. 1-D (p. 58) (as *Arthopyrenia halodytes*).

Thallus: entirely immersed or very sparse; **surface:** apparently white or whitish green; **photobiont:** a cyanobacterium, *Hyella*; cells: orange; **Perithecia:** to 0.2-0.6 (-1.5) mm diam. [on soft chalk, half-immersed by erosion of the substratum, to 1 mm on limestone and then subsessile (even on hard rock)]; black; ostioles not prominent; **involucrellum:** brown-black, extending part way down over the exciple and spreading; exciple: hyaline to pale brown, to 200 µm diam.; **hamathecium:** much-branched paraphysoid network, somewhat persistent; **asci:** subcylindrical to cylindrical, *c.* 8-spored; **ascospores:** narrowly ovoid, hyaline, 1-septate, cells une-

qual in size, 12-20 (-24) x 5-7 (-10) µm; **Spot tests:** all negative; **Secondary metabolites:** none detected.

Substrate and ecology: on calcareous rocks amongst seaweeds in the sublittoral zone, especially ridges uncolonized by barnacles, and on shells (barnacles and limpets); **World distribution:** Europe, west coast in North America, and New Zealand; **Sonoran distribution:** coastal California [reported from central part; may also occur in southern part].

Notes: In many treatments prior to 1992 this species was treated as a synonym of *C. halodytes*. Santesson (1992) distinguishes the species on the basis of the immersed thallus. However, *C. sublitoralis* has a whitish thallus and larger, more prominent perithecia. This species is not yet reported from the area, but it is likely to occur.

CULBERSONIA

by T. L. Esslinger

Culbersonia Essl., Bryologist 103: 771 (2000).

Family: Physciaceae. Type: *Culbersonia nubila* (Moberg) Essl. (= *Culbersonia americana* Essl.); No. species: only one world-wide; Selected lit.: Esslinger (2000b).

Note: Because the genus is monotypic, a generic description would simply recapitulate the specific description given below.

The Species

Culbersonia nubila (Moberg) Essl., **comb. nov.**

Basionym: *Pyxine nubila* Moberg, Norw. J. Bot. 27: 189 (1980); Synonym: *Culbersonia americana* Essl.; Illustrations: Esslinger (2000b), p. 772 as *Culbersonia americana*; and Fig. 47 to right.

Life habit: lichenized; **Thallus:** foliose, appressed but loosely adnate, up to 3 or 4 cm in diameter, but somewhat difficult to measure in the irregular, often non-rosette forming thallus; **lobes:** 1-3 mm broad, ± flat to irregularly concave, rounded and irregularly overlapping to somewhat elongate; 120-180 µm thick, upper cortex distinctly paraplectenchymatous, 17-40 µm thick, lower cortex irregularly prosoplectenchymatous, 12-35 µm thick, in part intergrading with and poorly delimited from the medulla; **upper surface:** gray (distinctly green when wet!), usually with a bluish tint, especially in younger areas, darkening with a bluish to greenish tint in older central areas, the entire upper surface evenly to somewhat unevenly pruinose, mostly smooth on the lobes and only slightly roughened or cracked inwardly;

Fig. 47. *Culbersonia nubila*, photo by T. Esslinger.

soredia: granular (25-50 µm diam.), bluish-gray, in small soralia (0.5-1.5 mm); soralia: marginal first and then also laminal in older regions, rounded on the lamina, rounded to irregular on the margins; **medulla:** white; **photobiont:** primary one a *Trebouxia*, secondary photobiont absent; **lower surface:** mostly pale, white to slightly tan, peripheral areas with a conspicuous broad region on the lobes with the same bluish pigment as the upper cortex (and the same spot tests, below), older parts often becoming dar-

kened (necrotically), sometimes to almost black; moderately rhizinate (but rhizines not evenly distributed, sparse to rather abundant in different areas), the rhizines simple to irregularly furcate, up to 0.5-1 mm long, concolorous with the lower surface; **Ascomata:** not seen (but one apothecium reportedly seen by Moberg 1980b); **Conidiomata:** pycnidial, rare; **conidia:** ± cylindrical to weakly fusiform (faintly wider in the middle), 5-6.5 x 1µm; **Spot tests:** bluish-greenish regions (of both the upper and lower cortex) are K+ rose-violet, C+ faint but quickly bleaching, N+ rose (fading somewhat); medulla K-, C-, KC-, P-; **Secondary metabolites:** none detected.

Substrate: in the study area known only on acidic rock; **World distribution:** Arizona, Peru, Africa, Saudi Arabia, Tasmania; **Sonoran distribution:** known only from several sites in the Mount Baldy Wilderness Area in east-central Arizona, above 2900 m.

Notes: Based on the characters of the single observed apothecium, Moberg (1980b) placed this species in *Pyxine*, but noted that its pale lower surface, lack of secondary chemistry, and bluish pigmentation were unique for that genus. He did not find pycnidia (present however in Krog 3K18/110 from Kenya), and therefore did not observe that the conidia of this species are larger (5-6.5 µm vs. 3-4 µm) and different in shape (cylindrical to weakly fusiform vs. bacilliform to weakly bifusiform) than other species of *Pyxine*. Regardless of the apothecial or spore types, this list of distinctions seems to me sufficient basis for separation of *C. nubila* from *Pyxine*.

This unusual species is more likely to be identified as a species of *Physconia*, primarily because of its darkened and K- (or at least not yellow) upper cortex and its distinctive pruina. However, the unusual bluish or greenish gray pigments (K+ rose-violet) found in both the upper and lower cortex, and the mostly pale lower surface with simple or sparsely furcate rhizines, will clearly distinguish *Culbersonia* from all species of *Physconia* as well as all other foliose species in the area.

DENDROGRAPHA

by A. Tehler

Dendrographa Darb., Ber. Deutsch. Bot. Ges. 13: 321. (1895).

Family: Roccellaceae; Type: *Dendrographa leucophaea* (Tuck.) Darb.; No. species: two world-wide; Selected lit.: Darbishire (1898), Sundin and Tehler (1996), and Lohtander et al. (1998).

Life habit: lichenized; **Thallus:** fruticose, erect, repeatedly branched with branch tips ecorticate, sometimes anastomosing, often with lateral ecorticate branchlets breaking through the cortex; **lobe surface:** brown to creamy-grayish to pale gray; soredia and isidia absent; **cortex:** with hyphae periclinally arranged, 50-80 µm thick; **medulla:** white, byssoid or coalescent; **photobiont**: primary one a *Trentepohlia*, secondary photobiont absent; **Ascomata:** apothecioid, numerous to absent, solitary, erumpent, lateral, circular in outline, sessile with constricted base; disc: exposed, convex or rarely flat, white with a pruinose layer, smooth; thalloid exciple: whitish and formed by the disintegrating of the cortex but margin may be intact on the under side of the ascomata (algae excluded at least in the upper part); proper exciple: a thin parathecium, not well developed; epithecium: 25-60 µm thick with brownish, intertwined, richly branched paraphysoids; hymenium: 100-120 µm thick with paraphysoids that are *c.* 1 µm diam, hyaline and sparsely branched; hypothecium: dark-brown (carbonaceous); **asci:** clavate, 70-80 x 15-18 µm, 8-spored; **ascospores:** fusiform, curved, smooth, 3-septate, hyaline; **Conidiomata:** pycnidial, black, solitary, lateral, immersed or rarely elevated, 0.1 mm diam; **conidia:** filiform, semicircular to almost straight, hyaline; **Secondary metabolites:** ß-orcinol depsides, one unknown depside and one other unknown substance; **Geography**: coastal regions with Mediterranean climates in SW North America; **Substrate**: on bark and rock.

Key to the species of ***Dendrographa*** in the Sonoran region:

1. Medulla byssoid; terminal branches and lateral ecorticate branchlets ± complanate; conidia *c.* 11-15 µm long 2
1. Medulla coalescent; terminal branches and lateral ecorticate branchlets ± terete; conidia *c.* 10-12 µm long 3
   2. Lateral ecorticate branchlets missing; internode length *c.* 4-20 mm, ascomata rarely absent .... ***D. leucophaea*** f. ***leucophaea***
   2. Lateral ecorticate branchlets present; internode length up to 5 mm, ascomata nearly always absent..... .....***D. leucophaea*** f. ***minor***
3. Apothecia present; main branches often more or less complanate ..... ***D. alectoroides*** f. ***alectoroides***
3. Apothecia usually absent; main branches terete .... ***D. alectoroides*** f. ***parva***

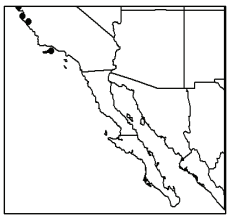
The Species

Dendrographa alectoroides Sundin & Tehler, Bryologist 19: 26 (1996).

Illustrations: Sundin and Tehler (1996), pp. 25, 27 & 29.

Thallus: fruticose, attached by a holdfast; main branches: terete to complanate; terminal branches: terete, up to 1 mm thick and up to 2 mm broad, almost always with terete lateral ecorticate branchlets; **lobe surface:** brown or grayish brown to pale gray, smooth with a thin white pruina; prothallus: not seen; **cortex:** with smooth, brown or hyaline hyphae, 50-70 µm thick; gel: clear, hyaline, also as epicortex with uppermost 2-3 µm granular layer; **medulla:** white to brown, coalescent, composed of mainly periclinally arranged hyphae, with hyaline thallus gel; hyphae: hyaline, ± conglutinated; **"Apothecia":** 0.8-3.0 mm diam; epithecium: 50-60 µm; hymenium: 100-120 µm high; paraphysoids: sparsely branched, hyaline, *c.* 1 µm in diam.; hypothecium *c.* 400 µm thick, often extending down into medulla; **asci:** clavate, 70-80 x 15-18 µm; **ascospores:** fusiform, (18-) 21-25 (-28) x (5-) 6-8 (-9) µm; **Pycnidia:** black, solitary, lateral, immersed, often in small protuberances, *c.* 0.3 mm diam.; **conidia:** filiform, (8-) 11-15 (-18) x < 1 µm; **Spot tests:** thallus K-, C-, KC-, P+ orange; **Secondary metabolites:** fumarprotocetraric acid, protocetraric acid and succinprotocetraric acid, one unknown depside and one unknown other substance.

Substrate and ecology: near the ocean on trees and rocks, preferably on the vertical, north-facing sides; **World** and **Sonoran distribution:** from Monterey, San Francisco and Marin Counties in California and, thus, lies on the border of the Sonoran region.



Notes: *Dendrographa alectoroides* is distinguished from *D. leucophaea* by its more terete branches (especially the terminal parts). Sometimes, especially in *Dendrographa alectoroides* f. *alectoroides*, the main branches are distinctly flattened. In these cases a determination is best achieved by checking the lateral branchlets, which are always terete in *Dendrographa alectoroides*, and the medulla, which is always coalescent. Transitional forms with ascomata are more common in *Dendrographa alectoroides* f. *parva* (see below) than in *D. leucophaea* f. *minor*.

Dendrographa alectoroides f. **alectoroides**

Illustrations: Sundin and Tehler (1996), pp. 25, 27 & 29.

Thallus: with ascomata.

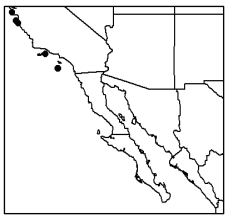
Substrate and ecology: growing near the sea on trees and rocks, usually on the vertical, northern side; **World** and **Sonoran distribution:** from Monterey, San Francisco and Marin Counties in California, and, thus, lies somewhat north of the Sonoran region.

Dendrographa alectoroides f. **parva** Sundin & Tehler, Bryologist 19: 26 (1996).

Illustrations: Sundin and Tehler (1996), p. 27.

Thallus: without ascomata.

Substrate and ecology: near the sea on trees and rocks, usually on the vertical, northern side; **World** and **Sonoran distribution:** from California in Monterey, San Francisco and Marin Counties in the north and extending south to Santa Cruz Island in Santa Barbara County.

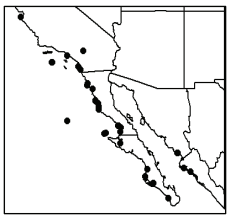


Dendrographa leucophaea (Tuck.) Darb., Ber. Deutsch. Bot. Ges. 13: 321 (1895).

Basionym: *Roccella leucophaea* Tuck., Am. J. Arts Sci. 25: 423 (1858); Illustrations: Sundin and Tehler (1996), pp. 21, 25, 27 & 29.

Thallus: fruticose, attached by a holdfast; main branches: complanate to broadly complanate; terminal branches: complanate to terete, often anastomosing, up to 1 mm thick and up to 10 mm broad, with or without complanate lateral ecorticate branchlets; **lobe surface:** brown to creamy gray, smooth with a thin white pruina; holdfast only as an attachment; prothallus: not seen; **cortex:** with verrucose or smooth, hyaline or brown hyphae, 50-80 µm thick; epicortex: the uppermost 2-3 µm, granular, hyaline; **medulla:** white, byssoid, without thallus gel; hyphae: hyaline, forming a loose network oriented in all directions; **"Apothecia":** 0.3-1.5 mm diam; epithecium: 25-45 µm; hymenium: 100-120 µm high; paraphysoids: sparsely branched, hyaline, *c.* 1 µm in diam.; hypothecium: 200-300 µm, only rarely extended into medulla; **asci:** clavate, 70-80 x 15-18 µm; **ascospores:** fusiform, (17-) 20-24 (28) x (4-) 6-8 (-9) µm; **Pycnidia:** black, solitary, lateral, immersed, often in low, warty protuberances, 0.1-0.3 mm diam; **conidia:** filiform, (8-) 10-12 (-16) x < 1 µm; **Spot tests:** thallus K-, C-, KC-, P+ orange; **Secondary metabolites:** fumarprotocetraric acid, protocetraric acid and succinprotocetraric acid, one unknown depside and one other unknown substance.

Substrate and ecology: locally abundant on various trees, shrubs and cacti as well as on cliffs and rocks near the ocean, but above the littoral and well away from direct salt spray; **World** and **Sonoran distribution:** restricted to the west coast of North America in Baja California, Sonora, Sinaloa and southern California.

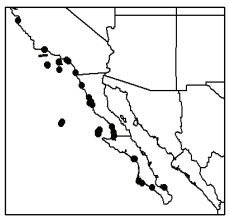


Notes: The major morphological differences between *Dendrographa leucophaea* f. *leucophaea* and *D. leucophaea* f. *minor* are that the latter has shorter internodes, frequent lateral branchlets and lacks ascomata. Old herbarium material contains few transitional forms between *Dendrographa leucophaea* f. *leucophaea* and *D. leucophaea* f. *minor*, probably due to selective collecting. In the field, though, it is rather easy to find transitional forms. Hypothesized transitional forms include specimens: a) with ascomata, main branches with short internodes and many lateral branchlets; b) with or without ascomata, some main branches with short internodes, carrying many lateral branchlets and some main branches with longer internodes and ± without lateral branchlets; and c) with or without ascomata, main branches with long internodes and with few and small lateral branchlets. *Dendrographa leucophaea* f. *leucophaea* and *D. leucophaea* f. *minor* have been observed growing from the same holdfast, suggesting that an individual can change morphology from one branch to another. On the basis of the observed gradient populations Sundin and Tehler (1996) proposed that *Dendrographa leucophaea* f. *minor* consists of clonal populations of *D. leucophaea* formed by fragmentation of branchlets. That hypothesis was recently corroborated by molecular data (Lohtander et al. 1998).

Dendrographa leucophaea f. **leucophaea**

Illustrations: Sundin and Tehler (1996), pp. 21, 25, 27 & 29.

Thallus: with ascomata, internodes (2-) 4-20 (-30) mm, rarely with lateral branchlets.



Substrate and ecology: common on shrubs, especially on dead branches, often found in more exposed microhabitats than *Dendrographa*

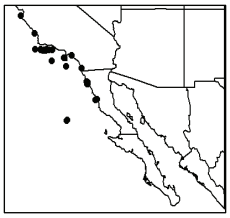
leucophaea f. *minor* (see below); **World** and **Sonoran distribution:** ranges from southern Baja California Sur to Monterey County, California but not collected north of Santa Barbara Island later than 1885 (Sundin and Tehler 1996).

Dendrographa leucophaea f. **minor** (Darbish.) Sundin & Tehler, Bryologist 99: 19 (1996).

Basionym: *Dendrographa minor* Darb., Bibliotheca Botanica 9(45): 67 (1898); Illustrations: Sundin and Tehler (1996), pp. 21 & 27; Brodo et al. (2001), p. 296.

Thallus: without ascomata, internodes 1-5 mm, with abundant lateral branchlets.

Substrate and ecology: abundant on shaded, north-exposed rocks, also often on bark in shaded situations; **World** and **Sonoran distribution:** somewhat more restricted than that of *D. leucophaea* f. *leucophaea*, occurring from Monterey Co., California to Baja California; more common than *Dendrographa leucophaea* f. *leucophaea* in the northern part of the range.



DIBAEIS

B. D. Ryan & K. Kalb

Dibaeis Clem., Genera of Fungi: 78, 175 (1909).

Family: Icmadophilaceae; Type: *Dibaeis baeomyces* (L. fil.) Rambold & Hertel; No. species: 13 world-wide; Selected lit.: Gierl and Kalb (1993), Rambold et al. (1993), Thomson (1967 & 1984), and Purvis et al. (1992).

Life habit: lichenized; **Primary thallus:** crustose, smooth and continuous (to indistinct or within the substrate) to rimose-areolate, areolate, verrucose or granular, thin to thick (up to 1 mm), pseudocorticate; **surface:** chalky white (when calcium oxalate crystals present), pale gray, beige, or greenish, continuous or rimose; soredia, schizidia or isidia-like tubercles sometimes present; **photobiont** primary one a chlorococcoid alga, secondary photobiont absent; **secondary thallus:** podetia sometimes present, arising laminally on the primariy thallus, short (mostly under 2 cm tall), erect, usually unbranched, ± hollow; **Ascomata:** apothecial, up to 4-7 mm diam., usually occurring on podetia, without a thalline margin; disc: roundish, pink to almost white, plane or soon swollen (dome-shaped to partly irregularly folded, or spherical); proper margin: not or slightly prominent; true exciple: hyaline, not distinct from the interior of the stipe; hymenium gel: I+ blue; paraphyses: not branched or anastomosing, little thickened above; hypothecium: hyaline; **asci:** cylindrical, thin-walled, unitunicate, with a thin, K/I+ blue apical cap, (4-) 8-spored; **ascospores:** mainly simple (occasionally indistinctly 1-3-septate), cylindrical-ellipsoid, fusiform, or citriform, obtuse or apiculate at the poles, *c.* 7-24 (-30) x (2-) 2.7-5 (-8) µm, wall hyaline, smooth or halonate with multilayered appendages, without distinctly developed endospore thickening, I-; **Conidiomata:** pycnidial, immersed in warts, laminal to lateral; **conidia:** short bacilliform, formed pleurogenously; **Secondary metabolites:** thallus, stipes and apothecia with ß-orcinol depsides; **Geography:** mostly tropical to subtropical in both hemispheres, and one species (*D. baeomyces*) holarctic and temperate; **Substrate:** on soil, detritus or non-calciferous, siliceous rock.

Notes: *Dibaesis* is segregated from *Baeomyces* on the basis of such characters as apothecial color, amyloidy of the hymenium, ascus type and secondary chemistry (depsides rather than depsidones). *Dibaeis* is divided into two subgenera: subg. *Dibaeis* with stalked, clavate to capitate (domed to spherical) apothecia, fusiform to aciculate ascospores and nonlichenized to lichenized stipes, and subg. *Apoda* with flat, sessile or stalked apothecia, ellipsoid ascospores, and mostly non-lichenized stipes. The subg. *Apoda*, which includes *D. absoluta*, is also characterized by a poorly developed horizontal thallus, simple asco-

spores, and asci showing only weak tendencies of reduction of the amyloid ring. Rambold et al. (1993) placed *Dibaeis* in a new family Icmadophilaceae, while Tehler (1996) didn't mention *Dibaeis* but treated *Baeomyces* and *Icmadophila* under the family Baeomycetaceae.

The Species

Dibaeis absoluta (Tuck.) Kalb & Gierl in Gierl and Kalb, Herzogia 9: 613 (1993).

Basionym: *Baeomyces absolutus* Tuck., Am. Journ. Art. Scienc. 28: 201 (1859); Synonyms: see Gierl and Kalb (1993); Illustrations: Gierl and Kalb (1993), figs. 4 & 13.

Primary thallus: mostly forming only a thin, varnish-like film over the substrate, inconspicuous, often scarcely visible; **surface:** emerald green to gray when fresh, becoming brownish to beige, mostly smooth, scarcely cracked, rarely with calcium oxalate excretions, without soredia; **podetia:** absent or very short, often immersed in the substrate, up to 1 mm tall, 0.5-1 mm diam., narrow at the base, wider above, finally going over the disc margin, weakly but distinctly channeled or longitudinally folded, mostly concolorous with the apothecia.; **Apothecia:** solid in longitudinal section, rose, pale rose to pale beige or ivory white, round, 0.5-2 (-3) mm diam.; disc: plane to uneven, often slightly funnel-shaped, pruinose in the center; margin: sometimes visible, narrow, swollen, rose-red [in non-Sonoran material], becoming convex towards the inside; hymenium: *c.* 120 µm, the upper 20 µm with lichen substances; **asci:** 65-80 x 8 µm wide, (4-) 8-spored; **ascospores:** ovoid to oblong-ellipsoid, hyaline, simple, (9-) 1.7 ± 1.38 x 4.58 ± 0.64 µm, L:W = 3; **Spot tests:** thallus and apothecia K+ yellow, C-, KC+ orange, P+ orange, UV+ orange; **Secondary metabolites:** baeomycesic and squamatic acids (both major), and barbatic acid (accessory).

Substrate and ecology: on rock, soil, loam, loamy rock walls, sandstone; **World distribution:** pantropical to subtropical, particularly in the Americas, Asia and Australasia; **Sonoran distribution:** known from several collections from a single locality in central Sinaloa, 2300-2320 m, on soil over acidic rock in pine-oak forest, and on road bank.

Notes: This species is characterized by an inconspicuous, smooth thallus that contrasts with the pale, rose-colored, plane, small, almost sessile, rounded apothecia.

DICTYONEMA

by B. D. Ryan

Dictyonema C. Agardh. in Kunth., Synops. plant. aequinoct. Orbis novi 1: 1 (1822).

Family: Thelephoraceae [Tehler, 1996; Meruliaceae according to Hawksworth et al. 1995]; Type: *Dictyonema excentricum* C. Ag. (= *D. sericeum* (Sw.) Berk.); No. species: five world-wide; Selected lit.: Parmasto (1978).

Thallus: usually not evident as a distinct structure, but basidiomata originating from tangled hyphae which in some species form a dark greenish, crust-like growth that may be visible even when basidiomata are absent; **Basidiomata:** "crustose" (forming a matt-like cover of appressed or erect branched fibrils) to "foliose", often forming semicircular brackets, which are sessile, standing out from the substrate, or resupinate (partly attached, partly lifted up and bent backwards), single or united in rosettes, soft or paper-like, small or to 20 (-25) cm diam.; **upper surface:** blue- to gray-green, gray to dark or olive green, or whitish or yellowish, often with concentric markings, sometimes unevenly thickened or sulcate (grooved) or zoned, smooth to frequently roughened, or becoming villose, hispid or fibrillose (appearing "combed" hairy or shaggy) due to irregularly to radially arranged filaments of the photobiont; **photobiont:** primary one a cyanobacterium (*Scytonema* or sometimes *Chroococcus* or similar genera), secondary photobiont absent, usually in a well-developed layer in the basidiomata, the filaments sur-

rounded by a coating of longitudinally arranged hyphae; **lower surface:** smooth and even, to warty or granular, without gills or pores; hymenophores (hymenium-bearing parts) soon or eventually produced, scattered to reticulate or forming low concentric bands, dehiscent, white, cream or buff, smooth to ± tomentose, continuous or broken up; **basidiomata anatomy:** with monomitic hyphal system, consisting only of diploid (dikaryotic) generative hyphae (giving rise to other hyphal types and to the hymenium) which are thin- to thick-walled, hyaline or yellowish, septate, irregularly branched or at times dichotomous, with or without clamp connections , 3-11 (-13) µm diam.; without sterile bodies (cystidia and gleocystidia); hymenium organized into an irregular but definite palisade layer with thick increments of basidia and basidioles (immature basidia); **basidia:** in bundles, clavate or subcylindrical, not constricted, 15-30 x 5-9 µm, bearing four slender, slightly curved sterigmata (spore-producing structures); **basidiospores:** simple, hyaline or yellowish brown, ellipsoid to subcylindrical or almost boat-shaped, smooth, I-, 6-10 x 2.8-5 µm, thin-walled, non-amyloid; **Secondary metabolites:** none detected; **Geography:** mostly tropical or subtropical, but some species occurring in boreal-temperate areas; **Substrate:** trees, mossy rocks and soil.

Notes: Although this genus lacks a true thallus (in the sense of a distinctly developed "vegetative plant body"), some authors have referred to the basidioma, which contains the photobiont, as being the thallus.

The Species

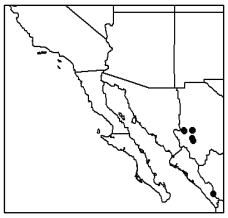
Dictyonema glabratum (Sprengel) D. Hawksw., Lichenologist 20: 101 (1988).

Basionym: *Thelephora glabrata* Spreng., Kgl. Vetensk. Akad. Handl. 1820: 51 (1820); Synonyms: *Cora pavonia* (Sw.) Fr., *Dictyonema pavonia* (Sw.) Parm., *D. montanum* (Sw.) Parm. in Follmann & Redón (not validly published); and see Parmasto (1978); Illustrations: Henssen and Jahns, (1974), fig. 13.58a & b as *Cora pavonia*; Larcher and Vareschi (1988), figs. 1-2; see Parmasto (1978) for additional figure citations.

Basidiomata: sessile, solitary or imbricate and united in rosettes up to 20 cm or more in diam. (to over 60 cm across the longer axis in some specimens, but mostly under 5 cm across in Sonoran region material); the individual pilei (bracket-like units) flabelliform, semicircular, or reniform, rarely almost stalked, frequently laterally fusing, 1-6 (-8) x 1-6 (-8) cm across (mostly 1-2 cm across in our material), thin, 0.18-1.2 (-1.4) mm, membranaceous or almost paper-like, brittle when dry; **upper surface:** usually distinctly and densely but shallowly sulcate-zonate (but in our material rather plane and even but sometimes with fine, concentric wrinkles), without radial fibrils, smooth, under a lens slightly villose (appearing faintly powdery-roughened), in live state glossy blue-green or greenish blue, in herbarium becoming creamy white to whitish gray, grayish yellow, or (especially outside the Sonoran region) grayish green, gray-blue-green, blue-green, or bluish gray, in central part usually darker, the outer 2-3 mm usually ochraceous-cream-colored (more yellowish than rest of upper surface), or greenish or ink-green at the edge; **margin:** usually with few and coarse, rounded lobes, acute (thinning towards edge), at the edge when dry narrowly but strongly involute downward; **photobiont:** a "*Chroococcus*" (Rivulariaceae); cells: green or yellowish, irregularly ellipsoidal or almost polygonal, oblong, (8-) 10-15 um long, without a mucous shell; forming a layer *c.* 150-200 um thick; **lower surface:** densely concentrically zonate, gray to greenish or blue-gray (somewhat darker than upper surface), under a lens appearing granulose or faintly white-arachnoid; **hymenophores:** at first scattered, 0.2-0.4 mm, then up to 1 mm diam. and 0.3-0.6 (-1) mm high, 1-2 mm distant from each other, irregularly cup-like or apothecium-like, later uniting to form interrupted concentrical ridges, finally polygonally or almost reticulately cracked; surface initially deep cream color, then pale ochraceous or dull yellowish-grayish-reddish; in old specimens the hymenial spots fall away beginning from the margin and thus the lower surface becomes sterile again; **basidiomatal anatomy:** context (hyphal mass between upper surface and subhymenium): layered; subhymenium: (30-) 50-150 (-200) µm thick; hymenium: consisting of very numerous basidioles and scattered basidia; basidioles: 4-7 µm diam.; **hyphae:** without clamps; **basidia:** often few or absent, 15-20 (-25) x (5.5-) 6-8.5 µm; sterigmata (spore-bearing projections): 4 or rarely 2, slightly subconical, 5-

7.5 µm long, soon collapsed; **basidiospores:** often few and in poor condition, ellipsoid-teardrop-shaped, slightly boat-shaped, with lateral apiculus (projection for attachment to the sterigma), without droplets, (6.5-) 7.5-8.5 x (3.8-) 4-4.5 (-5) µm; spore print: white; **Spot tests:** all negative; **Secondary metabolites:** none detected.

Substrate and ecology: on soil or mosses (sometimes over acidic rocks) and trees, rarely on bare loam; in sheltered to rather sunny and arid habitats; **World distribution:** U.S.A. (Florida, Hawaii); widely distributed in southern to north-central Mexico, Central America, the Caribbean, and South America; Africa (Mauritius Island, E of Madagascar); early reports (Berkeley and Curtis [1869]) from "west Africa" and the Indian subcontinent ("Hindustan") need to be confirmed; **Sonoran distribution:** Chihuahua (2000-2300 m) and occasional in Sinaloa (1700 m), generally on shaded, mossy acidic rocks (often rhyolite) in pine-oak forests.



Notes: The internal anatomy of this species is described more fully by Parmasto (1978). As discussed in that treatment, although this species (over its full distribution range) is highly variable, especially in the color of the upper surface and in the external structure of the hymenium, the microscopic characters are much more uniform, and most apparent variations in the spores reported in the earlier literature [e.g, 10-15 x 6-12 µm, given by Fink (1935)] are based on extraneous spores or conidia from other fungi. The basidiomata in our material tend to be rather small, and with a rather paler and smooth upper surface, but fall well within the range of variation exhibited by material from other areas. This species is similar to *D. sericeum* (which occurs further south in Mexico) in the bracket-like (not crustose) form and lack of clamp connections, but *D. glabratum* differs by the densely sulcate-zonate upper surface, lack of radial fibrils, and narrowly but strongly involute margin of the basidiocarp, and photobiont not *Scytonema*.

DIGITOTHYREA

by M. Schultz

Digitothyrea Moreno & Egea, Lichenologist 24: 216 (1992).

Family: Lichinaceae; Type: *Digitothyrea rotundata* (Henss., Büdel & Wessels) Moreno & Egea; No. species: three world-wide; Selected lit.: Henssen (1986a), Henssen et al. (1985) and Moreno and Egea (1992b).

Life habit: lichenized; **Thallus:** umbilicate, foliose, fruticose, with deeply divided lobes, gelatinous when wet; **surface:** black, smooth or covered by numerous globose to scale-like isidia; **anatomy:** ecorticate, heteromerous, with a compact central strand of periclinally arranged hyphae and reticulate anatomy at the thallus periphery; **photobionts:** primary one a chroococcoid cyanobacterium, secondary photobiont absent; **Ascomata:** apothecial, laminal on thallus or marginal, orbicular, half-immersed to sessile or stipitate; margin: distinct to prominent, with thalloid rim; **ontogeny:** hemiangiocarpous, ascogonia arising in a tangle of generative hyphae beneath the thallus surface; **anatomy:** exciple: absent; epithecium: brownish yellow; hypothecium: hyaline; **asci:** prototunicate, wall thin, nonamyloid, 8-spored but sometimes fewer; **ascospores:** simple, ellipsoid, broad ellipsoid to globose; 9-15 x 7-9 µm; walls: thin, hyaline; **Conidiomata:** pycnidial, laminal, immersed; **conidia:** ellipsoid, bacilliform or globose, *c.* 3 x 1 µm; **Secondary metabolites:** not detected; **Geography:** world wide in arid to semi-arid regions; **Substrate:** calcareous or siliceous rock.

Notes: The genus differs from *Thyrea* in its deeply divided, tongue shaped lobes, its sessile to stipitate apothecia and its type of ascoma development starting with a tangle of generative hyphae.

Key to the species of ***Digitothyrea*** from the Sonoran region:

1. Thallus forming cushions of erect, repeatedly branched lobes with diverging tips, lobes narrow, 0.5-1 mm wide ..... **D. divergens**
1. Thallus forming flat rosettes (rarely ± erect) of sparingly branched lobes, lobes broader, 0.5-1.5 mm wide, the tips usually broadened or shortly furcate, not conspicuously diverging ..... ***D. polyglossa***

The Species

Digitothyrea divergens (Henss.) Moreno & Egea, Lichenologist 24: 223 (1992).

Basionym: *Thyrea divergens* Henss., Mycotaxon 25: 497 (1986); Illustrations: Henssen (1986a), p. 496; Moreno and Egea (1992b), p. 224, and Fig. 48 below.

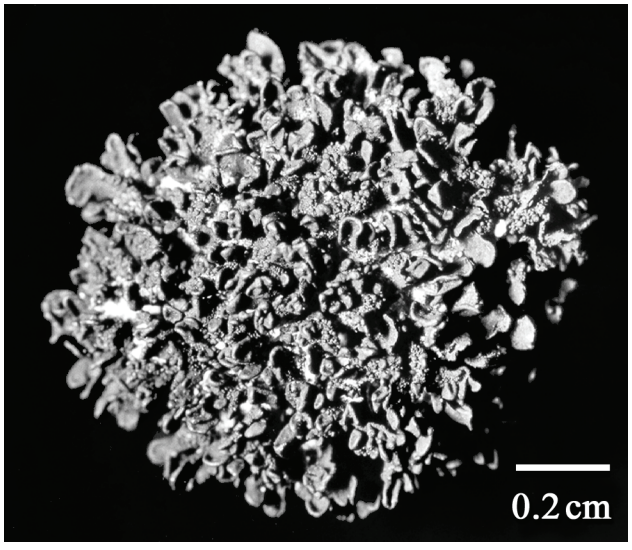
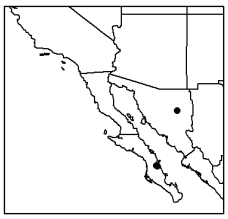


Fig. 48. *Digitothyrea divergens*, photo by M. Schultz.

Thallus: fruticose, umbilicate, deeply branched, polyphyllous cushions; **lobes:** predominantly erect, 0.5-1 mm wide, repeatedly branched; branchlets: diverging, rarely broadened or furcate at tips; **upper surface:** black, rough due to numerous small globose isidia (50-250 µm) that may become scale-like (up to 0.5 mm wide); **lower surface:** furrowed; **Apothecia:** not seen in Sonoran samples; elsewhere, marginal, stipitate, lecanorine, up to 1 mm wide, with persisting thalline margin; disc: dark red, open; exciple: lacking; hymenium: up to 100 µm high, amyloid; paraphyses: distinctly septate, sparingly branched and anastomosing, apical cells indistinctly thickened; hypothecium: ± inverse cone-shaped, elongated as a stipe into the central strand; **asci:** 8-spored, sometimes fewer; **ascospores:** simple, hyaline, broadly ellipsoid, often poorly developed, 12-14 x 7-8 µm; walls: thin; **Pycnidia:** immersed, marginal, ± globose, *c.* 0.15 mm wide; **conidia:** cylindrical, hyaline, 2.5-4 x 1 µm; **Spot tests:** all negative; **Secondary metabolites:** none detected.

Substrate and ecology: on volcanic rocks, with *D. polyglossa* on steep rock faces rocky slopes; (presumably coastal to) montane; **World distribution:** Kenya, Cape Verde Islands, South Yemen, Socotra Island, SW North America; **Sonoran distribution:** Baja California Sur and Sonora.



Notes: It is difficult to separate from *D. polyglossa*, see notes below.

Digitothyrea polyglossa (Nyl.) Moreno & Egea, Lichenologist 24: 223 (1992).

Basionym: *Omphalaria polyglossa* Nyl., Flora 59: 558 (1876); Synonyms: *Thyrea polyglossa*; Illustrations: Henssen (1986a), p. 496; Moreno and Egea (1992b), p. 224, and Fig. 49 on next page.

Thallus: foliose (to fruticose), umbilicate, deeply branched rosettes or cushions, lobules usually flat on the substrate, central lobules in very polyphyllous thalli ± erect, 0.5-1.5 mm wide, stretched, sparingly branched, often with broadened or furcate tips,

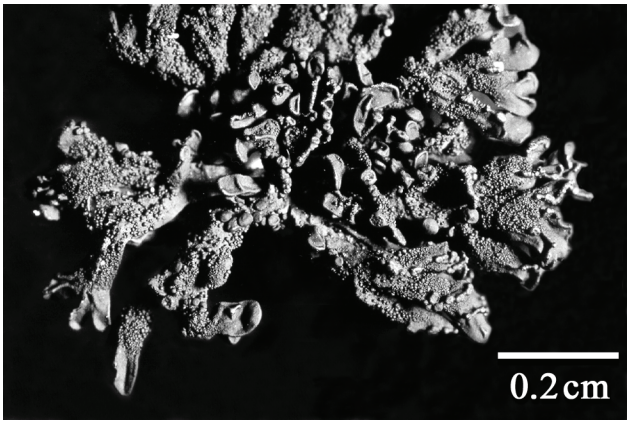
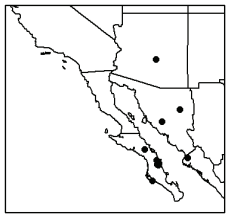


Fig. 49. *Digitothyrea polyglossa*, photo by M. Schultz.

upper surface: black, with coarse globose isidia (50-250 µm) that usually become scale-like (*c.* 0.5 mm), **lower surface:** furrowed; **Apothecia:** rare, sessile to stipitate, marginal, rarely on laminal folds, lecanorine, 0.25-0.6 mm wide, with a persisting thalline margin; disc: dark red; exciple: lacking; hymenium: up to 140 µm high, hyaline, amyloid; paraphyses: distinctly septate, sparingly branched and anastomosing, apical cells indistinctly thickened; hypothecium: ± inverse cone-shaped, up to 70 µm high, hyaline; **asci:** 8-spored; **ascospores:** rarely well developed, simple, hyaline, broadly ellipsoid, sometimes curved, 9.5-14 x 4.5-9.5 µm; walls: thin; **Pycnidia:** immersed, ± globose, *c.* 0.25 mm wide; pycnidial wall: convoluted with age; **conidia:** cylindrical, hyaline, 2.5-4 x 1 µm; **Spot tests:** all negative; **Secondary metabolites:** none detected.

Substrate and ecology: on (calcareous) volcanic rocks, limestone or siliceous rock; on steep, sheltered or shaded rock faces, in clefts and along seepage tracks; coastal to montane; **World distribution:** SW North and Central America; **Sonoran distribution:** obviously confined to strictly Sonoran Desert habitats in Arizona, Sonora, Sinaloa and Baja California Sur, not extending northwards onto the Colorado Plateau or high altitudes in southern Arizona.



Notes: It is distinguished from *D. divergens* by the predominatly flat rosettes with fewer lobules, and the more sparingly branched and slightly broader lobes with less pronounced diverging tips that are often broadened or shortly furcate.

DIPLOSCHISTES

by H. T. Lumbsch

Diploschistes Norman, Nyt. Mag. Naturvid. 7: 232 (1853).

Family: Thelotremataceae; Type: *D. scruposus* (Schreb.) Norman; No. species: 21 world-wide; Selected lit.: Lumbsch (1989).

Life habit: primarily lichenized, but lichenicolous and parasitic stages exist in some species; **Thallus:** crustose, continuous to cracked-areolate; **upper surface:** gray-white to gray or yellowish, smooth to verrucose, often pruinose; **epinecral layer:** thin, gelatinous; **medulla:** white; of irregularly interwoven hyphae, I+ bluish or I-; **photobiont:** primary one a *Trebouxia*, secondary photobiont absent; layer: horizontally continuous; algal cells: 7-18 µm in diam.; **lower cortex:** absent; **lower surface:** firmly attached to the substrate with bundles of hyphae penetrating into it; **Ascomata:** apothecial but at first perithecia-like, later urceolate, lecanoroid, or remaining perithecioid when mature, laminal, immersed, exciple: brown to dark brown; paraphyses: simple, lax; hymenial gel: non-amyloid; lateral paraphyses: present, simple, brownish or hyaline; **asci:** elongate-clavate to subcylindrical, the wall ± evenly thickened when mature, with a somewhat abrupt apical thickening with a thin, internal apical beak or a downward, convex swelling when young, lacking any apical apparatus, the contents I+ orange-red, the walls I-,

not fissitunicate; 1-8-spored; **ascospores:** broadly ellipsoid, brown to dark brown or purplish black, muriform, smooth, lacking a distinct perispore or gelatinous sheath, I- or I+ bluish; **Conidiomata:** pycnidial, in slightly raised warts, black; **conidia:** elongate-ellipsoid or bacilliform, 4-7 x 1-1.5 µm; **Secondary metabolites:** para-depsides and ß-orcinol depsidones; **Geography:** cosmopolitan, but with the center of distribution in semi-arid subtropical regions; **Substrate:** soil, moss, detritus or rocks.

Key to the species of ***Diploschistes*** in the Sonoran region:

1. Ascomata immersed to semi-immersed, perithecioid, opening only by a small ostiolum 2
1. Ascomata sessile, urceolate, disc open, concave 7

2. Thallus C-, lacking secondary metabolites 3
2. Thallus C+ red, containing lecanoric or gyrophoric acids 4

3. Thallus whitish, relatively thick, asci 6 (-8)-spored, apothecial margin radially ridged ..... ***D. arabiensis***
3. Thallus grayish, very thin, asci (6)-8-spored, apothecial margin not ridged ..... ***D. euganeus***

4. Thallus brownish, containing gyrophoric or lecanoric acid 5
4. Thallus grayish to whitish gray, containing lecanoric acid 6

5. Thallus containing gyrophoric acid, relatively thick (1.5-2.4 mm), apothecia up to 2.5 mm in diam., asci 4-6-spored ..... ***D. badius***
5. Thallus containing lecanoric acid, relatively thin (1.0-1.8 mm), apothecia up to 0.8 mm in diam., asci 6-8-spored ..... ***D. euganeus***

6. Thallus whitish gray to gray, spores 16-32 x 10-20 µm ..... ***D. actinostomus***
6. Thallus dark gray to gray, spores 28-45 x 12-25 µm .. .. ***D. caesioplumbeus***

7. Thallus terricolous or muscicolous, whitish to grayish, pruinose, K+ yellow to red (diploschistesic 8
7. Thallus usually saxicolous, grayish, epruinose, K- or yellow to red (diploschistesic acid present or absent) .... ***D. scruposus***

8. Juvenile parasite on *Cladonia* spp., hymenium 80-120 µm high, asci 4-spored, spores 18-32 x 6-15 µm .... ***D. muscorum***
8. Thallus not lichenicolous, hymenium 110-180 µm high, asci 4-8-spored, spores 20-38 x 9-17 µm .... ***D. diacapsis***

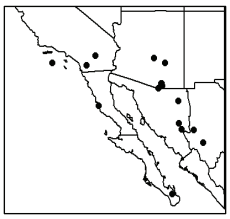
The Species

Diploschistes actinostomus (Ach.) Zahlbr., Hedwigia 31: 34 (1892).

Basionym: *Verrucaria actinostoma* Ach., Lich. Univ. 288 (1810); Illustrations: Lumbsch (1989), pp. 140 & 156; Guderley and Lumbsch (1996), p. 271.

Thallus: rimose-areolate; areoles: 0.5-1.5 mm in diam., plane, thin; **upper surface:** whitish gray to gray, smooth, shiny or dull, epruinose; **Ascomata:** perithecioid, immersed, up to 3 mm in diam.; disc: blackish, plane; proper exciple: up to 70 µm thick; hymenium: 120-160 µm high; **asci:** cylindrical to subclavate, 4-8-spored; **ascospores:** brown, muriform, ellipsoid, 16-32 x 10-20 µm; transverse septa 4-6, longitudinal septa 1-3 per transverse segment; **Pycnidia:** immersed; **conidia:** bacilliform, 4-7 x 1.0 µm; **Spot tests:** K-, C+ red, KC-, P-, UV-; **Secondary metabolites:** lecanoric acid (major), diploschistesic and orsellinic acids (both minor).

Substrate and ecology: on siliceous rocks; **World distribution:** subcosmopolitan in relatively open habitats in arid, semi-arid and Mediterranean areas; **Sonoran distribution:** scattered in mountains at *c.* 500- 2400 m in Arizona, Chihuahua, and Sonora, and about sea level at the coast in Baja California and California.



Notes: *Diploschistes actinostomus* is characterized by the perithecioid ascomata, the presence of lecanoric acid and the whitish gray to gray thallus. A similar species is *D. caesioplumbeus* which differs in having larger ascospores and darker thallus. Poorly developed thalli of *D. actinostomus* may be similar to *D. euganeus* which is readily

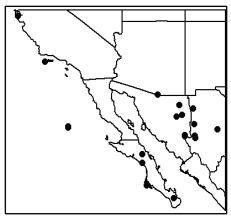
distinguished by the absence of secondary metabolites and the broadly ellipsoid ascospores.

Diploschistes aeneus (Müll. Arg.) Lumbsch, J. Hattori Bot. Lab. 66: 158 (1989).

Basionym: *Urceolaria actinostoma* var. *aenea* Müll. Arg., Rev. Mycol. 38: 12 (1888); Illustrations: Lumbsch (1989), p. 159; Guderley and Lumbsch (1996), p. 271.

Thallus: rimose-areolate; areoles: 0.4-1.8 mm in diam., plane, thin; **upper surface** grayish brown to brown, smooth, shiny or dull, epruinose; **Ascomata:** perithecioid, immersed, up to 2.5 mm in diam.; disc: blackish, plane; proper exciple: up to 70 µm thick; hymenium: 100-130 µm high; **asci:** cylindrical to subclavate, 4-6-spored; **ascospores:** brown, muriform, broadly ellipsoid, 16-26 x 8-18 µm; transverse septa 4-6, longitudinal septa 1-3 per transverse segment; **Pycnidia:** not seen; **Spot tests:** K-, C+ red, KC-, P-, UV-; **Secondary metabolites:** lecanoric acid (major) and orsellinic acid (minor).

Substrate and ecology: on siliceous rocks; **World distribution:** North and South America, southwestern Europe, and East Asia; **Sonoran distribution:** scattered in southern California and Arizona, Baja California (Guadalupe Island, Baja California Sur, Chihuahua and Sonora, occurring in mountainous regions at 270 to 2240 m.



Notes: *Diploschistes aeneus* has perithecioid ascomata, a brownish thallus, contains lecanoric acid, and has broadly ellipsoid spores. It may be confused with *D. badius*, a species that also has a brownish thallus, but can be distinguished by the presence of gyrophoric acid and the thicker thallus.

Diploschistes arabiensis Lumbsch, in Abu-Zinada et al., Arab Gulf Jour. Sci. Res. sp. Publ. 2: 15 (1986).

Illustrations: Abu-Zinada et al. (1986), p. 33; Lumbsch (1993), p. 229.

Thallus: rimose-areolate; areoles: 0.5-1.0 mm in diam., plane, thin; **upper surface:** white or whitish gray, rough, dull, slightly grayish and whitish pruinose; **Ascomata:** perithecioid, immersed to semi-immersed, up to 2.0 mm in diam.; disc: blackish, plane; proper exciple: up to 70 µm thick; hymenium: 120-140 µm high; **asci:** cylindrical to subclavate, 6 (-8)-spored; **ascospores:** brown, muriform, ellipsoid, 23-29 x 15-19 µm; transverse septa 5-6, longitudinal septa 2-3 per transverse segment; **Pycnidia:** not seen; **Spot tests:** K-, C-, KC-, P-, UV-; **Secondary metabolites:** none detected.

Substrate and ecology: on siliceous rocks; **World distribution:** Arabia and western North America; **Sonoran distribution:** rare, at 1600-2200 m in Arizona (and adjacent Colorado and Utah).

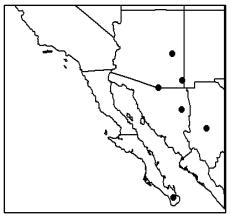
Notes: *Diploschistes arabiensis* is characterized by the lack of secondary metabolites and a relatively thick, whitish thallus. A similar species is *D. euganeus* which differs in having a thinner, more grayish thallus, unridged apothecia, and the predominantly 8-spored asci.

Diploschistes badius Lumbsch & Elix, Pl. Syst. Evol. 167: 196 (1989).

Illustrations: Lumbsch (1989), p. 159; Lumbsch and Elix (1989), p. 197.

Thallus: rimose-areolate; areoles: 0.6-2.0 mm in diam., plane, thick; **upper surface:** reddish brown to brown, smooth, shiny or dull, epruinose; **Ascomata:** perithecioid, immersed, up to 0.8 mm in diam.; disc: blackish, plane; proper exciple: up to 65 µm thick; hymenium: 120-140 µm high; **asci:** cylindrical to subclavate, 6-8-spored; **ascospores:** brown, muriform, broadly ellipsoid, 16-26 x 8-18 µm; transverse septa 4-6, longitudinal septa 1-2 per transverse segment; **Pycnidia:** not seen; **Spot tests:** K-, C+ red, KC-, P-, UV-; **Secondary metabolites:** gyrophoric and lecanoric acids (both major) and orsellinic acid (minor).

Substrate and ecology: on siliceous rocks; **World distribution:** endemic to southwestern North America; **Sonoran distribution:** rare, in mountainous regions at an elevation of *c.* 1300-2700 m in Arizona, Baja California Sur, Chihuahua and Sonora.



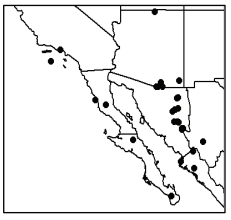
Notes: This species can be readily identified by the presence of gyrophoric acid, the brownish thallus, and the perithecioid ascomata. *Diploschistes badius* is similar to *D. aeneus* and the differences between the two species are discussed under the latter.

Diploschistes caesioplumbeus (Nyl.) Vain., Bot. Mag. Tokyo 35 : 70 (1921).

Basionym : *Urceolaria actinostoma* var. *caesioplumbea* Nyl., Bull. Soc. Linn. Normand., sér. 2, 6 : 264 (1872); Illustrations: Lumbsch (1989), pp. 149 & 162.

Thallus: rimose-areolate; areoles: 0.4-1.5 mm in diam., plane, thin or thick; **upper surface:** gray to dark gray, smooth, shiny or dull, epruinose; **Ascomata:** perithecioid, immersed, up to 1.6 mm in diam., disc: blackish, plane; proper exciple: up to 70 µm thick; hymenium: 130-170 µm high; **asci:** subclavate, 4-8-spored; **ascospores:** muriform, brown, broadly ellipsoid, 28-45 x 12-25 µm; transverse septa 4-9, longitudinal septa 2-5 per transverse segment; **Pycnidia:** not seen; **Spot tests:** K-, C+ red, KC-, P-, UV-; **Secondary metabolites:** lecanoric acid (major) and diploschistesic and orsellinic acids (both minor).

Substrate and ecology: on siliceous rocks; **World distribution:** temperate Europe, Mediterranean area, and western North America; **Sonoran distribution:** locally abundant in mountainous areas of Arizona, Baja California and Baja California Sur, California, Chihuahua, Sinaloa and Sonora at 650-2300 m, also occurring at the coast in Baja California and California.



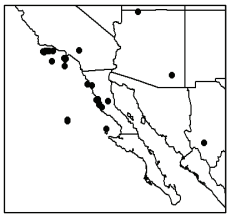
Notes: *Diploschistes caesioplumbeus* is characterized by the relatively large ascospores, the perithecioid ascomata, and the dark grayish thallus. It may be confused with the morphologically similar *D. actinostomus* which has smaller spores.

Diploschistes diacapsis (Ach.) Lumbsch, Lichenologist 20: 20 (1988).

Basionym: *Urceolaria diacapsis* Ach., Syn. Meth. Lich.: 339 (1810); Synonym: *Diploschistes albissimus* (Ach.) Dalla Torre & Sarnth., Flechten Tirol: 299 (1902); Illustrations: Lumbsch (1988), p. 22; Lumbsch (1989), pp. 137-8 & 166; Brodo et al. (2001), p. 303.

Thallus: rimose- to verrucose-areolate; areoles: 0.5-2.5 mm in diam., plane to subconvex, thick; **upper surface** whitish to whitish gray, rough, dull, scarcely to abundantly grayish or whitish pruinose; **Ascomata:** urceolate, sessile, slightly pruinose, up to 2.5 mm in diam.; disc: blackish, concave; proper exciple: up to 80 µm thick; hymenium: 110-180 µm high; **asci:** subclavate to cylindrical, 4-8-spored; **ascospores:** brown, muriform, broadly ellipsoid, 20-38 x 9-17 µm; transverse septa 3-6; longitudinal septa 1-2 per transverse segment; **Pycnidia:** immersed; **conidia:** bacilliform, 4-6 x 1.0-1.5 µm; **Spot tests:** K+ yellow to red, C+ red, KC-, P-, UV-; **Secondary metabolites:** diploschistesic and lecanoric acids (both major) and orsellinic acid (minor).

Substrate and ecology: on soil in open habitats; **World distribution:** subcosmopolitan in open habitats with Mediterranean to arid climate; **Sonoran distribution:** common in semi-arid exposed habitats and coastal areas at 5-250 m (and up to 800 m) in Baja California and southern California, and in open bushlands or open pine forests at an elevation of *c.* 1600-1800 m in Arizona and Chihuahua.



Notes: *Diploschistes diacapsis* is a terricolous species which is readily identified by the K+ yellow to red reaction of the thallus due to the presence of dip-

loschistesic acid as major constituent, the whitish pruinose thallus, (4-) 8-spored asci, and the ascospore size. A similar species is *D. muscorum* which differs in having always 4-spored asci, being a juvenile parasite on *Cladonia* spp., and having a thinner thallus. North American records of *D. ocellatus* belong to *D. diacapsis. Diploschistes ocellatus* does not occur in the western Hemisphere, it is easily distinguished from *D. diacapsis* by the lecanoroid ascomata and the presence of norstictic acid.

Diploschistes euganeus (A. Massal.) J. Steiner, Verh. zool. bot. Ges. Wien 69: 96 (1919).

Basionym: *Limboria euganea* A. Massal., Ric. Auton. Lich. crust.: 155 (1852); Illustrations: Lumbsch (1989), pp. 147 & 170; Guderley and Lumbsch (1996), p. 277.

Thallus: rimose-areolate; areoles: 0.3-1.5 mm in diam., plane, thin; **upper surface:** whitish gray, smooth, shiny or dull, epruinose; **Ascomata:** perithecioid, immersed to semi-immersed, up to 1.8 mm in diam.; disc: blackish, plane; proper exciple: up to 90 µm thick; hymenium: 100-140 µm high; **asci:** subclavate, (6-) 8-spored; **ascospores:** brown, muriform, broadly ellipsoid, 16-32 x 10-20 µm; transverse septa 3-6, longitudinal septa 1-4 per transverse segment; **Pycnidia:** not seen; **Spot tests:** K-, C-, KC-, P-, UV-; **Secondary metabolites:** none observed.

Substrate and ecology: on siliceous rocks; **World distribution:** subcosmopolitan in relatively open habitats. Mainly in semi-arid and arid regions, but also extending into the temperate zone; **Sonoran distribution:** rare, in Baja California at 150 m and Chihuahua at 1600 m.

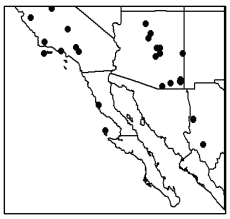
Notes: *Diploschistes euganeus* is characterized by the broadly ellipsoid ascospores and the thin thallus lacking secondary metabolites. The distinction from the similar *D. arabiensis* is discussed under that name.

Diploschistes muscorum (Scop.) R. Sant., in Hawksworth et al., Lichenologist 12: 106 (1980).

Basionym: *Lichen muscorum* Scop., Flora Carniol. indig. 2: 365 (1772); Synonym: *Diploschistes bryophilus* (Ach.) Zahlbr., Hedwigia 31: 34 (1892); Illustrations: Brodo et al. (2001), p. 304; Lumbsch (1989), pp. 138, 140 & 174; Wirth (1995), p. 379.

Thallus: rimose-to verrucose-areolate; areoles: 0.2-0.6 mm in diam., plane to subconvex, thin or thick; **upper surface:** white or whitish gray, rough; shiny or dull, scarcely or abundantly grayish or whitish pruinose; **Ascomata:** urceolate, sessile, slightly pruinose, up to 1.8 mm in diam.; disc: blackish, concave; proper exciple: up to 70 µm thick; hymenium: 80-120 µm high; **asci:** subclavate to cylindrical, 4-spored; **ascospores:** brown, muriform, ellipsoid, 18-32 x 6-15 µm; transverse septa 4-6, longitudinal septa 1-2 per transverse segment; **Pycnidia:** not seen; **Spot tests:** K+ yellow to red, C+ red, KC-, P-, UV-; **Secondary metabolites:** diploschistesic and lecanoric acids (both major) and orsellinic acid (minor).

Substrate and ecology: on soil or mosses, juvenile parasitic on *Cladonia* spp; **World distribution:** cosmopolitan in relatively open habitats in Mediterranean, temperate and polar regions and extending to high altitudes in the tropics; **Sonoran distribution:** common, occurs in the studied area at an elevation of *c.* 250-4100 m in Arizona, Baja California, California and Chihuahua.



Notes: The terricolous or muscicolous *Diploschistes muscorum* can be identified by the combination of 4-spored asci, juvenile parasitism, and the presence of lecanoric and diploschistesic acids. Similar species include *D. diacapsis* (distinction see under that species) and *D. scruposus.* The latter species is a saxicolous and is not lichenicolous. It has an epruinose thallus, (4-) 8-spored asci, and may or may not contain diploschistesic acid.

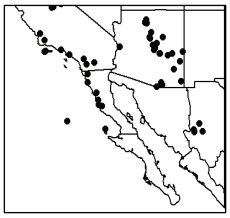
Diploschistes scruposus (Schreb.) Norman, Nyt. Mag. Naturvid. 7: 232 (1853).

Basionym: *Lichen scruposus* Schreb., Spic. Fl. Lips.: 133 (1771); Illustrations: Brodo et al. (2001), p. 304; Lumbsch

(1989), p. 186; Guderley and Lumbsch (1996), p. 289; Wirth (1995), p. 379.

Thallus: rimose-to verrucose-areolate; areoles: 0.4-1.5 mm in diam., plane to subconvex, thin or thick; **upper surface:** greenish or brownish gray, smooth, shiny or dull, epruinose; **Ascomata:** urceolate, sessile, slightly pruinose, up to 2.0 mm in diam.; disc: blackish, concave; proper exciple: up to 75 µm thick; hymenium: 100-140 µm high; **asci:** subclavate to cylindrical, (4-) 8-spored; **ascospores:** brown, muriform, ellipsoid, 25-40 x 10-20 µm; transverse septa 4-7, longitudinal septa 1-3 per transverse segment; **Pycnidia:** immersed; **conidia:** bacilliform, 4-6 x 1.0 µm; **Spot tests:** K- or + yellow to red, C+ red, KC-, P-, UV-; **Secondary metabolites:** diploschistesic acid (major or absent), lecanoric acid (major), and orsellinic acid (minor).

Substrate and ecology: usually on siliceous rocks; **World distribution:** cosmopolitan in relatively open habitats in Mediterranean, temperate and polar regions and extending to high altitudes in the tropics; **Sonoran distribution:** common, at an elevation of *c.* 0-2700 m in Arizona, Baja California, California and Chihuahua.



Notes: The saxicolous *Diploschistes scruposus* is characterized by an epruinose thallus and ureolate ascomata. A similar species is *D. muscorum* and the differences are discussed under that name.

DIRINA

by A. Tehler

Dirina Fr., Syst. orb. veg. 244. (1825).

Family: Roccellaceae; Type: *Dirina ceratoniae* Fr.; No. species: eight world-wide; Selected lit.: Tehler (1983) and Tehler et al. (1995).

Life habit: lichenized; **Thallus:** crustose, effuse sometimes slightly bullate, rimose; **surface:** usually creamy-white, smooth, usually slightly pruinose, soredia often developed; **cortex:** with anticlinally arranged hyphae; **medulla:** white, chalky; **photobiont**: primary one a *Trentepohlia*, secondary photobiont absent; **prothallus:** when free-growing byssoid, brown; when contiguous crust-like and black; **Ascomata:** apothecioid, numerous to absent, solitary, circular in outline, sessile or immersed; disc: exposed, convex or rarely flat, white with a smooth, pruinose layer; thalline exciple: often undulating or strongly undulating, with algae and cortex; proper exciple: a thin parathecium; epithecium: brown with intertwined and branched paraphysoids; hymenium: 50-140 µm thick; paraphysoids: parallel, sparsely branched, hyaline, 1 µm diam.; hypothecium: dark-brown (carbonaceous), not extending down to the substrate; **asci:** clavate, 70-120 x 15 µm; **ascospores:** fusiform, curved, hyaline, 3-septate; walls: smooth; **Conidiomata:** solitary, immersed, dark-brown, 0.1 mm diam; **conidia:** filiform, curved or semi-circled, hyaline, 10-16 µm long less than 1 µm thick; **Secondary metabolites:** orcinol depsides; **Geography:** coastal regions of Mediterranean and subtropical climates; **Substrate:** on bark or rock.

Key to the species of ***Dirina*** from the Sonoran region:

1. On bark ..... ***Dirina paradoxa*** subsp. ***approximata***
1. On rock 2

2. Apothecia sessile and/or thallus sorediate ..... ***Dirina catalinariae***
2. Apothecia immersed, thallus non-sorediate ..... ***Dirina mexicana***

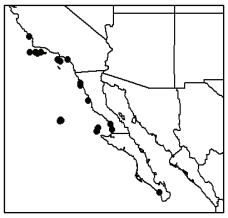
The Species

Dirina catalinariae Hasse, Bryologist 14: 102 (1911).

Illustrations: Tehler (1983), pp. 40 & 41.

Thallus: crustose but sometimes slightly bullate or nearly subfruticose, effuse, 0.2-1.1 mm wide; **surface:** varying from creamy white to grayish white, smooth, slightly pruinose; **soredia:** often present, granular, when young in punctiform soralia that becoming maculiform to capitate when old; **cortex:** 35-65 µm thick; **"Apothecia":** numerous, circular in outline, sessile, 0.5-2 mm diam.; exciple: usually undulating or strongly undulating sometimes to the extent that the ascomata may become stromatoid; hymenium: 50-140 µm high; paraphysoids: sparsely branched, parallel, hyaline, *c.* 1 µm in diam.; **asci:** clavate, 70-120 x 15 µm, 8-spored; **ascospores:** fusiform, hyaline, 3-septate, 23-29 x 5-6 µm; **Spot tests:** cortex K-, C+ red, KC+ red, P-; medulla K-, C+ red, KC+ red, P-; **Secondary metabolites:** erythrin, lecanoric acid, and an unknown substance.

Substrate and ecology: growing on vertical or overhang rocks and cliffs near the sea; occasionally abundant with individuals forming large mosaic patterns; **World** and **Sonoran distribution:** along the Californian coast from Monterey Co. in the north to Baja California Sur. The two forms, *Dirina catalinariae* f. *catalinariae* and *D. catalinariae* f. *sorediata* are sympatric throughout their respective ranges.



Dirina catalinariae f. catalinariae

Illustration*:* Tehler (1983), p. 35.

Thallus: without soredia.

Dirina catalinariae f. sorediata Tehler, Opera Bot. 70: 36 (1983).

Illustrations: Tehler (1983), p. 36; Brodo et al. (2001), p. 305.

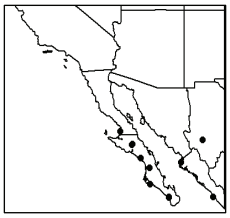
Thallus: with soredia.

Dirina mexicana Tehler, in Tehler et al., Lichenologist 27: 256 (1995).

Illustration: Tehler et al. (1995), p. 256.

Thallus: crustose but sometimes slightly bullate, effuse, 0.2-0.5 mm wide; **surface:** varying from yellowish white to white to grayish white, smooth, epruinose to slightly pruinose; soredia and isidia: not seen; **cortex:** 20-40 µm thick; **"Apothecia":** numerous, circular or elongated in outline, immersed or subimmersed, 0.4-0.8 mm diam.; exciple: usually immersed and coinciding with the thallus but often slightly elevated and distinguished from the thallus by a brownish marginal surface; hymenium: 50-140 µm high; paraphysoids: sparsely branched, parallel, hyaline, *c.* 1 µm in diam.; **asci:** clavate, 70-120 x 15 µm, 8-spored; **ascospores:** fusiform, hyaline, 3-septate, 21-27 x 5-6 µm; **Spot tests:** thallus K-, C+ red (and KC+ red) in rimulae and thalline margin otherwise C-, KC-, P-; medulla K-, C+ red, KC+ red, P-; **Secondary metabolites:** erythrin, lecanoric acid, orsellinic acid and two unknown substances.

Substrate and ecology: growing on vertical or overhang rocks and cliffs near the sea; occasionally abundant with individuals forming large mosaic patterns; **World** and **Sonoran distribution:** Baja California Sur, Baja California and Sinaloa on the mainland.



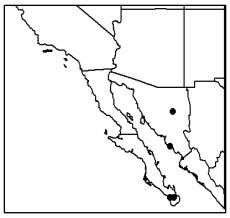
Notes: *Dirina mexicana* falls within the group with immersed ascocarps: *D. insulana*, *D. immersa* and *D. cretacea* (Tehler 1983). It is similar to the European species *Dirina insulana* and *D. immersa* but is distinguished from those two by the yellowish tinge of the thallus. However, this character is variable and sometimes the thallus is merely white or white-grayish. Another characteristic of *Dirina mexicana* is the often brownish color of the thin,

slightly elevated thalline margin. *Dirina mexicana* is partly sympatric with the other two *Dirina* species of the region, *D. paradoxa* and *D. catalinariae*, both of which have conspicuously sessile apothecia with constricted bases in contrast to *D. mexicana* with its immersed apothecia.

Dirina paradoxa subsp. **approximata** (Zahlbr.) Tehler, Lichenologist 18: 296 (1986).

Basionym: *Dirina approximata* Zahlbr., Ann. Mycol. 29: 78 (1931); Illustration: Tehler (1983), p. 40.

Thallus: crustose, effuse, 0.1-0.7 mm, **surface:** varying from white to creamy white, smooth, epruinose to slightly pruinose; soredia and isidia: not seen; **cortex** 10-50 µm thick; **"Apothecia":** numerous, circular in outline, sessile, 0.5-1.6 mm diam.; exciple: usually undulating; hymenium: 50-140 µm high; paraphysoids: sparsely branched, parallel, hyaline, *c.* 1 µm in diam.; **asci:** clavate, 70-120 x 15 µm, 8-spored; **ascospores:** fusiform, hyaline, 3-septate, 28-33 x 4-5 µm; **Spot tests:** cortex K-, C+ red, KC+ red, P-; medulla K-, C-, KC-, P-; **Secondary metabolites:** erythrin and lecanoric acid.



Substrate and ecology: growing on trees and shrubs near the sea; **World distribution:** only known from the Galapagos Islands outside of the Sonoran region; **Sonoran distribution:** known from Baja California Sur (Todos Santos area) and Sonora.

Notes: *Dirina paradoxa* subsp. *approximata* is similar to *Roccellina conformis* which also occurs on bark, but *D. paradoxa* is easily distinguished by its C+ red thallus. *Dirina paradoxa* includes two other subspecies, *D. paradoxa* subsp. *hioramii* in the Greater and Lesser Antilles, and *Dirina paradoxa* subsp. *africana* on the Canary Islands, the Atlantic coast of northern Africa and in Yemen and Socotra Island (Tehler 1983).

DISTOPYRENIS

by A. Aptroot

Distopyrenis Aptroot, Biblioth. Lichenol. 44: 41 (1991).

Family: Pyrenulaceae; Type: *Distopyrenis americana* Aptroot; No. species: three world-wide; Selected lit.: Aptroot (1991).

Life habit: non-lichenized, saprophytic; **Thallus:** absent or immersed in the substrate; **photobiont:** absent; **Ascomata:** perithecial, simple; **involucrellum:** dark brown to black, composed of fungal hyphae interspersed with bark cells; **ascomatal wall:** black, continuous below the hamathecium; true **exciple:** brown, entire below the perithecial cavity; **hamathecium:** unbranched paraphyses, amyloid (IKI+ blue); **asci:** bitunicate, cylindrical, ocular chamber rounded, tholus non-amyloid; **ascospores:** brown, ellipsoid, 1-septate with a median distoseptum, 12-17 x 5-9 µm; walls: not ornamented; **Conidiomata:** pycnidial; **conidia:** filiform, hyaline; **Secondary metabolites:** absent; **Geography:** SE U.S.A. to the neotropics; **Substrate:** only on bark.

Notes: It is characterized by the brown, 1-septate distoseptate ascospores and the unbranched paraphyses; differing from all other genera of the Pyrenulaceae in the consistently 1-septate, brown ascospores.

The Species

Distopyrenis americana Aptroot, Biblioth. Lichenol. 44: 42 (1991).

Illustrations: Aptroot (1991), pp. 143 & 154.

Thallus: absent or immersed in the substrate; **upper surface:** if present, a whitish gray discoloration relative to adjacent bark surface, dull; photobiont: absent; **Perithecia:** hemispherical or elongated due to the wood veins, black, semi-immersed in the substrate, *c.* 1 mm diam., often flattened; **ascomatal wall:** black, continuous below the hamathecium, ostiole papillate; **hamathecium:** unbranched paraphyses (or branched at tips), not anastomosing above the asci; filaments: *c.* 1 µm wide, not inspersed with oil droplets, gelatinized, IKI + blue; **asci:** clavate, *c.* 50-60 x 8-10 µm, with 8, uniseriately arranged ascospores; **ascospores:** brown, broadly ellipsoid, 1-septate with a median euseptum, cell walls much thickened leaving angular lumina, 13-16 x 6-8 µm; walls: not ornamented, without a gelatinous sheath; **Pycnidia:** black, immersed, wall blackened only in the upper part; **conidia:** filiform, hyaline, 6-10 x 0.2-0.4 µm; **Spot tests:** all negative, UV negative; **Secondary products:** none detected.

Substrate and ecology: on bark and wood of *Lycium*; **World distribution:** previously only known from SE USA and tropical America, but also recently found in Papua New Guinea (Aptroot, unpublished); **Sonoran distribution:** only collected once on the Channel Islands in southern California on *Lycium*.

ENDOCARPON

by O. Breuss

Endocarpon Hed., Descr. Adumbr. Muscor. Frond. 2: 56 (1789).

Family: Verrucariaceae; Type: *Endocarpon pusillum* Hed.; No. species: *c.* 60 world-wide; Selected lit.: McCarthy (1991) and Harada (1993).

Life Habit: lichenized; **Thallus:** squamulose to subfoliose, fruticose in one species; **squamules:** scattered to contiguous or imbricate, 0.5-10 mm (rarely more) wide, plane to concave or convex, rounded or variously lobed, closely appressed to the substrate or ascending (to erect), attached by folds of the lower side, basal ends of squamules, rhizines, or rhizohyphal wefts; **upper surface:** various shades of brown, smooth or rugulose to shallowly rimose, dull, lacking isidia and soredia; **upper cortex:** paraplectenchymatous, 10-100 µm thick, composed of roundish-angular cells, with or without an amorphous epinecral layer; **medulla:** white (yellow in one species), of intricately interwoven hyphae, filamentous to subparaplectenchymatous; **photobiont:** primary one a green alga (*Stichococcus*), secondary photobiont absent; algal cells 5-14 µm in diam.; algal layer: irregularly dispersed or in vertical columns; forming a continuous or discontinuous layer; **lower cortex:** (sub)paraplectenchymatous or lacking; rhizohyphae colorless or brown; **lower surface:** pale to carbonaceous, bare, or with rhizohyphal weft, or with rhizines; **Ascomata:** perithecial, laminal, immersed, broadly pyriform to subglobose, without involucrellum; exciple: hyaline, brown or brown-black to carbonaceous; interascal filaments: evanescent; hymenial gel: amyloid (I+ reddish or blue, KI+ blue); hymenial alga: present, globose to cuboid or elongate; ostiolar filaments (periphyses): present, simple to moderately branched, their walls becoming gelatinized in wet condition; **asci:** bitunicate, thin-walled, clavate or cylindro-clavate, usually bisporous (rarely mono- or tetrasporous), wall non-amyloid; **ascospores:** colorless or pale to dark brown, broadly ellipsoid to elongate-ellipsoid to subcylindrical; distal ascospore: mostly shorter and broader than the proximal one, thin-walled, smooth, without halo; **Conidiomata:** pycnidia, of *Staurothele*-type, laminally immersed; conidiogenous layer: simple to convoluted; **conidia:** bacilliform; **Secondary metabolites:** none detected; **Geography:** world-wide, mainly temperate; **Substrate:** soil, detritus, mosses, rocks, rarely bark.

Key to the species of ***Endocarpon*** from the Sonoran region:

1. Thallus subfruticose, composed of upright, flattened or almost cylindrical, dichotomously divided, tortuose lobes; medulla loosely filamentous; lower cortex of con-

glutinated cells in vertical columns; hymenial algal cells oblong to cylindrical ..... ***E. pulvinatum***

1. Thallus squamulose; medulla dense; lower cortex, if present at all, of irregular, not strongly conglutinated cells; hymenial algal cells ± globose 2

2. Medulla yellow ..... ***E. myeloxanthum***
2. Medulla not yellow 3

3. Rhizines present; asci mono- or bisporous 4
3. Rhizines lacking; asci always bisporous 6

4. Asci monosporous ..... ***E. simplicatum***
4. Asci bisporous 5

5. Rhizines black, with a carbonaceous outer layer and pale core; squamules with a black basal layer; lower surface black ..... ***E. pusillum***
5. Rhizines whitish or darkening, but not carbonaceous; lower side of squamules pale ..... ***E. loscosii***

6. Squamules small (0.5 - 1.5 mm), finely lobed, usually on rock 7
6. Squamules larger (up to 3 - 4 mm), usually on earth 9

7. Rhizohyphae 4 - 5 µm thick; hymenial algae 3 - 5 µm in diam. ..... ***E. schisticola***
7. Rhizohyphae thin (2.5 - 3.5 µm); hymenial algae small (2.5 - 3.5 µm in diam.) 8

8. Squamules loosely aggregated to imbricate, margins free, lower surface blackish ..... ***E. pallidulum***
8. Squamules dispersed to adjacent, not overlapping, broadly adnate ..... ***E. petrolepideum***

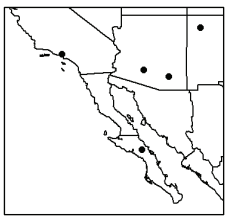
9. Lower surface pale; squamules attached by rhizohyphae. Medulla of filamentous hyphae ..... ***E. pallidum***
9. Lower surface dark; squamules attached by folds of lower side, rhizohyphal weft lacking, medulla subparaplectenchymatous ..... ***E. pseudosubnitescens***

The Species

Endocarpon loscosii Müll. Arg., Flora 55: 503 (1872).

Illustration: Etayo and Breuss (1996), p. 221.

Thallus: squamulose; **squamules:** 1-2 mm wide, 0.2-0.35 mm thick, solitary to adjacent and hardly overlapping, adnate, plane or with weakly elevated margins, shallowly to deeply incised; **upper surface:** grayish brown to medium brown, the edges often paler and appearomg as though gnawed; **upper cortex:** 30-50 µm thick, composed of anticlinally oriented hyphae; cells: in vertical columns, angular, isodiametrical and 5-10 µm in diam., or vertically elongated and up to 13 x 7 µm, amorphous layer up to 30 µm high; **medulla:** white, composed of interwoven hyphae divided into a varying number of spherical cells (7-11 µm in diam.); algal layer: *c.* 60-100 µm thick, unevenly delimited; algal cells: 7-12 µm in diam.; **lower cortex:** no true one developed, but more densely packed spherical cells found below; **lower surface:** whitish or darkening, attachment by rhizohyphal wefts and additionally rhizines; rhizohyphae: hyaline, 3-4.5 µm in diam., forming a rather loose hypothalline weft; rhizines: few per squamule, whitish or pale gray-brown, normally not blackening, long and slender, sparingly branched; main stems: 50-120 µm thick and up to 3 mm long, not linking squamules; **Perithecia:** broadly pyriform to almost globose, up to 0.45 mm broad; exciple: black, 20-30 µm thick; periphyses: 25-40 µm long; hymenial algal cells: subglobose to ellipsoid, 3-5 µm in diam.; **asci:** oblong-clavate, 75-95 x 20-28 µm, 2-spored; **ascospores:** muriform, pale to dark brown, 30-41 x 17-25/ 38-54 x 13-21 µm (distal/proximal spores); **Pycnidia:** rarely found; **conidia:** *c.* 5 x 1 µm; **Spot tests:** all negative; **Secondary metabolites:** none detected.



Substrate and ecology: in arid sites on fine-grained soil, rarely on weathered rock; **World distribution:** Europe (Spain, Austria, Russia) and western North America (from Washington south to Mexico); **Sonoran distribution:** Arizona, southern California and Baja California Sur.

Notes: *Endocarpon loscosii* resembles *E. pusillum* from which it is distinguished by pale undersides of squamules and whitish rhizines. Though the rhizines may darken with age, they never become carbonaceous as in *E.*

pusillum. Moreover, the smaller asci are distinctive (75-95 x 20-28 µm versus 90-125 x 20-33 µm in *E. pusillum*).

Endocarpon myeloxanthum Breuss, Österr. Z. Pilzk. 9: 148 (2000).

Illustration: Breuss (2000a), p. 150.

Thallus: squamulose; **squamules:** small (*c.* 1-2 mm wide and 0.1-0.2 mm thick), densely imbricate in several layers, adnate, lobed; **upper surface:** medium to dark brown, smooth, dull; **upper cortex:** 20-30 µm thick, composed of angular cells (4-9 µm in diam.), overlain by a thin amorphous layer; **medulla:** yellow, composed of densely interwoven hyphae divided into many spherical cells (5-9 µm in diam.), upper part densely inspersed with small crystals, (downwards less inspersed and darkening - thus merging into a thick dark basal layer); algal layer: averaging 50 µm in thickness, evenly delimited above, uneven below, horizontally continuous or slightly divided by vertical hyphal bundles; algal cells: *c.* 5-8 µm in diam.; **lower cortex:** not developed; **lower surface:** black, squamules attached by rhizohyphae; rhizohyphae: brownish, 3-5 µm thick; **Perithecia:** subglobose, up to 0.25 mm broad, deeply sunken into the dark basal layer of squamules; exciple: black throughout, *c.* 25 µm thick; periphyses: 20-35 µm long; hymenial algal cells: globose, 3-5 (-6) µm in diam.; **asci:** clavate, 70-80 x 15-20 µm, 2-spored; **ascospores:** muriform, hyaline to slightly brownish, 25-30 x 12-15 / 32-40 x 11-13µm (distal/proximal spores); **Pycnidia:** immersed; **conidia** *c.* 5 x 1 µm; **Spot tests:** all negative; **Secondary metabolites:** none detected.

Substrate and ecology: on rock; **World and Sonoran distribution:** known only from the type collection in Sonora.

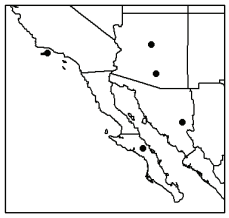
Notes: *Endocarpon myeloxanthum* is the only species known to have a yellow medulla, apparently caused by crystaline inclusions which are clearly visible in microscopical sections of well-developed, thicker squamules under polarized light. The inspersed upper part of medulla may be very poorly developed or even lacking in thin squamules.

Endocarpon pallidulum (Nyl.) Nyl. in Hue, Nouv. Archiv Mus., ser. 3, 4: 106 (1892).

Basionym: *Verrucaria pallidula* Nyl., Flora 57: 73 (1874); Synonym: *Endocarpon neopallidulum* Harada; Illustrations: Harada (1993), pp. 337 & 341 as *E. neopallidulum*.

Thallus: squamulose; **squamules:** 0.5-1.5 mm wide, 0.1-0.2 mm thick, loosely aggregated to imbricate, ± finely lobed, with margins free from the substrate and ± ascending, centrally attached; **upper surface:** pale brown, smooth; **upper cortex:** 20-40 µm thick, composed of rather large, angular cells (6-15 µm in diam.), lacking an amorphous layer; **medulla:** white, subparaplectenchymatous, composed of spherical cells (5-8 µm in diam.), becoming more closely packed with depth to form a paraplectenchymatous basal layer; algal layer: *c.* 40-60 µm thick, rather continuous; algal cells: 6-11 µm in diam.; **lower cortex:** weakly differentiated from the medulla, composed of more angular, closely packed and dark pigmented cells; rhizohyphae: hyaline to brownish, 2.5-3.5 µm thick, forming a few bundles (but not true rhizines); **lower surface:** black except for elevated marginal parts; **Perithecia:** subglobose, up to 0.3 mm wide, causing swellings on the lower side of the squamules; exciple: black, *c.* 20 µm thick; periphyses: 20-35 µm long; hymenial algal cells: globose, 2.5-3.5 µm in diam.; **asci:** clavate, *c.* 60-75 x 15-20 µm, 2-spored; **ascospores:** muriform, hyaline to faintly yellowish-brown, 25-30 x 12-15/ 27-35 x 11 - 13 µm (distal/proximal spores); **Pycnidia:** not seen; **Spot tests:** all negative; **Secondary metabolites:** none detected.

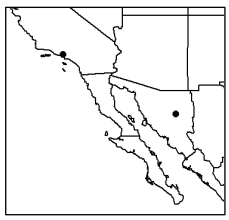
Substrate and ecology: on limestone and acidic rock or thin soil layer thereon; **World distribution:** Peru, West Indies, SW North America, Queensland and Japan; **Sonoran distribution:** Arizona, southern California, Sonora and Baja California Sur.



Notes: The distinction from *Endocarpon petrolepideum* may be difficult. The squamules of *E. pallidulum* tend to be somewhat larger and more or less imbricate, and are attached to the substrate only by their central parts, whereas those of *E. petrolepideum* are smaller, ± dispersed and broadly adnate.

Endocarpon pallidum Ach., Lich. Univ.: 301 (1810).

Thallus: squamulose; **squamules:** adjacent or slightly overlapping, 2-3 mm wide, 0.2-0.25 mm thick, adnate, the margins free from the substrate and slightly elevated, rounded to irregularly lobed; **upper surface:** pale brown, gray-brown or beige, smooth, dull; **upper cortex:** 20-40 µm thick, composed of angular cells (5-9 µm wide in upper part, their size continuously enlarging with depth up to 16 µm in diam.); **medulla:** composed of loosely interwoven, filamentous hyphae with a few spherical cells (in lowermost parts more tightly packed without forming a true cortex); algal layer: averaging 70 µm in height; algal cells: 7-14 µm in diam.; **lower cortex:** lacking, lowermost part of squamules composed of more tightly packed medullary hyphae (some of them bending into the substrate as rhizohyphae); rhizohyphae: hyaline, *c.* 2.5 µm in diam.; **lower surface:** whitish to pale brown; **Perithecia:** broadly pyriform to subglobose, up to 0.3 mm wide, perithecial apex concolorous with thallus or slightly darker, inconspicuous; exciple: brown to black, *c.* 30 µm thick; periphyses: *c.* 30-40 µm long; hymenial algal cells: globose, 3-5 µm in diam.; **asci:** clavate to cylindroclavate, 75-95 x 20-25 µm, 2-spored; **ascospores:** hyaline to slightly brownish, muriform, broadly ellipsoid to elongate, 28-34 x 13-16/ 30-40 x 11-13 µm (proximal/distal spores); **Pycnidia:** inconspicuous, small; **conidia:** shortly bacilliform, 3-5 x <1 µm; **Spot tests:** all negative; **Secondary metabolites:** none detected.



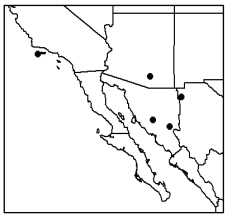
Substrate and ecology: mainly on soil, rarely on rock or bark in dry regions; the Mexican specimen was collected from a tree trunk; **World distribution:** central and southern Europe, N Africa, United States and Australia; **Sonoran distribution:** southern California and Sonora.

Notes: *Endocarpon pallidum* can be readily recognized by its loosely filamentous medullary tissue.

Endocarpon petrolepideum (Nyl.) Nyl. in Hue, Nouv. Archiv Mus., ser. 3, 4: 106 (1892).

Basionym: *Verrucaria petrolepidea* Nyl., Lich. Japon.: 88 (1890); Illustrations: Harada (1993), pp. 337 & 345.

Thallus: squamulose; **squamules:** scattered to adjacent, not overlapping, 0.5-1 mm wide, 0.1-0.25 mm thick, plane, broadly adnate with only the very edges slightly elevated, incised; **upper surface:** brown, smooth, often with darker rims; **upper cortex:** 10-30 µm thick, composed of angular cells (5-9 µm in diam.); **medulla:** composed of spherical cells 5-9 µm wide with small air spaces between them; algal layer: 30-60 µm high; algal cells: 6-10 µm in diam.; **lower cortex:** not delimited, composed of more closely packed medullary cells whose walls darken below; rhizohyphae: hyaline to faintly brownish, 2.5-3.5 µm thick; **lower surface:** pale brown to blackish; **Perithecia:** broadly pyriform, up to 0.25 mm wide; apex: concolorous with or paler than the thallus; exciple: dark brown to black, *c.* 20 µm thick; periphyses: *c.* 25-35 µm long; hymenial algal cells: (sub)globose, 2.5-3.5 µm in diam.; **asci:** clavate, *c.* 70 x 17 µm, 2-spored; **ascospores:** muriform, ellipsoid, colorless to very pale brownish when overmature; the proximal and distal spores of about the same length, 25-32 x 12-16/ 25-36 x 10-13 µm; **Pycnidia:** not seen; **Spot tests:** all negative; **Secondary metabolites:** none detected.



Substrate and ecology: on siliceous rock in dry and sun-exposed situations; **World distribution:** Japan and SW North America; **Sonoran distribution:** Arizona, California (Channel Islands) Chihuahua and Sonora.

Notes: The distinction from *E. pallidulum* may be difficult (see under that species).

Endocarpon pseudosubnitescens Breuss, **sp. nov.**

Diagnosis: *Endocarpon pusillum simile, sed differt rhizinis rhizohyphisque nullis.*

Type: MEXICO, Baja California Sur: N-facing conglomerate outcrops along pass through the Sierra de la Giganta 23.5 km SW of Loreto along dirt road to San Javier, 25º 57'N, 111º30'W, *c.* 580 m, 18 March, 1992, T. H. Nash III 30410 (ASU).

Other specimen examined: MEXICO, Sonora, 24 km W. of Río Yaquí along Sonoran Hwy 20, 450 m, 28º50'N, 110°00'W, 21 February, 1987, B. D. Ryan 21712 (ASU).

Synonym: *Endocarpon subnitescens* auct. non (Nyl.) Nyl.

Thallus: squamulose; **squamules:** contiguous or slightly overlapping, 1-3 mm wide, 0.15-0.3 mm thick, ± deeply lobate, closely adnate; **upper surface:** pale to dark brown, smooth, dull; **upper cortex:** 30-50 µm thick, composed of angular cells (4-9 µm wide), in ± vertical columns, with a thin amorphous, epinecral layer; **medulla:** white, subparaplectenchymatous, composed of roundish cells (6-11 µm in diam.); algal layer: *c.* 50-100 µm thick; algal cells: 6-11 µm in diam., in vertical rows; **lower cortex:** paraplectenchymatous, brown-black, 30-40 µm thick; **lower surface:** black, bare, without rhizohyphae or rhizines; squamules attached by folds of their undersides; **Perithecia:** subglobose, up to 0.4 mm broad; exciple: dark brown to black, *c.* 25 µm thick; periphyses: 40-60 µm long, simple or sparingly branched; hymenial algal cells: globose, 4-5 µm in diam. or ellipsoid and 5-7 x 3-4 µm; **asci:** oblong-clavate, 2-spored; **ascospores:** muriform, hyaline to pale brown, broadly ellipsoid to oblong-subcylindrical; 30-50 x 14-25/ 40-60 x 13-18 µm (distal/proximal spores); **Pycnidia:** immersed, ovoid, up to 0.2 mm wide; **conidia:** bacilliform, 5-7 x 1 µm; **Spot tests:** all negative; **Secondary metabolites:** none detected.

Substrate: soil; **World** and **Sonoran distribution:** uncertain, only known from NW Mexico, probably to be found elsewhere.

Notes: The type specimen of *Endocarpon subnitescens* has conspicuous black rhizines and agrees also in all other details with *E. pusillum*, however, the name *E. Subnitescens* has long been erroneously used for an erhizinate taxon (*c.* Poelt 1974). Accordingly, a new name is required. *Endocarpon pseudosubnitescens* is clearly distinct from *E. pusillum* in having neither rhizines nor rhizohyphae. Its squamules are fastened to the substrate by folds or knobs of their naked lower side, which is clearly set off the substrate, whereas *E. pusillum* has a more or less thick dark basal layer that merges into a weft of rhizohyphae penetrating the substrate though the squamules are mainly anchored by ± conspicuous black rhizines. Moreover, the conidia of *E. pseudosubnitescens* are longer, and the ascospores tend to be paler.

Endocarpon pulvinatum Th. Fr., Nova Acta Reg. Soc. Sci. Upsal. ser. 3, 3: 357 (1861).

Synonyms: *Endocarpon tortuosum* Herre, *Pyrenothamnia spraguei* Tuck.; *Pyrenothamnia brandegei* (Tuck.) Zahlbr.; Illustrations: Brodo et al. (2001), p. 308; Thomson (1984), p. 222.

Thallus: subfruticose, consisting of upright, elongate squamiform or subcylindrical lobes forming cushions up to 2 cm wide (or larger aggregates); **lobes:** bifacial, tortuose nodulate, ± stipitate, up to 7 mm tall, 0.15-0.3 mm thick, repeatedly dichotomously branched, several of them rising from a common holdfast; **upper surface:** medium to dark brown or brown-black, dull; **upper cortex:** 20-30 µm thick, composed of roundish-angular cells (4-8 µm in diam.), lacking an amorphous layer; **medulla:** white, loosely filamentous with large air spaces especially in nodular parts of lobes, hyphae *c.* 3 µm thick; algal layer: 50-100 mm high, uneven above and below, horizontally discontinuous; algal cells: *c.* 7-9 µm in diam., interstitial hyphae paraplectenchymatous above, rather loosely arranged below; **lower cortex:** abruptly delimited, paraplectenchymatous, 25-45 µm thick, hyaline to pale brownish, composed of rather thick-walled, conglutinated, angular cells (5-10 µm wide) in distinct vertical columns; rhizohyphae: lacking; **lower surface:** paler than upper side, rugose, bare; squamules attached by holdfasts;

Perithecia: innate in distal parts of lobes, causing swellings on the underside, broadly pyriform, up to 0.3 mm wide; exciple colorless or very pale brownish; periphyses: 50-80 µm long; hymenial algal cells: ellipsoid-oblong to mostly elongate, 5-8 x 2.5-3 µm, up to 12 µm long when in division; **asci:** narrowly clavate, *c.* 100-130 x 25-33 µm, 2-spored; **ascospores:** strongly muriform, at first hyaline but becoming dark brown with age, 45-57 x 21-25/ 45-60 x 13-20 µm (distal/proximal spores); **Pycnidia:** not seen; **Spot tests:** all negative; **Secondary metabolites:** none detected.

Substrate and ecology: on calcareous or non-calcareous rocks; **World distribution:** mainly northern, scattered in North America, Greenland, Scandinavia; **Sonoran distribution:** collected only once in the Sierra San Pedro Martir at 2800 m in Baja California.

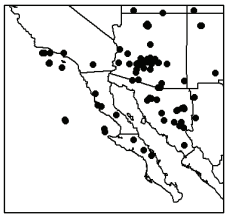
Notes: *Endocarpon pulvinatum* is unique in being subfruticose, in the construction of its lower cortex of strictly vertically arranged hyphae, and in having elongate hymenial algal cells.

Endocarpon pusillum Hed., Descr. Adumbr. Muscor. Frond. 2: 56 (1789).

Synonyms: *Endocarpon lepidallum* Nyl., *Endocarpon subnitescens* (Nyl.) Nyl.; Illustrations: McCarthy (1991), p. 38; Harada (1993), p. 347; Brodo et al. (2001), p. 308.

Thallus: squamulose; **squamules:** scattered to contiguous but hardly overlapping, *c.* 1-3 mm wide, 0.15-0.25 mm thick, usually weakly to deeply lobate, plane and fully adnate, more rarely concave with margins turned upward, with conspicuous black rhizines anchoring and linking squamules; **upper surface:** pale ochraceous brown to dark brown or with an olivaceous tinge or red-brown, smooth, dull; **upper cortex:** 30-70 µm thick, composed of angular cells (5-10 µm in diam.), in ± distinct vertical rows, isodiametrical or vertically elongated, composed of equal sizes throughout or becoming somewhat larger (up to 12 µm) with depth, overlain by a thin to thick amorphous layer; **medulla:** white, subparaplectenchymatous, composed of roundish cells (5-10 µm in diam.); algal layer: *c.* 50-80 µm high, unevenly delimited below, horizontally continuous; interstitial hyphae: paraplectenchymatous; algal cells: 6-10 µm in diam., in vertical rows; **lower cortex:** brown-black, ± paraplectenchymatous in upper part, merging into a ± thick, dark basal layer composed of interwoven hyphae interspersed with substrate particles; rhizohyphae: hyaline to brown; **lower surface:** black, rhizinate; rhizines: usually conspicuous, moderately to richly branched, black, with a carbonaceous envelop and a white core, with main stems up to 0.25 mm thick and up to several mm long; ramifications: partly anastomosing thus linking squamules; **Perithecia:** (sub-) globose, up to 0.4 mm wide; exciple: brown-black to black, 20-30 µm thick; periphyses: 40-60 µm long, simple; hymenial algal cells: subglobose and (2.5-) 3-4 (-5) µm wide to ellipsoid-oblong and 4-6 (-7) x 2.5-3 (-4) µm; **asci:** clavate to cylindro-clavate, 90-125 x 20-33 µm, 2-spored (very rarely 1-spored); **ascospores:** muriform, hyaline to dark brown, broadly ellipsoid to elongate-ellipsoid to subcylindrical, 35-53 (-60) x 16-26/40-65 x 13-18 µm (distal/proximal spores); **Pycnidia:** immersed, up to 0.2 mm wide, opening indistinct or crateriform; **conidia:** bacilliform, 3-5 x <1 µm; **Spot tests:** all negative; **Secondary metabolites:** none detected.

Substrate and ecology: on bare or mossy soil and soil cover over rocks, rarely on crumbling rock, over both calcareous and non-calcareous substrate, from low to high elevations; **World distribution:** cosmopolitan; **Sonoran distribution:** common but never abundant in Arizona, California, Baja California, Baja California Sur, Chihuahua and Sonora.



Notes: *Endocarpon pusillum* is quite variable considering thallus morphology, development of upper cortex, thickness of the dark basal layer, and ascospore size and pigmentation. Black rhizines, a black basal layer and bisporous asci is the diagnostic combination of characters. The rhizines are usually conspicuous, but may be stubby in poorly developed thalli or thalli growing directly on (crumbling) rock. These specimens are easily confused with *Endocarpon pseudosubnitescens* auct. (see under that species). Specimens of *Endocarpon loscosii* with unusual dark undersides and rhizines can easily be dis-

tinguished by their notably shorter asci (75-95 x 20-28 µm as against to 90-125 x 20-33 µm in *E. pusillum*). The type material of both *Endocarpon lepidallum* and *E. subnitescens* agrees in all aspects with *E. pusillum* and is therefore reduced to synonymy.

Endocarpon schisticola de Lesd., Bull. Soc. Bot. France 84: 282 (1937).

Thallus: squamulose; **squamules:** 1-1.5 mm wide, 0.2-0.25 mm thick, plane, contiguous to ± overlapping, incised; **upper surface:** brown, smooth, dull; **upper cortex:** *c.* 30 µm thick, cells 5-8 µm wide; **medulla:** white, subparaplectenchymatous, composed of roundish cells (5-8 µm in diam.), with small interhyphal spaces; algal layer: *c.* 60-80 µm thick; algal cells: 5-11 µm in diam.; **lower cortex:** thin, composed of 1-3 layers of roundish-angular cells (5-7 µm in diam. with brown-black walls); rhizohyphae: hyaline to faintly brown, 4-5 µm thick; **lower surface:** pale brown; **Perithecia:** broadly pyriform, up to 0.3 mm broad; exciple: at first pale but soon darkening, black in old perithecia; periphyses: stout, 15-25 µm long; hymenial algal cells: subglobose, 3-5 µm in diam.; **asci:** clavate, *c.* 65-85 x 17-22 µm, 2-spored; **ascospores:** muriform, colorless to pale brownish, 25-38 x 15-18/ 30-42 x 13-16 µm (distalproximal spores); **Pycnidia:** rarely found; **conidia:** bacilliform, *c.* 5 x 1 µm; **Spot tests:** all negative; **Secondary metabolites:** none detected.

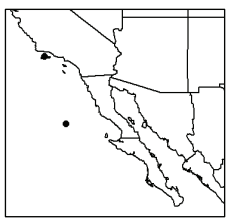
Substrate and ecology: on rock (schist or limestone); **World distribution:** previously known only from Italy (Liguria); **Sonoran distribution:** collected once in Arizona.

Notes: *Endocarpon schisticola* is a rare and little-known species characterized by small saxicolous squamules with pale undersides, and short periphyses. From the other small, saxicolous species of the region (*E. pallidulum* and *E. petrolepideum*) it is separable, besides its stout periphyses, by its thicker rhizohyphae and larger hymenial algal cells.

Endocarpon simplicatum (Nyl.) Nyl., Revue Bot. 6: 104 (1888).

Basionym: *Verrucaria simplicata* Nyl, Flora 67: 390 (1884); Illustration: McCarthy (1991), p. 46.

Thallus: squamulose; **squamules:** scattered or adjacent, 1.5-4 mm wide, 0.25-0.4 mm thick, rounded or deeply lobate, plane and fully adnate or concave with upturned and often undulate margins, ± distinctly black-rimmed, fastened by conspicuous black rhizines; **upper surface:** medium to dark brown, smooth or somewhat rugulose, dull, margins blackened and often slightly thickened; **upper cortex:** 30-50 µm thick; cells: angular, isodiametrical and *c.* 5-8 µm in diam. or anticlinally slightly elongated and then up to 11 x 8 µm wide, overlain by an amorphous layer (10-30 µm thick); **medulla:** white, composed of interwoven hyphae divided into many spherical cells (5-9 µm in diam.), with filamentous parts in thick squamules; algal layer: *c.* 50-80 µm thick, evenly delimited above, uneven below; algal cells: 5-9 µm in diam., ± in vertical columns; **lower cortex:** paraplectenchymatous, brown-black, 25-40 µm thick; cells: 5-9 µm wide; **lower surface:** black throughout, lacking rhizohyphae, rhizinate; rhizines: externally black, with a white core, 50-100 µm in diam. and up to more than 10 mm long, originating centrally or from most of the underside, usually branched, anchoring and linking squamules; **Perithecia:** broadly pyriform, up to 0.4 mm broad, causing swellings on the underside of squamules; exciple: *c.* 30 µm thick, black, often pale near the apex; periphyses: 40-60 µm long; hymenial algal cells: globose, 2-3 (-4) µm in diam. or ellipsoid and up to 5 x 3 µm; **asci:** clavate, 1-spored (very rarely 2-spored); **ascospores:** muriform, yellowish brown to brown, elongate-ellipsoid or narrowly clavate, (55-) 65-92 x 23-36 µm; **Pycnidia:** immersed, up to 0.2 mm wide, roundish, conidiogenous layer convoluted; **conidia:** bacilliform, 3-4.5 x <1 µm. **Spot tests:** all negative; **Secondary metabolites:** none detected.



Substrate and ecology: on soil in areas with Mediterranean climates; **World distribution:** SW Europe, Australia and SW North America; **Sonoran distribution:** southern California and Baja California.

Notes: The 1-spored asci are distinctive.

EVERNIA

by B. D. Ryan

Evernia Ach., Lich. Univ.: 84 (1810).

Family: Parmeliaceae; Type: *Evernia prunastri* (L.) Ach.; No. species: 10 world-wide; Selected lit.: Purvis et al. (1992), Bird (1974), Thomson (1984), & Keissler (1960).

Life habit: lichenized; **Thallus:** fruticose, or subfruticose ("elongate-foliose"), semi-erect to erect and caespitose, to subpendent or pendent and beardlike, up to 40-150 (-300) mm long, moderately to very flaccid, soft, and pliant, or sometimes stiffer (with hard and brittle cortex or denser medulla); weakly to richly branched, isotomic to anisotomic; **branches:** 1-4 mm wide, in cross-section semiterete and angular or strongly flattened and ± dorsiventral; without rhizines, attached by a basal disc or draped over the substrate; **(upper) surface:** ochraceous-yellowish to greenish yellow or ± greenish gray (rarely whitish mineral gray), often brownish to black at the tips; matt, epruinose, continuous, broadly wrinkled or ridged; rounded to effigurate pseudocyphellae sometimes present, white; with or without soredia, isidia; **cortex:** thin, of branched, septate, anticlinal hyphae, cells small and indistinct; **medulla:** white, thick, lax or dense, without strands; **photobiont:** primary one a *Trebouxia*, below at least the upper cortex, secondary photobiont absent; (**lower) surface:** (dorsiventral species) paler than upper (often whitish), grooved, soredia absent or present along marginal rim formed by rolled-down upper surface; **lower cortex:** similar to upper one, but sometimes very thin and unpigmented; **Ascomata:** apothecial, rare, marginal, lateral or terminal, shortly and stoutly stipitate, concave; disc: red-brown; thalline exciple: prominent, irregular, crenate; outer-ascomatal filaments absent; exciple: hyaline; hypothecium: hyaline; hymenium: hyaline, upper part brown or ochraceous-yellowish; paraphyses: thick, septate, unbranched; ostiolar filaments absent; **asci:** clavate, *Lecanora*-type, unitunicate; tholus I+ blue; 8-spored; **ascospores:** simple, hyaline, thin walled, 7-11 x 4-6 µm, ellipsoid, obtuse at the poles; wall thin, smooth, without distinct endospore thickening, not amyloid; **Conidiomata:** pycnidial, rare, laminal and marginal, immersed, rounded, blackened around the ostiole; conidiophores: ± type V of Vobis (1980); **conidia:** acicular, formed pleurogenously; **Secondary metabolites:** cortex with ß-orcinol depsides and usually usnic acid; medulla with orcinol depsides; **Geography:** arctic to temperate in the Northern Hemisphere; **Substrate:** bark, wood, or occasionally calcareous rocky soil or non-calciferous rock.

Notes: It differs from the fructicose genus *Ramalina* in having simple spores and in usually having a flaccid, often dorsiventral, thallus. Although the foliose genus *Pseudevernia* can also be caespitose, the latter genus has a canaliculate lower surface, always has a gray upper surface and has stiff thallus.

Key to the species of ***Evernia*** from the Sonoran region:

1. Branches distinctly flattened and usually paler below; with soredia and sometimes pseudoisidia; thallus caespitose to subpendent; medulla with evernic acid; southern California ..... ***E. prunastri***
1. Branches semiterete to angular, not flattened, similarly colored on all sides; without soredia; thallus usually pendent; medulla with divaricatic acid; Arizona ..... ***E. divaricata***

The Species

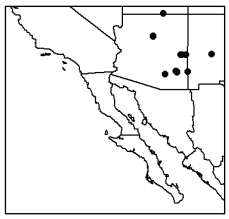
Evernia divaricata (L.) Ach., Lich. Univ. 441 (1810).

Basionym: *Lichen divaricatus* L., Syst. Veg. edit. 12: 713 (1768); Synonym: *Letharia divaricata* (L.) Hue; see Keissler (1960) for further synonymy; Illustrations: Bird (1974), fig. 4; McCune and Goward (1995), p. 100; Goward (1999), p. 173.

Thallus: usually pendulous, without evident base, 5-15 (30) cm long, not dorsiventral, concolorous on all sides,

richly but irregularly branched, with mostly obtuse and rounded axils, becoming entangled, or sometimes main branches mostly parallel and matting together into strands; **branches:** subterete to angular, or ± flattened just below the axils, very soft and flaccid, 0.5-1 (-2) mm wide, strap-shaped, within a given order of branching rather evenly thickned; with numerous but scattered; side branches: almost perpendicular but often curved away from the axil (divaricate), at first short and thorn-like, then becoming elongated (up to 2 cm) and further divided in a similar way, subcylindrical and towards the tips becoming subulate or often abruptly acuminate; **surface:** greenish gray to grayish yellowish green or pale yellowish green when fresh (in herbarium turning grayish yellow or creamy yellow or mottled whitish, or eventually yellowish or reddish brown), often with irregularly elongated and branched maculae of a paler, more yellowish color than the rest, the finer branches becoming gray-brown, darkest at the extreme tips; smooth or often with one or several shallow to deep longitudinal grooves or channels separated by low, rounded ridges, sometimes also with small depressions and wrinkles, but without a distinctly reticulate pattern; cortex matt, often degenerating and roughened in places, and (especially in age) frequently cracking transversely, exposing the medulla; soredia and isidia absent; **medulla:** fibrous to arachnoid and loose but often cohering as a strand *c.* 0.1-0.3 mm wide (usually less than half the width of the branch); **Apothecia:** very rare, sessile, lateral on the main branches, weakly margined, 2-6 mm diam.; disc: chestnut brown, roundish, plane; thalline margin (on underside): concolorous with thallus, rather flat, with wrinkles and veins throughout; hymenium: hyaline, upper part pale brown; paraphyses: short, dense, little branched, not septate, soon gelatinizing, *c.* 3 µm wide; hypothecium: hyaline; **asci:** short, clavate, not stalked, 8-spored, *c.* 40-45 x 12-15 µm; **ascospores:** adhering together, hyaline, somewhat greenish, moderately thick-walled, oblong-roundish, *c.* 6 x 3-4 µm, or when mature up to 8-10 x 4.5-5.5 µm; **Pycnidia:** very rare, laminal, immersed; **Spot tests:** cortex K-, C-, KC+ yellow, P-; medulla K-, KC+ yellow, P-, UV+ ice-blue; **Secondary metabolites:** cortex with usnic acid; medulla with divaricatic acid.

Substrate and ecology: pendulous, on stems or more often branches or twigs, mostly of conifers (especially spruce), in humid locations in montane to subalpine forests; **World distribution:** western North America (rather sporadic), Europe; Near East, China; **Sonoran distribution:** central to SE Arizona, 2700-3400 m, on *Abies concolor*, *A. lasiocarpa*, *Picea engelmannii*, *Pinus aristata* and *Pseudotsuga menziesii*.



Notes: This species is sometimes entangled with *Usnea* spp., and can be superficially rather similar to *Usnea cavernosa*, which has a central strand and can occur in similar habitats. Although the exposed medulla of *E. divaricata* can resemble the axial strand of an *Usnea*, the remaining pieces of cortex in the *Evernia* tend to be rather loosely attached to it, and have mostly longitudinal grooves rather than roundish foveolae. At least in the Sonoran region, *E. divaricata* shows very little morphological variation compared to most fruticose lichens. Farther north an alpine variant is prostrate on ground and is usually less than 5 cm long.

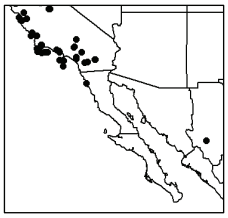
Evernia prunastri (L.) Ach., Lich. Univ. 442, tab. X, fig. 1 (1810).

Basionym: *Lichen prunastri* L., Spec. Pl. 1147 (1753); Synonyms: see Keissler (1960) for synonyms; Illustrations: Bird (1974), fig. 8; Hale and Cole (1988), pl. 3d; McCune and Goward (1995), p. 100; McCune and Geiser (1997), p. 113; Goward (1999), p. 173.

Thallus: (sub-)fruticose, erect and tufted to drooping and subpendent, (1-) 2-3 (-5) cm tall or in non-Sonroan regions occasionally pendent to 7-10 cm long, usually somewhat flaccid and pliant, occasionally very small, with very short, rosette-like aggregated branches occasionally with very short; axils: acute and V-shaped to almost right-angled (but rounded); **branches:** few to numerous, flattened, strap-shaped to very narrow and linear usually dorsiventral, mostly (0.5-) 1-1.5 (-3) mm wide, often ± broadened at major axils in the lower parts, to *c.* 5 mm wide there elongated, ± palmately branched to rather regularly dichotomous (dichotomies annual), often twisted, ultimate branches usually 1-2 (-3) mm long, 0.1-

0.2 mm wide, blunt or pointed, often forked; **upper surface:** green-gray to pale greenish yellow or pale yellowish green (slowly turning grayish yellow or finally brownish yellow in herbarium), or occasionally distinctly yellow, with age (or when damaged) bleaching to ash-gray to finally almost white but near the base itself often brownish yellow, extreme tips often darkened (brown); matt, sometimes (especially on smaller branches) with weak to strong mottling by paler, irregularly elongated and branched maculae, smooth to rather strongly rugose and pitted, often with an incomplete network of elongate ridges centrally spreading towards the margins; cortex degenerating and weakly cracked in places; **soredia:** finely to coarsely granular marginally, often on ridges and/or margins, or occasionally spreading and confluent usually white (often slightly bluish or blackish-speckled and distinctly contrasting with rest of the surface, but sometimes concolorous with it); **medulla:** uniformly loose, without hyphal bundles; **photobiont:** mainly confined to a layer just below the greenish side, in small groups, with at most a few clusters of algae near the underside; **lower surface** concolorous with upper side or more often paler or white (becoming creamy to slightly orange-yellow in herbarium), often dotted or blotched greenish especially towards the tips (more visible without lens than with it), broadly channeled, often with rims formed by the curved-down edge of the upper side (and then often sorediate), but mostly less wrinkled/ridged and pitted than then the upper surface; **Apothecia:** very rare (not seen in material from the Sonoran Region) marginal, substipitate, bowl-shaped then plane, 0.2-0.5 (-1.5) cm diam.; disc: red-brown, thalline margin: slightly crenate, underside concolorous with thallus, pitted and wrinkled; hymenium: hyaline, upper part reddish or brownish; paraphyses: conglutinate, filamentous, unbranched, 1 µm thick, tips broadened, yellowish or reddish; hypothecium: pale reddish to brownish, to almost hyaline; **ascospores:** ellipsoid, 7-11 x 4-6 µm; **Pycnidia:** very rare, *c.* 0.3 mm diam., marginal, immersed, roundish, ostioles dark or black; **conidia:** formed pleurogenously, acicular, straight, 6-7 x 0.5 µm; **Spot tests:** cortex K- (rarely K+ yellow), C-, KC+ yellow (rarely KC-), P-, UV-; medulla P-, K- or + yellow, KC-, C-, UV- or + pale blue; **Secondary metabolites:** cortex with usnic acid (usually major, sometimes ± absent), atranorin, and chloroatranorin, medulla with evernic acid.

Substrate and ecology: usually on neutral to acidic bark (stems, branches and twigs), especially of oaks and other broadleaf trees or shrubs (only occasionally on conifers), usually at lower elevations (but up to 1675 m) in areas with high humidity but mainly in sunny, often windswept; **World distribution:** incompletely circumpolar: western North America, Europe; northern Africa and Japan; **Sonoran distribution:** southern California, oak woodland and chaparral, now largely extinct south of Santa Barbara, 60-1400 m, on *Quercus* or occasionally *Baccharis*, *Heteromeles arbutifolia*, *Pinus nemorata*; occasional in Baja California.



Notes: The upper cortex is usually yellowish or greenish, with usnic acid, but rarely (e.g, the Channel Islands) it can be partly or entirely dirty ash-gray or bluish. See Keissler (1960) for formal description of forms and varieties. Forms with narrow lobes (often in more shaded habitats) and green specimens may be confused with *Ramalina* species (especially *R. farinacea*, with which it is often intermixed), but can distinguished by its more limp thallus and often dichtomous branching. A somewhat unusual morph found occasionally in the Sonoran region has numerous, narrow, elongate, and densely sorediate branches arising mostly near the tips of broad, scarcely branched and mostly non-sorediate lower branches. The relatively few specimens found today in mainland areas around the Los Angeles area are often rather small, poorly developed and distorted.

EVERNIASTRUM

by T. H. Nash III, B. D. Ryan and J.A. Elix

Everniastrum Hale *ex* Sipman, Mycotaxon 26: 237 (1986).

Family: Parmeliaceae; Type: *Everniastrum cirrhatum* (E. Fr.) Hale *ex* Sipman; No. species: *c.* 27 world-wide; Selected lit.: Elix (1994c), Sipman (1986), and Culberson and Culberson (1981).

Life habit: lichenized; **Thallus:** foliose to subfruticose, lobate, separate, loosely imbricate; **lobes:** linear-elongate, canaliculate; apices: usually truncate, ciliate; **upper surface:** light gray to gray, smooth, plane to rugulose, shiny or matt, maculate or not, usually epruinose; with or without isidia or soredia; pseudocyphellae absent; **upper cortex:** thin, *c.* 30 µm thick; pored epicortex, paraplectenchymatous; **medulla:** white, loosely packed, cell walls containing isolichenan; **photobionts:** primary one a *Trebouxia*, secondary photobiont absent; **lower surface:** brown to black, rhizinate or not; rhizines: long, simple, sparse, concolorous; cyphellae, pseudocyphellae and tomentum absent; **Apothecia:** laminal on thallus, orbicular, cup-shaped, subpedicellate or pedicellate; stipe: hollow; margin: prominent with thalloid rim; disc: imperforate, brown to dark brown; exciple: gray or hyaline; epithecium: brown or brownish yellow; hypothecium: hyaline; **asci:** lecanoral, wall layers of apex thickened, apex amyloid, relatively large (mean of 50 x 23 µm), *c.* 8-spored; **ascospores:** simple, ellipsoid; 10-28 x 4-12 µm; walls: thin, hyaline, not amyloid; **Conidiomata:** pycnidial, laminal or marginal, immersed or emergent sessile; **conidia:** bifusiform, 4-10 x 1 µm, or rarely filiform, 13-21 x 1 µm; **Secondary metabolites:** upper cortex atranorin and chloroatranorin; medulla some combination of orcinol depsides or depsidones, ß-orcinol depsides or depsidones, benzyl esters, or aliphatic acids; **Geography:** pantropical and extending into subtropical, montane regions, most diverse in Central and South America; **Substrate:** mostly bark, particularly common on conifers, rarely on rock.

Notes: The use of paraplectenchymatous to describe the upper cortex follows the use of that term by Hale (e.g. see Elix 1993a), but Culberson and Culberson (1981) designated it prosoplechtenchymatous. Because of the relative sparsity of true rhizines, the marginal cilia may sometimes touch the substrate, and consequently some authors have referred them as marginal rhizines. The related genus *Cetrariastrum* (not in the Sonoran region) has irregularly branched lobes, apothecia with solid stalks, smaller asci and a thicker hypothecium. Within the Sonoran region the only confusable genus is *Pseudevernia*, that lacks cilia entirely, has smaller ascospores and contains *Cetraria*-type lichenan in the hyphae cell walls.

Key to the species of ***Everniastrum*** in the Sonoran region:

1. Rhizines present, sparingly or dense (*nepalense* group). ..... ***E. pseudonepalense***
1. Rhizines absent (*cirrhatum* group) 2

2. Upper surface isidiate, sorediate, or both 3
2. Upper surface neither sorediate nor isidiate 4

3. Upper surface sorediate but never soredio-isidiate .... ***E. sorocheilum***
3. Upper surface isidiate or (in rare forms) soredio-isidiate ..... ***E. vexans***

4. Medulla with norstictic acid major ***E. neocirrhatum***
4. Medulla usually lacking norstictic acid (trace reported in one specimen) ..... ***E. cirrhatum***

The Species

Everniastrum cirrhatum (E. Fr.) Hale *ex* Sipman, Mycotaxon 26: 239 (1986).

Basionym: *Parmelia cirrhata* E. Fr., Syst. Orb. Beg. 1: 283 (1825); Synonym: *Cetrariastrum cirrhatum* (E. Fr.) W. L. Culb. & C. F. Culb.; Illustration: Culberson and Culberson (1981), p. 282.

Thallus: foliose to subcaespitose, very loosely adnate, up to 15 (-25) cm across, richly dichotomously or subdichotomously lobate; **lobes:** 0.5-2 (-4) mm broad, strongly to moderately involute or flat or nearly so; apices: abundantly ciliate; cilia: up to 4 mm long, simple or more commonly branched; **upper surface:** pale gray to gray; not sorediate or isidiate; **lower surface:** black or brown or pale brown at the tips of the lobes, mostly erhizinate but some specimens with a few short, usually simple, black rhizines; **Apothecia:** relatively infrequent, 4-6 mm diam.; **asci:** clavate, 8-spored; **ascospores:** ellipsoid or slightly reniform, 16-21 x 8-10 µm; **Pycnidia:** common, 0.1-0.2 mm diam.; **conidia:** bacilliform, straight, 5-7 (-8) x <1 µm; **Spot tests:** upper cortex K+ yellow, C-, KC-, P+ yellow; medulla K+ yellow then turning deep red, C-, KC-, P+ yellow then orange; **Secondary metabolites:** cortex with atranorin and chloroatranorin; medulla with salazinic acid (major), consalazinic acid (minor), galbinic and protocetraric acids (accessory) and a fatty acid.

Substrate and ecology: on trees and shrubs, rarely on rock or soil; **World distribution:** Mexico, Central and South America, southern Asia; **Sonoran distribution:** Sierra Madre Occidental of Chihuahua.

Everniastrum neocirrhatum (Hale & M. Wirth) Hale *ex* Sipman, Mycotaxon 26: 241 (1986).

Basionym: *Parmelia neocirrhata* Hale & M. Wirth, Phytologia 22: 37 (1971); Synonym: *Cetrariastrum neocirrhata* (Hale & M. Wirth) W. L. Culb. & C. F. Culb.; Illustration: Culberson and Culberson (1981), p. 288.

Thallus: foliose to subcaespitose, very loosely adnate, up to 13 (-19) cm across, dichotomously or subdichotomously lobate; **lobes:** 1-2 (-3) mm broad, strongly to moderately involute or occasionally nearly flat; apices: ciliate; cilia: sparse to moderately abundant, up to 2.5 mm long, usually simple; **upper suface:** pale gray; not sorediate or isidiate; **lower surface:** black or brownish colored at the tips of the lobes or pale throughout with darker zones here and there, smooth and slightly wrinkled, very rarely with a few short scattered rhizines; **Apothecia:** abundant, 3-10 mm diam.; **asci:** clavate, 8-spored; **ascospores:** ellipsoid to reniform, (14-) 16-22 x (6-) 8-10 µm; **Pycnidia:** abundant, 0.1-0.2 mm diam., immersed; **conidia:** bacilliform, straight, 6-7 x 1 µm; **Spot tests:** upper cortex K+ yellow, C-, KC-, P+ yellow; medulla K+ yellow then red, C-, P+ orange; **Secondary metabolites:** cortex with atranorin and chloroatranorin; medulla with salazinic acid (major), norstictic and consalazinic acids (minor) and a fatty acid.

Substrate and ecology: common on trees and relatively rare on rocks; **World distribution:** common only in Mexico; **Sonoran distribution:** Sierra Madre Occidental of Sinaloa.

Everniastrum pseudonepalense (Hale & M. Wirth) Hale *ex* Sipman, Mycotaxon 26: 242 (1986).

Basionym: *Parmelia pseudonepalensis* Hale & M. Wirth, Phytologia 22: 40 (1971); Synonym: *Cetrariastrum pseudonepalensis* (Hale & M. Wirth) W. L. Culb. & C. F. Culb.; Illustration: Culberson and Culberson (1981), p. 302.

Thallus: robust, foliose to subcaespitose, very loosely adnate, up to 8 (exceptionally to 12) cm across, dichotomously or subdichotomously lobate; **lobes:** (1-) 2-4 (-6) mm broad, subinvolute to flat; apices: ciliate; cilia: frequent, up to 3 mm long, simple or branched; **upper surface:** pale and inconspicuously white-stippled; not sorediate or isidiate; **lower surface:** black, brown-colored at the tips of the lobes, densely to very sparsely rhizinate; rhizines: to 1 mm long, simple or branched; **Apothecia:** common, up to 8 (-14) mm diam., the largest ones perforate; **asci:** clavate, 8-spored; **ascospores:** ellipsoid to slightly reniform, 16-21 (-23) x 7-10 µm; **Pycnidia:** abundant, 0.2-0.3 mm broad; **conidia:** bacilliform, straight, 5-8 x 1 µm; **Spot tests:** upper cortex K+ yellow, C-, KC-, P+ yellow; medulla K+ yellow then turning dark red, C-, P+ orange to orange-red; **Secondary metabolites:** cortex with atranorin and chloroatranorin; medulla with salazinic acid (major), consalazinic acid (minor), norstictic acid (minor or accessory) and a fatty acid.

Substrate and ecology: on trees (*Quercus, Alnus* and *Pinus*); **World distribution:** Mexico and Hawaii; **So-**

noran distribution: Sierra Madre Occidental of Chihuahua.

Notes: Based on presence or absence of rhizines there is potential confusion with *E. neocirrhatum,* but *E. pseudonepalense* usually has trace quantities of protocetraric acid (not in *E. neochirrhatum*). Although norstictic acid may be found in both species, it is major in *E. neocirrhatum* and minor or accessory in *E. pseudonepalense*. Furthermore, the minor acids also help to differentiate *E. pseudonepalense* with norstictic acid from *E. cirrhatum* with galbinic acid.

Everniastrum sorocheilum (Vain.) Hale *ex* Sipman, Mycotaxon 26: 242 (1986).

Basionym: *Parmelia sorocheila* Vain., Hedwigia 38: 123 (1899); Synonym: *Cetrariastrum sorocheilum* (Vain.) W. L. Culb. & C. F. Culb.; Illustrations: Culberson and Culberson (1981), p. 293; Swinscow and Krog (1988), plate 7; Elix (1994c), p. 38.

Thallus: foliose to subcaespitose, very loosely adnate, up to 7 (exceptionally to 9) cm across, subdichotomously lobate; **lobes:** 0.5-2.5 (-4) mm broad, flat to involute, inferquently ciliate; cilia: 0.5-1 (-2) mm long, simple or sparingly branched; **upper surface:** pale, sometimes inconspicuously white-stippled, sometimes blackened in part, sorediate**: soredia:** farinose to granular, in soralia at the lobe tips or along the subterminal edge of the lobes; **lower surface:** black or pale- or brown-colored at the tips of the lobes, smooth or obscurely wirnkled transversely, particularly on the older lobes; **Apothecia:** very rare, to 1 mm diam.; **asci:** clavate, 8-spored; **ascospores:** not seen; **Pycnidia:** infrequent, to 0.15 mm diam.; **conidia:** bacilliform, straight, 4-6 x 1 µm; **Spot tests:** upper cortex K+ yellow, C-, KC-, P+ yellow; medulla K+ yellow then red, C-, P+ orange; **Secondary metabolites:** cortex with atranorin and chloroatranorin, medulla with salazinic acid (major), consalazinic acid (minor), galbinic acid (accessory) and a fatty acid.

Substrate and ecology: on trees and shrubs, especially angiosperms; **World distribution:** pantropical and extending into adjacent subtropical regions, particularly in the mountains; **Sonoran distribution:** Sierra Madre Occidental of Sinaloa.

Everniastrum vexans (Zahlbr. *ex* Culb. & C. Culb.) Hale *ex* Sipman, Mycotaxon 26: 242 (1986).

Basionym: *Parmelia vexans* Zahlbr., Fedd. Rep. Spec. Nov. Reg. Veg. 33: 55 (1933); Synonym: *Cetrariastrum vexans* Zahlbr. *ex* W. L. Culb. & C. F. Culb.; Illustration: Culberson and Culberson (1981), p. 293.

Thallus: foliose to subcaespitose, very loosely adnate, up to 12 (exceptionally to 17) cm across, dichotomously or subdichotomously lobate; **lobes:** 0.5-2 (-4) mm broad, divided, strongly to moderately involute or flat; apices: ciliate; cilia: abundant, up to 4 (-6) mm long, simple or branched; **upper surface:** pale gray to gray; slightly to densely isidiate: **isidia:** up to 1 mm, often bearing a lateral (rarely terminal) black hairs [0.2-0.5 (-2) mm long]; **lower surface:** black, brown- or pale-colored at the tips, usually naked but with a few short, usually simple, black rhizines in some specimens; **Apothecia:** very rare, up to 6 mm diam.; **asci:** clavate, 8-spored; **ascospores:** ellipsoid, 12-13 x (5-) 6-8 µm; **Pycnidia:** rare, 0.1-0.2 mm diam., immersed; **conidia:** bacilliform, straight, *c.* 5-7 x 1 µm; **Spot tests:** upper cortex K+ yellow, C-, KC-, P+ yellow; medulla K+ yellow then red, C-, P+ yellow then orange; **Secondary metabolites:** cortex with atranorin and chloroatranorin, medulla with salazinic acid (major), consalazinic acid (minor), galbinic and norstictic acids (accessory) and a fatty acid.

Substrate and ecology: on trees and shrubs, rarely rocks in montane forests; **World distribution:** pansubtropical and extending into adjacent subtropical regions, particularly in the mountains; **Sonoran distribution:** Sierra Madre Occidental of Sinaloa.

FLAVOPARMELIA

T. H. Nash III and J. A. Elix

Flavoparmelia Hale, Mycotaxon 25: 603 (1986).

Family: Parmeliaceae; Type: *Flavoparmelia caperata* (L.) Hale; No. species: over 20 world-wide; Selected lit.: Hale (1976c & 1986a), Elix (1993a & 1994d).

Life habit: lichenized; **Thallus:** foliose, *c.* circular in outline, lobate; **lobes:** usually subirregular, apices: usually rotund, cilia absent; **upper surface:** yellow green to yellow (rarely green to blue green), smooth, plane to rugulose, shiny or dull, often with soredia or pustules, emaculate, usually epruinose, pseudocyphellae absent; **upper cortex:** pored epicortex, palisade plectenchymatous; **medulla:** white, sometimes lower part pigmented; cell walls: containing isolichenan; **photobionts**: primary one a *Trebouxia*, secondary photobiont absent; **lower surface:** black, frequently with a brown margin, plane to sometimes wrinked, attachment by simple rhizines, cyphellae, pseudocyphellae and tomentum absent; **Ascomata:** apothecial, imperforate, laminal on thallus, orbicular, cupshaped, sessile, margin prominent with thalloid rim; exciple: gray or hyaline; epithecium: brown or brownish yellow; hypothecium: hyaline; **asci:** lecanoral, with thickened wall layers towards the apex; apex: amyloid, with wide, axial body divergent towards apex; 8-spored; **ascospores:** simple, ellipsoid; 14-20 x 7-10 µm; wall thin, hyaline; **Conidiomata:** absent or present, pycnidial, laminal, immersed; **conidia:** bacilliform, bifusiform or fusiform, 6-10 x 1 µm; **Secondary metabolites:** upper cortex with usnic acid, rarely also atranorin and chloroatranorin; medulla with some combination of orcinol depsides, ß-orcinol depsides, ß-orcinol depsidones, (higher) aliphatic acids, antraquinones or other quinones, secalonic acids or amino acid derivatives; **Geography:** cosmopolitan outside of polar and moist tropical regions; **Substrate:** mostly bark or non-calciferous rock.

Notes: This is a segregated from *Pseudoparmelia*, sensu Hale (1976c) and is characterized by having broad lobes, black lower surface, larger ascospores, short pycnospores, a yellow-green upper surface (usnic acid).

Key to species of ***Flavoparmelia*** in the Sonoran region:

1. Isidiate-pustulate (sometimes appearing sorediate), southern Arizona; primarily on rock ..... ***F. baltimorensis***
1. Not isidiate or pustulate; primarily on bark 2

2. Sorediate (very rarely non-sorediate); apothecia very rare 3
2. Not sorediate; apothecia very common ... ***F. rutidota***

3. Thallus 5-20 cm broad, ± loosely adnate towards center; lobes broad (5-13 mm across) ..... ***F. caperata***
3. Thallus smaller, often more closely adnate; lobes narrower (< 5 mm across) ..... ***F. subcapitata***

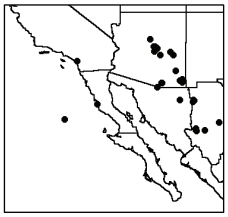
The Species

Flavoparmelia baltimorensis (Gyeln. & Fóriss) Hale, Mycotaxon 25: 604 (1986).

Basionym: *Parmelia baltimorensis* Gyeln. & Fóriss, Ann. Crypt. Exotiq. 4: 167 (1931); Synonym: *Pseudoparmelia baltimorensis* (Gyeln. & Fóriss) Hale; Illustrations: Hale (1976c), p. 19 as *Pseudoparmelia baltimorensis*; Brodo et al. (2001), p. 316.

Thallus: adnate to loosely adnate, foliose, 6-15 cm in diam., often fusing to cover large areas, irregularly lobate; **lobes:** sublinear to irregular, elongate, plane to subconvex, separate, 3-8 mm wide; apices: subrotund, crenate, eciliate; **upper surface:** yellow-green, smooth but becoming rugose with age, dull to somewhat shiny, epruinose and emaculate; **pustulae:** abundant, laminal crateriform, isidioid, breaking open apically but not sorediate; true isidia and soredia absent; **medulla:** white with continuous algal layer; **lower surface:** black centrally and toward margin, narrow brown zone peripherally, smooth to papillate; rhizines: sparse to moderately abundant, black, simple; **Apothecia:** rare, laminal on thallus, sessile,

1-4 mm wide; disc: brown; margin: pustulate, pruina and soredia absent; **asci:** clavate, 8-spored; **ascospores:** simple, ellipsoid, hyaline, 13-15 x 6-7 µm; **Spot tests:** upper cortex K-, C-, KC+ yellow, P-; medulla K-, C+ red, KC+ red, P+ red; **Secondary metabolites:** upper cortex with usnic acid; medulla with protocetraric acid (major) and gyrophoric acid (minor to accessory).

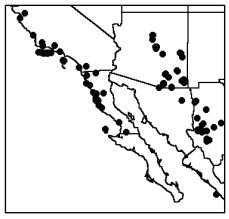


Substrate and ecology: commonly on acidic rock, rarely tree bases; **World distribution:** eastern and SW North America; **Sonoran distribution:** central Arizona south along the Sierra Madre Occidental, Southern California and Baja California.

Flavoparmelia caperata (L.) Hale, Mycotaxon 25: 604 (1986).

Basionym: *Lichen caperatus* L., Sp. Pl.: 1147 (1753); Synonyms: *Parmelia caperata* (L.) Ach., *Parmelia herreana* Zahlbr., *Pseudoparmelia caperata* (L.) Hale and see Hale (1976c) for further synonyms under *Pseudoparmelia caperata*; Illustrations: Hale (1976c), p. 19 as *Pseudoparmelia caperata*; Wirth (1995), pp. 32 and 639 as *Parmelia caperata* ; St. Clair (1999), p. 80; Brodo et al. (2001), p. 317.

Thallus: adnate to loosely adnate, foliose, 5-20 cm in diam., sometimes forming extensive patches, irregularly lobate; **lobes:** subirregular, elongate, plane to subconvex, separate, 5-13 mm wide, contiguous to somewhat imbricate; apices rotund, crenate, eciliate; **upper surface:** yellow green to pale yellow, occasionally green-gray (in shade), smooth but becoming rugose and folded with age, dull to somewhat shiny; epruinose and emaculate; **soredia:** laminal, granular to wart-like, initially in circular soralia but becoming diffuse and confluent; isidia: absent; **medulla:** white with continuous algal layer; **lower surface:** black centrally, brown and naked peripherally; rhizines: dense to sparse centrally to edge of brown zone, black, simple, sometime brown or white tipped; **Apothecia:** rare, up to 8 mm wide, laminal, sessile; disc: brown; margin: smooth but sorediate sometimes; **asci:** clavate, 8-spored; **ascospores:** simple, ellipsoid, hyaline, 15-24 x 8-13 µm; **Pycnidia:** laminal, immersed; **conidia:** weakly bifusiform, 6 x 1 µm; **Spot tests:** upper cortex K-, C-, KC+ yellow, P-; medulla K-, C-, KC-, P+ red; **Secondary metabolites:** upper cortex with usnic acid (major) and atranorin (trace); medulla with protocetraric acid (major) and caperatic acid (minor).



Substrate and ecology: on broad leafed trees, shrubs and fence posts in open habitats, coastal to montane up to 2000m, rarely on rocks; **World distribution:** North and South America, Europe, Asia, Africa; **Sonoran distribution:** common on oaks, particularly in coastal California and Baja California, occasionally in central Arizona southwards into the Sierra Madre Occidental of Sonora and Chihuahua.

Flavoparmelia rutidota (Hook. f. & Taylor) Hale, Mycotaxon 25: 605 (1986).

Basionym: *Parmelia rutidota* Hook. f. & Taylor, London J. Bot. 3: 645 (1844); Synonyms: *Pseudoparmelia rutidota* (Hook. f. & Taylor) Hale and see Elix (1994d); Illustrations: Hale (1976c), p. 43 as *Pseudoparmelia rutidota*; Elix (1994d), p. xiii.

Thallus: adnate to loosely adnate, foliose, 4-20 cm in diam., irregularly lobate; **lobes:** subirregular, elongate, plane to subconvex, separate, 2-8 mm wide, lobulate or not; apices rotund, crenate, eciliate; **upper surface:** yellow green to pale yellow, smooth but becoming rugose with age, dull to slightly shiny, epruinose and emaculate; soralia, isidia, and pustulae absent; **medulla:** white and occasionally yellow patches, with continuous algal layer; **lower surface:** black centrally, brown peripherally; rhizines sparse, black, simple; **Apothecia:** common, up to 8 mm wide, laminal on thallus, sessile; disc: cinnamon-brown to dark brown, epuinose; margin: smooth; **asci:** clavate, 8-spored; **ascospores:** simple, ellipsoid, hyaline, 12-20 x 7-11 µm; **Pycnidia:** common, immersed; **conidia:** bacilliform, 7-8 x 1 µm; **Spot tests:** upper cortex K-, C-, KC+ yellow, P-; medulla K-, C-, KC-, P+ red; **Se-**

condary metabolites: upper cortex with usnic acid (major) and atranorin (accessory), medulla with protocetraric acid (major), caperatic acid (minor), secalonic acid A (accessory).

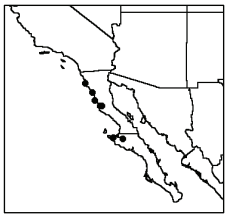
Substrate and ecology: bark of shrubs and small trees in open habitats**; World distribution:** North and South America, Texas to Argentina; Australasia; **Sonoran distribution:** arid woodlands in foothills of the Sierra Madre Occidental in Sinaloa.

Flavoparmelia subcapitata (Nyl. *ex* Hasse) Hale *ex* DePriest & B. Hale, Mycotaxon 67: 202 (1998).

Basionym: *Parmelia subcapitata* Nyl. *ex* Hasse, Contr. US Nat'l Herb. 17: 103 (1913).

Thallus: adnate to tightly adnate, foliose, 4-6 (-8) cm in diam., irregularly lobate; **lobes:** subirregular, elongate, plane to subconvex, separate, 1-3 (-5) mm wide; apices: rotund, crenate, eciliate; **upper surface:** yellow green to pale yellow, occasionally green-gray (in shade), smooth but becoming rugose with age, dull to slightly shiny; epruinose and emaculate; **soredia:** farinose to granular, common, in circular, laminal soralia that rarely become confluent; isidia, pustulae and dactyls absent; **medulla:** white with continuous algal layer; **lower surface:** black centrally, brown peripherally; rhizines sparse, black, simple; **Apothecia** and **Pycnidia:** not seen; **Spot tests:** upper cortex K-, C-, KC+ yellow, P-; medulla K+ yellow turning red,C-, KC-, P+ red; **Secondary metabolites:** upper cortex with usnic acid; medulla with with protocetraric acid (major) and caperatic acid (minor).

Substrate and ecology: on coastal shrubs, occasionally cacti; **World distribution:** southern and western Europe; Macaronesia; North and South America, central and southern Africa, New Zealand; **Sonoran distribution:** apparently limited to NW Baja California and previously in southern California.



Notes: *Flavoparmelia subcapitata* is somewhat similar to *F. caperata* but its thallus is smaller and more closely adnate, its lobes are narrower, and its soredia are less diffuse.

FUSCOPANNARIA

by P. M. Jørgensen

Fuscopannaria P. M. Jørg., Journ. Hattori Bot. Lab. 76: 202 (1994).

Family: Pannariaceae; Type: *Fuscopannaria leucosticta* (Tuck.) P. M. Jørg.; No. species: *c.* 40 world-wide; Selected lit.: Jørgensen (1978, 1994 & 2000a).

Life Habit: lichenized; **Thallus:** subcrustose to squamulose, resting on a thin blackish hypothallus; **upper surface:** usually olivaceous to brownish; **photobiont:** primary one a *Nostoc*, secondary photobiont absent; **Ascomata:** apothecial, with or without a thalline margin; hymenium: hemiamyloid, I+ blue-green, turning red-brown; **asci:** with an amyloid apical plug [tubes in subg. *Fuscopannaria* or sheets in subg. *Micropannaria*], 8-spored; **ascospores:** simple, hyaline, usually ellipsoid, sometimes with distinct epispore with apical thickenings or "tails"; **Conidiomata:** pycnidial, pale brown; **conidia:** simple, bacilliform, colorless; **Secondary metabolites:** sometimes with atranorin and/or aliphatic acids and terpenoids, or no substances; **Geography:** widespread in temperate, forested habitats, primarily in the Northern Hemisphere and with a center of distribution along the Pacific coast of North America; **Substrate:** on soil, rocks and bark.

Notes: This is a difficult genus where the species tend to be superficially very similar, and microscopic studies are often necessary for definite identification. Particularly in the field, they may be difficult to distinguish from *Parmeliella* species which also has small-squamulose species, most of

which are gray-blue with thinner, smoother thallus. Apothecia of *Parmeliella* invariably lack a thalline margin and have an amyloid hymenium, as well as asci with amyloid apical tubes. On the basis of ascal characters, *Fuscopannaria* is closer to *Psoroma* than *Pannaria* or *Parmeliella*.

Key to the species of ***Fuscopannaria*** from the Sonoran region:

1. Thallus sorediate 8
1. Thallus not sorediate 2

2. Thallus on soil; often with upturned margins or with isidioid protruberances 3
2. Thallus on rocks; with flat margins 4

3. Thallus uniformily brown; with isidioid protuberances; without secondary metabolites; lowlands of California ..... ***F. coralloidea***
3. Thallus brownish, often with the bluish lower surface of the upturned margins visible; with terpenoids and aliphatic acids; high mountains of Arizona ..... ***F. praetermissa***

4. Squamules white-margined or pruinose; containing secondary metabolites 5
4. Squamules uniformily brown; without secondary substances 6

5. Squamules bluish, pruinose; containing atranorin and lacking terpenoids or aliphatic acids; spores 14-18 x 7-10µm ..... ***F. leucostictoides***
5. Squamules brown with white margins; lacking atranorin but containing terpenoids and aliphatic acids; spores larger (23-27 x 9-11 µm) ..... ***F. leucosticta***

6. Thallus thick to 0.5 mm, often forming cushions 7
6. Thallus thinner, mostly forming expanding crusts ..... ***F. leucophaea***

7. Apothecial discs black; thalline margin well developed; spores 10-12 x 6-7 µm; alpine ..... ***F. hookerioides***
7. Apothecial discs brown, thalline margin variable, often surrounded by lobules; spores 17-25 x 7-10 µm; dry rock outcrops (non-alpine) ..... ***F. californica***

8. Thallus growing on soil, forming a thick crust; marginally completely dissolved into soredia ..... ***F. cyanolepra***
8. Thallus growing on bark or rocks, spreading over the substrate; with marginal soralia 9

9. Thallus bluish, pruinose; containing atranorin but lacking terpenoids and aliphatic acids; soredia corse-grained ..... ***F. pulveracea***
9. Thallus olivaceous, smooth; lacking atranorin but containing terpenoids and aliphatic acids; bluish, "woolly" soralia ..... ***F. mediterranea***

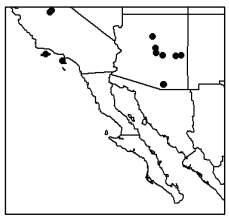
The Species

Fuscopannaria californica (Tuck.) P. M. Jørg., Bryol. 103: 679 (2000).

Basionym: *Pannaria microphylla* f. *californica* Tuck., Syn. N. Am. Lich.I: 12 (1882); Illustrations: Goward et al. (1994), p. 90 as *Parmeliella cheiroloba*; Jørgensen (2000a), p. 680.

Thallus: squamulose; forming strongly convex structures up to 2 cm diam., usually lacking a hypothallus; **squamules:** very thick, up to 0.5 mm thick and up to 2 mm wide, peripherally often with convex lobes, centrally becoming pulvinate; **upper surface:** brownish, smooth; **upper cortex:** paraplectenchymatous with irregularly thickened cell walls, 20-30 µm thick; **Apothecia:** common, often proliferating; up to to 1.5 mm diam, with variously developed thalline margin; disc: brown, convex; exciple: subparaplectenchymatous, often 80-100 µm thick; hymenium: I+ blue-green, turning red-brown, 100-120 µm high; **asci:** clavate, with apical amyloid sheets, 8-spored; **ascospores:** simple, colorless, ellipsoid, 17-25 x 7-10 µm; **Pycnidia:** not observed; **Spot tests:** all negative; **Secondary metabolites:** none detectable.

Substrate and ecology: dry rock outcrops of granite or ultrabasic rocks, mainly at lower or middle altitudes (possibly also in the higher mountains); **World distribution:** only known from western North America from New Mexico to California and north to British Columbia; **Sonoran distribution:** central and eastern Arizona and southern California.



Notes: It is characterized by the very thick squamules and a tendency to develop numerous secondary lobules around the apothecia. The larger spore size distinguishes it from extreme forms of *F. hookerioides*, which is mainly a high altitude species. *Fuscopannaria leucophaea* is a much thinner species of moist river valleys.

Fuscopannaria coralloidea P. M. Jørg., Bryol. 103: 681 (2000).

Synonym.: *Pannaria corallophora* auct. non sensu orig.; Illustration: Jørgensen (2000a), p. 678.

Thallus: squamulose, effuse, forming rosettes up to 4 cm diam., lacking a distinct hypothallus, **squamules:** usually deeply divided with coralloid protuberances, often apically swollen; **upper surface:** brown, smooth; **upper cortex:** paraplectenchymatous with irregularly thickened cell walls, 20-30 µm thick; **Apothecia:** rather common, up to 1.5 mm diam.; usually without thalline margin; disc: convex, brown; exciple: subparaplectenchymatous, usually 60-80 µm thick; hymenium: I+ blue-green and rapidly turning red-brown, 100-120 µm high; **asci** clavate with apical amyloid tubes, 8-spored; **ascospores:** simple, hyaline, ovoid, 16-20 x 8-10 µm; **Spot tests:** all reactions negative; **Secondary metabolites:** none detected.

Substrate and ecology: on moist, often clayey soil on riverbanks or road-cuts in coastal regions; **World distribution:** most possibly endemic to Pacific North America; **Sonoran distribution:** as yet only known from the Channel Islands in southern California.

Notes: It is a species of the *Fuscopannaria praetermissa* complex and may show some similarity to certain forms of that species, but it is always found in the lowlands. It is distinctly coralloid, never with "sorediate" upturned lobe-margins and lacks secondary substances.

Fuscopannaria cyanolepra (Tuck.) P. M. Jørg., Bryol. 103: 682 (2000).

Basionym: *Pannaria cyanolepra* Tuck., Lich. Calif.: 17 (1866); Illustration: Jørgensen (2000a), p. 678.

Thallus: squamulose, forming a extensive crusts over the ground, up to 10 cm diam., lacking a distinct hypothallus; **squamules:** often 1-2 mm diam. but not always distinct, imbricate, marginally dissolved in bluish soredia, only with a cortex centrally; **upper surface:** lead blue to brownish, smooth where corticate; **upper cortex:** paraplectenchymatous with irregularly thickened cell walls, 20-30 µm thick; **Apothecia:** rare (not observed in Sonoran material), laminal, with an excluded margin that sometimes is sorediate; disc: brown, mostly convex; exciple: subparaplectenchymatous, narrow, usually 40-50 (-80) µm thick; hymenium: I+ blue-green and rapidly turning red-brown, up to 100 (-150) µm high; **asci:** with apical amyloid tubes, 8-spored; **ascospores:** simple, colorless, ellipsoid, 16-22 x 7-9 µm; **Pycnidia:** not observed; **Spot tests:** all reactions negative; **Secondary metabolites:** none detected.

Substrate and ecology: on soil, mostly on road-cuts or river banks, possibly a rather short-lived colonizer; **World distribution:** endemic to Pacific regions of North America.; **Sonoran distribution:** only known from a few collections in southern California.

Notes: *Fuscopannaria cyanolepra* is a true sorediate species in the *F. praetermissa* complex. It somewhat resembles *Moelleropsis nebulosa*, a species that is paler gray-blue and lack any cortical development of the thallus. Potentially it may be confused with the rare *F. mediterranea*, a species that occurs on bark. The latter species also has lead-gray soredia, but they are more fine-grained and they do not totally dissolve the margin. Furthermore, the squamules of *F. mediterranea* are more olivaceous and the corticate portion of the squamules more swollen. When wet *F. cyanolepra* looks similar to a *Collema*.

Fuscopannaria hookerioides P. M. Jørg., Bryol. 103: 682 (2000).

Illustration: Jørgensen (2000a), p. 680.

Thallus: squamulose, forming small cushions, up to 2 cm broad, on a poorly developed hypothallus; **squamules:** up to 2 mm diam.; **upper surface:** dark greenish brown, une-

ven; **upper cortex:** paraplectenchymatous with irregularly thickened cell walls, 20-30 µm thick; **Apothecia:** black, with a strongly developed thalline margin; disc: flat and distinct; exciple: often poorly developed, subparaplectenchymatous, up to 50 µm thick; hymenium: I+ blue-green and rapidly turning red-brown, up to 100 µm high; **asci:** clavate, with apical amyloid sheets, 8-spored; **ascospores:** simple, colorless, fairly thick-walled, often with one or two oil droplets, ellipsoid, 10-12 x 6-7 µm; **Pycnidia:** not observed; **Spot tests:** all reactions negative; **Secondary metabolites:** none detected.

Substrate and ecology: mostly on wet, acidic rocks at high altitudes; **World distribution:** arctic-alpine, mainly known from the Rocky Mountains, Greenland , Labrador and rarely in Fennoscandia; **Sonoran distribution:** rare, only collected once in the high peaks of eastern Arizona (Escudilla Mt.) above 3000 m.

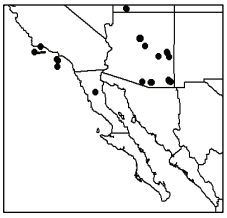
Notes: Previously this material was placed with the arctic-alpine *Pannaria hookeri* on the basis of the strongly margined, black apothecia found in both species. However, the thallus of *F. hookerioides* is more pulvinate and squamulose, and it lacks the marginal lobes and whitish striae found in *P. hookeri*. Also *P. hookeri* has an amyloid hymenium and asci that lack amyloid apical structures. *Fuscopannaria hookerioides* is the only truly arctic-alpine species of the *F. leucophaea*-complex and is easily recognized by its characteristic apothecia and the small spores. Extreme specimens with narrow lobes approach those of *F. californica*, which has much larger spores.

Fuscopannaria leucophaea (Vahl) P. M. Jørg., J. Hattori Bot. Lab. 76: 205 (1994).

Basionym: *Lichen leucophaeus* Vahl, Fl. Dan. 6, fasc.16: 8 (1787); Synonym: *Parmeliella microphylla* (Sw.) Müll. Arg., *nom. inval.*; Illustrations: Jørgensen (1978), p. 40; Jørgensen (2000a), p. 689; Wirth (1995), p. 634; Brodo et al. (2001), p. 322.

Thallus: crustose to squamulose, forming a crust-like cover, up to 150 µm thick and 2 cm diam., on a thin, blue-black hypothallus that is often poorly developed in dry habitats; **squamules:** up to 2 mm diam., remaining discrete at the margin of the crust, often (particularly in drier habitats) becoming imbricate and caespitose in central parts; **upper surface:** usually gray-brown (or gray to blackening); **upper cortex:** paraplectenchymatous with irregularly thickened cell walls, 15-20 µm thick; **Apothecia:** common, up to 1 mm diam., frequently proliferating and forming clusters, with or without a thalline margin (even on the same specimen); disc: brown to blackish (lighter in shade forms), often becoming convex; exciple: variously developed, up to 60 µm thick, subparaplectenchymatous; hymenium: brown-black above, otherwise hyaline, I+ blue-green and turning red-brown, 100-120 µm high; **asci:** clavate to subcylindrical, 8-spored with apical amyloid sheets; **ascospores:** simple, colorless, lacking an epispore, with numerous internal oil droplets that may give the spore the impression of being septate, 13-15 (-17) x 5-6 µm; **Spot test:** all negative; **Secondary metabolites:** none detected.

Substrate and ecology: on rocks (often sandstone) by rivers or in forested valleys, most common at middle altitudes (up to 2000 m); **World distribution:** widespread in temperate parts of the Northern Hemisphere; **Sonoran distribution:** primarily at mid-elevations in Arizona, southern California and Baja California.



Notes: It is a variable species, that is sometimes difficult to recognize. The variation in thallus form is mostly environmental. The form with a distinct hypothallus is principally found on shaded, moist rocks in narrow river-ravines. The thicker forms are from rocks (often sandstone) in forests. In its typical form it has discrete, brownish squamules on a thin distinct blackish hypothallus. However, only a few specimens in the Sonoran region correspond to that description. One of them (Nash 38109) surprisingly has a few granular soralia marginally. I interpret this as a local variation rather than representing a new species., although it might be recognized as a form. All other characters are typical of the species. Most specimens form thicker crusts or cushion-like aggregations, morphologically approaching *F. californica* and *F. hookerioides*. From the latter species it is easily distinguished in usually having brownish convex apothecia with irregular, often excluded thalline margin. *Fuscopannaria californica* is definitely thicker, builds conspicuous cushions

and has larger spores. The three also occupy different ecological niches.

Fuscopannaria leucosticta (Tuck.) P. M. Jørg., J. Hattori Bot. Lab. 76: 205 (1994).

Basionym: *Parmelia leucosticta* Tuck. in Darlington: Flora cestrica 3. ed.: 441 (1853); Illustrations: Jørgensen (2000a), p. 689; Brodo et al. (2001), p. 322.

Thallus: squamulose, usually 3-5 cm diam., usually occurring on a blackish, well developed hypothallus; **squamules:** rounded to 2-3 mm diam. but sometimes with elongated marginal ones that are up to 3-4 mm long; **upper surface:** brown to chestnut brown, sometimes paler, with white-felted tomentose margins; **upper cortex:** paraplectenchymatous with irregularly thickened cell walls, 40-50 µm thick; **Apothecia:** common, up to 1.5 mm diam. with brown, often with a white-felted thalline margin; disc: brown, plane and distinct; exciple: subparaplectenchymatous, 20-30 µm thick; hymenium: I+ blue-green and rapidly turning red-brown, *c.* 100 µm high; **asci:** clavate to subcylindrical, with an internal amyloid tubes, 8-spored; **ascospores:** simple, colorless, ellipsoid, with a conspicuous epispore which is broadly acuminate at both apices, 23-27 x 9-11 µm (with epispore; otherwise 14-18 x 8-9 µm); **Spot tests:** all reactions negative; **Secondary metabolites:** containing terpenoids and aliphatic acids.

Substrate and ecology: on rocks (rhyolite) in oak/pine forest at 2200 m, elsewhere commonly on bark; **World distribution:** temperate parts of eastern North America (including the West-Indies), SE Asia (as far South as New Guinea) and Mediterranean Europe (though extinct there since about 1900, see Jørgensen [1978], p. 43); **Sonoran distribution:** rare, only collected once in the western Chihuahua.

Notes: Curiosly it is often confused with *Pannaria rubiginosa* which is a much more large-lobed, grayer species with P+ orange thallus, and quite different hymenial characters. Perhaps easier confused with *Pannaria subfusca* which has smaller, P- lobes, but still with different hymenial characters and different thallus chemistry, and really not as distinctly small-squamulose without a white-felted margin.

Fuscopannaria leucostictoides (Ohlsson) P. M. Jørg., J. Hattori Bot. Lab. 76: 205 (1994).

Basionym: *Pannaria leucostictoides* Ohlsson, Bryologist 76: 379 (1973); Illustrations: Jørgensen (2000a), p. 685; Brodo et al. (2001), p. 323.

Thallus: squamulose, usually small, up to 3 cm diam., on a well developed hypothallus that extends beyond the margin; **squamules:** up to 1 mm broad, with crenulate to effigurate margins; **upper surface:** gray to grayish blue, smooth to slightly roughened, pruinose, esorediate; **upper cortex:** paraplectenchymatous with irregularly thickened cell walls, 40-50 µm thick; **Apothecia:** common, up to 1.5 mm diam., with a grayish, squamulose thalline margin; disc: brown; exciple: subparaplectenchymatous, 60-80 µm thick; hymenium: I+ blue-green and turning red-brown, 110-140 µm high; **asci:** clavate with apical amyloid ring structure, 8-spored; **ascospores:** simple, colorless, ellipsoid, 14-18 (-20) x 7-10 µm, smooth with thin epispore; **Spot tests:** K+ yellow, C-, KC- and P-; **Secondary metabolites:** with atranorin and two triterpenes.

Substrate and ecology: usually on bark of conifers, rarely found on alders and rocks; **World distribution:** Pacific North America from California to British Columbia; **Sonoran distribution:** Santa Catalina Island in the Channel Islands of southern California.

Notes: Due to its bluish gray, pruinose thallus, it may be confused with small specimens of *Pannaria malmei*, a species found locally in central California as well as Central and South America. However, that *Pannaria* does not contain atranorin, its hymenium does not turn red-brown with I, and it lacks an apical ring structure in its asci.

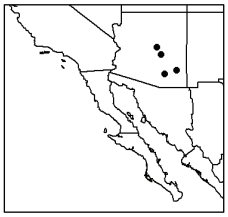
Fuscopannaria mediterranea (Tav.) P. M. Jørg., J. Hattori Bot. Lab. 76: 205 (1994).

Basionym: *Pannaria mediterranea* Tav., Port. Acta Biol. (B) 8: 5-6 (1965); Illustrations: Jørgensen (1978), p. 44;

Jørgensen (2000a), p. 676; Thor and Arvidsson (1999), p. 296.

Thallus: minutely squamulose, 2-3 mm in diam., crust-like, swollen, usally occurring on a thin, blue-black hypothallus; **squamules:** often irregularly rounded and incised, margin often upturned; **upper surface:** blue gray to olive-brown, often white-felted to tomentose marginally (in the herbaria often with crystals of terpenoids); **soredia:** granular, lead-gray, in soralia that are formed on the upturned margins; **upper cortex:** paraplectenchymatous with irregularly thickened cell walls, 30-40 µm thick; **Apothecia:** rare and not yet known in American collections, up to 2 mm diam., with distinct thalline, sorediate margin; exciple: subparaplectenchymatous, 20-30 µm thick; hymenium: I+ blue-green and rapidly turning red-brown, up to 100 µm high; **asci:** clavate to subcylindrical, with apical amyloid tubes, 8-spored; **ascospores:** ellipsoid, with a thick epispore and broadly attenuated apices, 17-23 x 8-9 µm (with epispore; otherwise 14-16 x 7-8 µm); **Spot tests:** all negative; **Secondary metabolites:** terpenoids and aliphatic acids (see Jørgensen 1991).

Substrate and ecology: on coarse, acidic bark (*Alnus* and *Quercus* spp.), often on the dry side of the trees; **World distribution:** mainly in the regions with a Mediterranean or oceanic climate in Europe, North and South America, but also extending as far south as Tierra del Fuego, and as far north as the Lappmark region in Scandinavia (where it is saxicolous); **Sonoran distribution:** rare, only collected in forested valleys of Arizona (Pinaleño Mts.) at about 2000 m.



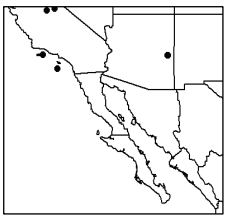
Notes: It is an easily recognized species due to its unique color and is not likely to be confused with any other species known from the region, except for stunted specimens of *Pannaria conoplea* which are paler gray-blue, and never olive-brown, and reacts P+ orange (pannarin). Further north (Oregon and Washington) there is a similar species, *Fuscopannaria leprosa* P. M. Jørg. & Tønsberg, that totally dissolves into soredia. The latter species appears to require cooler, damper habitats than those available in the Sonoran region and is not likely to occur here. The terricolous *Fuscopannaria cyanolepra* (Tuck.) P. M. Jørg., on the other hand, may grow on river banks in the Sonoran region. In addition to its different ecology, *F. cyanolepra* is recognizable by its very thick, crust-forming squamules that are mostly dissolved into soredia, because it is corticate only in central parts.

Fuscopannaria praetermissa (Nyl.) P. M. Jørg., J. Hattori Bot. Lab. 76: 205 (1994).

Basionym: *Pannaria praetermissa* Nyl. in Chydenius and Furuhjelm Not. Sällsk. Faun. Fl. Fenn. Förh. 4: 97 (1858); Illustrations: Jørgensen (2000a), p. 678; Brodo et al. (2001), p. 323.

Thallus: squamulose, often lobate, forming a continuous crust over the substrate, several cm in diam., usually lacking a hypothallus; **squamules:** thick, up to 0.4 mm wide and up to 3 mm diam., rounded, incised, densely compacted or imbricate; **lobes:** ascending and digitate, appearing like soralia or isidia and acting as dispersal units; **upper surface:** dark brown, margin often white due to terpenoid crystals; **upper cortex:** paraplectenchymatous with irregularly thickened cell walls, 20-30 µm thick; **Apothecia:** often abundent, brown, up to 1.5 mm diam., with or without and excluded thallus margin; disc: convex, brown; exciple:, subparaplectenchymatous, 60-80 µm thick; hymenium: I+ blue-green and turning red-brown, 100-120 µm high; **asci:** clavate to subcylindrical, with apical amyloid ring structure, 8-spored; **ascospores:** simple, colorless, ovoid, 18-22 x 9-11 µm, with a distinct epispore, often with one large oil droplet; **Spot tests:** all negative; **Secondary metabolites:** unidentified aliphatic acids and triterpenoids.

Substrate and ecology: primarily on mosses over calcareous ground, but also occasionally on burned stumps and decomposing logs; **World distribution:** circumpolar, arctic and alpine, following the Rocky Mountains south to Arizona and in the Sierra Nevada of California; **Sonoran distribution:** high elevations in Arizona, California (Channel Islands).



Notes: Typically it forms richly imbricate squamules over mosses and is often richly fertile.

Fuscopannaria pulveracea (P. M. Jørg. & Henssen) P. M. Jørg., J. Hattori Bot. Lab. 76: 205 (1994).

Basionym: *Pannaria pulveracea* P. M. Jørg. & Henssen, Opera Bot. 45: 115 (1978); Illustration: Jørgensen (2000a), p. 676.

Thallus: squamulose, up to 2 cm diam., sometimes with radiating peripheral lobes, usually not occurring on a hypothallus; **upper surface:** blue-gray, pruinose to scabrid, especially on the marginal lobes, sorediate; **soredia:** coarsely granular, in marginal soralia; **upper cortex:** paraplectenchymatous with irregularly thickened cell walls, 40-50 µm thick; **Apothecia:** rare, up to 1 mm in diam.; thalline margin: bluish, sorediate; disc: brown; exciple: subparaplectenchymatous, 50-60 µm thick; hymenium: I+ blue-green and turning red-brown, 100-120 µm high; **asci:** clavate with apical amyloid sheets, 8-spored; **ascospores:** simple, colorless, ellipsoid, not known fully developed; **Spot tests:** K+ yellow, C-, KC- and P-; **Secondary metabolites:** atranorin and terpenoids.

Substrate and ecology: mainly occurring on coarse-barked trees; **World distribution:** southern to northern California; **Sonoran distribution:** only known from one collection in the San Gabriel Mountains of southern California.

Notes: It is characterized by a bluish, pruinose and sorediate thallus and the occurrence of atranorin. It may be the sorediate counterpart of *F. leucostictoides*. It is only known from a very old collection from southern California and may now be extinct there. Although it is chemically different from *F. mediterranea*, it is morphologically quite similar. However, *F. pulveracea* is distinctly pruinose and it lacks the olivaceous tinge found in *F. mediterranea*.

GLOEOHEPPIA

by M. Schultz

Gloeoheppia Gyeln. emend. Henss., Lichenologist 29: 268 (1995).

Family: Gloeoheppiaceae; Type: *Gloeoheppia turgida* (Ach.) Gyeln.; No. species: four world-wide; Selected lit.: Henssen (1995a).

Life habit: lichenized; **Thallus:** umbilicate, squamulose, crustose, subfruticose, subgelatinous when wet, sometimes with marginal soralia; **surface:** blackish-brown to olive-brown, sometimes grayish pruinose, smooth, granulose, rimose or cracked; **anatomy:** ecorticate, homoiomerous, hyphae densely reticulate, sometimes with internal air spaces; **photobionts:** primary one a chroococcoid cyanobacterium, secondary photobiont absent; **Ascomata:** apothecial, laminal on thallus, orbicular, immersed to sessile; margin: indistinct to distinct, with thalloid rim; **ontogeny:** hemiangiocarpous, ascogonia arising in a tangle of generative hyphae beneath the thallus surface; **anatomy:** exciple: hyaline; epithecium: brownish yellow; hypothecium: hyaline; **asci:** prototunicate, wall thin, non-amyloid, 8-32-spored; **ascospores:** simple, ellipsoid, broadly ellipsoid to globose; 5-14 x 4-9.5 µm, wall thin, hyaline; **Conidiomata:** absent or present, pycnidia laminal, immersed; **conidia:** cylindrical, *c.* 3 x 1 µm; **Secondary metabolites:** not detected; **Geography:** in arid, semi-arid to warm temperate regions of the Northern Hemisphere; **Substrate:** soil crust over limestone and calcareous rock or on siliceous rock.

Notes: The subgelatinous thallus consistency and the occasional presence of soredia are similar to *Peltula* and *Heppia*, but its unstratified anatomy with reticulately arranged hyphae is similar to the Lichinaceae.

The Species

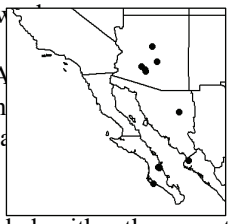
Gloeoheppia polyspora Henss., Lichenologist 27: 277 (1995).

Illustrations: Henssen (1995a), p. 274; and Fig. 50 below.

Fig. 50. *Gloeoheppia polyspora*, photo by M. Schultz.

Thallus: crustose-areolate to squamulose, subgelatinous due to air spaces in thallus, rarely ± pulvinate, surface of areoles/squamlues smooth, grooved when ± pulvinate due to the erect growth of tiny, compressed lobules; **areoles** or **squamules:** (0.25-) 0.5-2 (-3) mm wide, densely aggregated; **attachment:** by rhizoidal strands or small, indistinct umbilicus; **surface:** blackish brown when dry, dirty brownish olive or brownish yellow when moistened; **Apothecia:** semi-immersed to sessile, zeorine, up to 0.5 mm wide, with persisting thalline margin; disc: at first punctiform, later open, often depressed, brownish; exciple: distinct, of strongly gelatinized hyphae, 12.5-20 µm wide, hyaline; epihymenium: yellowish-brown; hymenium: up to 125 µm high, hyaline, iodine reaction variable; paraphyses: distinctly septate, branched and anastomosing, apical cells thickened (3.5-5 µm); **asci:** 16-32-spored; **ascospores:** small, simple, hyaline, broadly ellipsoid to globose, 5 (-7.5) x 5 µm; walls: thin; **Pycnidia:** immersed, globose, 0.075-0.1 mm wide; pycnidial wall: convoluted with age; **conidia:** cylindrical, hyaline, 3 x 1 µm; **Spot tests:** all negative; **Secondary metabolites:** none detected.

Substrate and ecology: on granite, rhyolite, rarely on calcareous crusts over siliceous rock (caliche) or limestone; on sheltered or shaded boulders in rocky slopes, w etc.; coastal to montane; **distribution:** SW North A **Sonoran distribution:** cen southern Arizona; Baja Ca Sur, Sonora and Sinaloa.



Notes: It grows intermingled with other crustose-squamulose species (e.g. *Phloeopeccania* spp.) and sometimes it is hard to separate. Moistening identifies the subgelatinous nature of the thallus because of a distinct change in color from blackish brown to lighter brownish olive or brownish yellow.

GLYPHOLECIA

by B. D. Ryan

Glypholecia Nyl., Ann. Sci. Nat. Bot. 317 (1853).

Family: Acarosporaceae; Type: *Glypholecia scabra* (Pers.) Müll. Arg.; No. species: one world-wide; Selected lit.: Magnusson (1936) and Thomson (1979 & 1984).

Note: Because the genus is monotypic, it would be repetitious to have a separate generic description.

The Species

Glypholecia scabra (Pers.) Müll. Arg., Hedwigia 31: 156 (1892).

Basionym: *Urceolaria scabra* Pers., Ann. Wetteruaischen Ges. Gesammte Naturk. 2: 10 (1911); Synonyms: *Acarospora saxicola* Fink, and see Thomson (1997) for further synonomy; Illustrations: McCune and Goward (1995), p. 102; Thomson (1997), p. 236.

Life habit: lichenized; **Thallus:** peltate-subumbilicate to ± areolate in appearance but all attached together; thalli *c.* 1-3 mm wide, 0.3-0.8 (-1.2) mm thick, usually monophyllous, attached with a broad, central stipe, appressed, rarely almost crustose, often with deep cracks between them; sometimes lobate; **lobes:** broadly rounded, up to 5 mm, partly ascending, concave or slightly convex, the margins rolled under; **upper surface:** white or bluish white when dry, reddish brown when moist, spottily to densely pruinose; **upper cortex:** paraplectenchymatous, 40-50 µm thick, grayish, the outer 7-11 µm reddish or yellowish brown; cells indistinct, thick-walled, 2-3(-5) µm diam.; epinecral layer irregular, up to 50 µm thick; **medulla:** chalky, densely filled with calcium oxalate crystals; hyphae: very loose, arachnoid, thick-walled, 3.5-4.5 µm wide, becoming thicker towards the lower side; **photobiont:** primary one a *Trebouxia*, secondary photobiont absent; algal layer: 50-75 µm thick with ± continuous layer, algae 8-14 µm diam.; **lower cortex:** lacking; **lower surface:** pale, sordid whitish to somewhat brownish, or light yellowish brown near the margin, matt, smooth to finely powdery-roughened, cracked here and there, without rhizines; umbilicus: very wide; **Ascomata:** apothecial, common, compound, forming multiple structures, the individual apothecia punctiform to circular or elongate, each with a proper exciple; with a pruinose net between, 0.7-1 (-2.5) mm diam.; disc: epruinose, scabrid, red-brown to dark brown, becoming slightly higher than the thallus surface; cortex between discs: similar in structure to that of thallus; "exciple": composed of parallel hyphae, I+ blue, 20-25 µm thick; epihymenium: yellow-brown; hymenium: 100 µm, hyaline, I+ blue; hypothecium: 40-50 µm thick, I+ blue; paraphyses: in water rather indistinct, with coherent tips, in HCl distinct, septate, 2-2.5 um wide, the tips clavate, 3.5-4 µm; algal layer below the apothecia strongly interrupted; **asci:** clavate, *Acarospora*-type, with tholus I+ slightly blue, without axial structures, without distinct ocular chamber, 55-65 x 15-17µm, *c.* (50-) 100-spored; **ascospores:** spherical, 3.5-4 µm diam.; wall: hyaline, thick; **Pycnidia:** very rare, 150 µm deep, 100 µm wide, simple, flask-shaped; conidiophores 10 µm long; **conidia:** *c.* 2 x 1 µm; **Spot tests:** upper cortex and medulla K-, C+ red, KC+ red (at least upper medulla), P-; **Secondary metabolites:** gyrophoric acid (an orcinol tridepside).

Substrate and ecology: in arid to semi-arid regions, on calcareous slate and siliceous limestone, on steep surfaces, ± exposed, usually on the end surface of larger boulders; **World distribution:** Arctic to cool temperate regions; Europe, northern Africa; southern Asia, North America; **Sonoran distribution:** Arizona, on limestone, 1900-2230 m (several collections from the Grand Canyon; see Boykin and Nash [1994] for specimen data).

Notes: The compound apothecia and the subfoliose, umbilicate thallus distinguish this genus from *Acarospora*. In a sense the species is part of a transition group between the crustose growth form and foliose; the lack of a lower cortex and multiple attachment structures (e.g. rhizines) argues against calling it foliose.

HEPPIA

by B. Büdel, M. Schulz and T. H. Nash III

Heppia Nägeli *ex* A. Massal., Geneac. Lich.: 6/8 (1854). Family: Heppiaceae; Type: *Heppia adglutinata* (Kremp.) A. Massal.; No. species: six world-wide; Selected lit.: Henssen (1994), and Wetmore (1970).

Life habit: lichenized; **Thallus:** squamulose, crustose or peltate; margin: appressed or raised; **upper surface:** olive, brownish, gray, or blackish, plane to deeply concave, smooth, corrugate or cracked; **cortex:** when present composed of predominantly anticlinally oriented hyphae; cells: cylindrical, globose or isodiametric; **medulla:** normally not separated from the algal layer, primarily composed of anticlinally arranged hyphae; **photobiont:** primary one a filamentous, heterocyst-containing cyanobacterium (*Syctonema*-like), secondary photobiont absent; **lower surface:** paler than upper surface, attached to substrate by numerous rhizoidal hyphae; **Ascomata:** apothecial, immersed; **ontogeny:** developing from a hyphal web of generative tissue with numerous ascogonia; disc: red or red-brown, urceolate, flat or slightly convex; exciple: sometimes present, then 20-60 µm thick; hymenium: 100-195 µm high; paraphyses: well developed, short-celled at the base, slightly branched in the upper part with characteristically enlarged top cells in older material; subhymenium: 10-60 µm; **asci:** prototunicate, cylindrical to obovoid, 70-170 x 15-30 µm, (4-)8-spored; **ascospores:** simple, frequently with a central plasma-bridge, often mistaken as a central septum, ellipsoid to fusiform, 14-32 x 4.5-13 µm; **Conidiomata:** pycnidial, immersed, solitary, simple to cerebriform in shape, 190-280 µm tall and 150-330 µm wide; **conidia:** simple, fusiform to bacilliform, terminally produced, hyaline, 2.5-3.5 x 1-1.5 µm; **Secondary metabolites:** none detected; **Geography:** predominately in arid and semi-arid regions of the world, but occurring wherever arid microclimates are found; **Substrate:** acidic or calcareous rocks or soil.

Notes: Although he recognized much of the variation used to distinguish the species below, Wetmore (1970) recognized only one species, *H. lutosa*, which was circumscribed broadly. *Heppia* occurs in similar habitats to those in which *Peltula* occurs. Differences in spore number (8/ascus in *Heppia* and 16-100+/ascus in *Peltula*) and ascus structure are definitive ways to tell the genera apart.

Key to the species of ***Heppia*** from the Sonoran region:

1. Thallus homiomerous or marginally with a rudimentary cortex, easily breaking in vertical direction; ascus wall intensely blue in iodine ..... ***H. lutosa***
1. Thallus heteromerous with a distinct upper or lower cortex; ascus wall blue **or** red in iodine 2
    2. Thallus with a lower cortex formed by periclinally arranged hyphae; hymenium reddish in iodine .... ***H. adglutinata***
    2. Thallus with broad, pseudoparenchymatous upper cortex, lower cortex (if present) marginal only; hymenium blue in iodine but reddish above ascus tips 3
3. Thallus yellow-olive or brown with pale depressions, margin not granular ..... ***H. despreauxii***
3. Thallus grayish pruinose or brownish; margin often granular to almost sorediate ..... ***H. conchiloba***

The Species

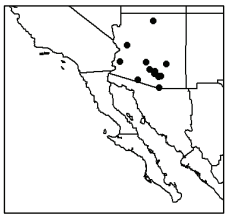
Heppia adglutinata (Kremp.) A. Massal., Geneac. Lich.: 8 (1854).

Basionym: *Lecanora adglutinata* Kremp., Flora 24: 675 (1851); Synonyms: see Henssen (1994); Illustrations: Henssen (1994), pp. 60, 62, 67 & 68.

Thallus: squamulose or peltate, forming multiple rosettes in aggregate up to 6 cm in diam. (individual rosettes 3-10 mm in diam.), lobate; **lobes:** individual ones up to 6 mm in diam., heteromerous, adnate or with raised margins; margins: entire or broken; **upper surface:** yellow-olive or brown; **upper cortex:** partially developed, 12-50 µm thick; epinecral layer: on aged lobes, 7-12 µm thick; **medulla:** with hyphal cells predominantly anticlinally arranged, cylindrical to globose, 4.5-12 µm wide; cyanobacteria distributed throughout; **lower cortex:** 13-40 µm thick, with 1-4 rows of enlarged cells; cells: 6-18 µm in diam.; **Apothecia:** one to several per squamule; disc: red-brown, up to 2 mm in diam., deeply urceolate or more rarely flat; exciple: 20-50 µm thick; hymenium: I+ reddish, (95-) 120-195 µm tall; subhymenium: 10-35 µm thick; **asci:** cylindrical to obovoid, 8-spored; **ascospores:** simple (rarely 1-septate), ellipsoid to fusiform, (15-) 18-

24 (-30) x 6-10.5 (-12) µm; **Pycnidia:** immersed; **conidia:** fusiform, 2.5-3.5 x 1-1.5 µm; **Spot tests:** all negative; **Secondary metabolites:** none detected.

Substrate and ecology: usually on soil, sometimes on soil over acidic rocks, occasionally in calcareous areas; **World distribution:** western and SE North America and southern Africa; **Sonoran distribution:** desert areas of Arizona.

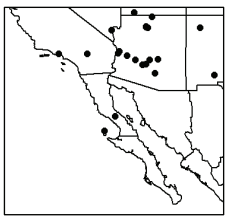


Heppia conchiloba Zahlbr., Beih. Bot. Centralbl. 13: 157 (1902).

Synonym: *Heppia macrospora* de Lesd.; Illustrations: Henssen (1994), pp. 68 & 70; Brodo et al. (2001), p. 333.

Thallus: peltate, irregularly orbicular or oval in outline, lobate; **lobes:** up to 8 mm in diam., frequently deeply concave; margins: incurved or raised and easily broken; **upper surface:** grayish pruinose or rarely brownish when without pruina; margin: rough, sometimes appearing granular or almost sorediate; **upper cortex:** pseudoparenchymatous, 8-50 µm thick, cells 5-12 µm wide; epinecral layer: 20-50 µm thick; **medulla:** with anticlinally arranged hyphae, 3.5-8 µm thick, at the base with enlarged globose cells (up to 12 µm in diam.); cyanobacteria distributed throughout; **lower cortex:** not developed; **Apothecia:** one to several per lobe; disc: red-brown, at first deeply urceolate and subsequently becoming shallowly concave, up to 1.5 mm diam.; exciple: 45-60 µm thick; hymenium: 115-160 µm tall, I+ blue, in part reddish; subhymenium: 28-60 µm thick; **asci:** cylindrical to obovoid, 8-spored; **ascospores:** simple, ellipsoid to fusiform, 18-20 x 8-13 µm; **Pycnidia:** immersed; **conidia:** fusiform, 2.5-3.5 x 1-1.5 µm; **Spot tests:** all negative; **Secondary metabolites:** none detected.

Substrate and ecology: usually on soil, sometimes on soil over acidic rocks, occasionally in calcareous areas; **World distribution:** SW and intermountain areas of western North America; **Sonoran distribution:** desert areas of Arizona, California, and Baja California.



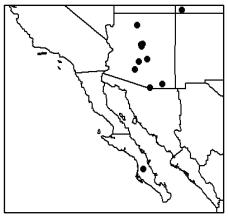
Notes: The species is often collected sterile, but its gray, deeply concave thallus and rough margin are sufficiently distinctive that it can be readily recognized. Most other *Heppiae* and *Peltulae* are olive or brownish-olive colored.

Heppia despreauxii (Mont.) Tuck., Gen. Lich. 46 (1872).

Basionym: *Solorina despreauxii* Mont., Hist. Nat. Isl. Canar. 3: 104 (1840); Synonyms: see Henssen (1994); Illustrations: Henssen (1994), pp. 68 & 70.

Thallus: peltate, irregularly orbicular, lobate; **lobes:** 2-8 mm in diam., heteromerous; margins: downcurved or raised, entire or broken; **upper surface:** yellow to brown-olive, with pale *c.* 40 µm deep depressions in a reticulate pattern; **upper cortex:** 25-50 (-75) µm thick; cells: 5-13 µm in diam.; epinecral layer: up to 45 µm thick; **medulla:** composed of anticlinally oriented hyphae, 3-8 µm thick, basally with globose, enlarged cells (up to 14.5 µm in diam.); cyanobacteria distributed throughout; **lower cortex:** not developed or only rudimentary at the margin of young lobes; **Apothecia:** one to several per lobe; disc: red-brown, urceolate, up to 2 mm diam.; exciple: 25-70 µm thick; hymenium: (115-) 140-175 µm tall, I+ blue or in part reddish; subhymenium: 20-50 µm thick; **asci:** cylindrical to obovoid, 8-spored; **ascospores:** simple, ellipsoid to fusiform, (15-) 17-29 (-32) x (5-) 8-10.5 (-12) µm; **Pycnidia:** immersed; **conidia:** fusiform, 2.5-3.5 x 1-1.5 µm; **Spot tests:** all negative; **Secondary metabolites:** none detected.

Substrate and ecology: usually on soil, sometimes on soil over acidic rocks, occasionally in calcareous areas; **World distribution:** SW North America, SW Europe, northern Africa and Australasia; **Sonoran distribution:** Arizona and Baja California Sur.



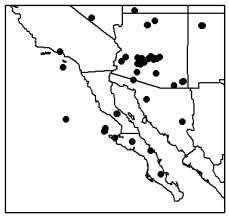
Note: The mottled, superficial appearance of this species due to the deep, reticulate depressions in the upper surface is a feature by which the species can be readily recognized.

Heppia lutosa (Ach.) Nyl., Syn. Lich. 2: 45 (1863).

Basionym: *Collema lutosum* Ach., Syn. Lich. 309 (1814); Synonyms: see Henssen (1994); Illustrations: Henssen (1994), pp. 62 & 64.

Thallus: squamulose to granulose, 1-2 (-4) µm in diam. (granules: 0.1-5 mm diam.), somewhat gelatinous, translucent when moistened; **squamules:** up to 200 µm thick, with an irregular outline, homoiomerous, often concave when young; margins: downcurved in older thalli; **upper surface:** blackish or brownish; **upper cortex:** absent; **medulla:** with predominantly anticlinally arranged hyphae; cells: 6-7 µm in diam.; cyanobacteria distributed throughout; **lower cortex:** sometimes present in juvenile squamules at the margins; cells: 3-5 µm thick; **Apothecia:** one to several per squamule; disc: dark red, up to 1.7 mm in diam., urceolate, flat or convex; exciple: 20-60 µm thick; hymenium: 115-150 µm tall; subhymenium: 20-35 µm thick; **asci:** cylindrical to obovoid; walls: I+ intensely blue (with hymenial gelatin becoming secondarily brownish); 8-spored; **ascospores:** simple, ellipsoid to fusiform, 14-18 (-26) x (4.5-) 6-10.5 µm; **Pycnidia:** immersed; **conidia:** fusiform, 2.5-3.5 x 1-1.5 µm; **Spot tests:** all negative; **Secondary metabolites:** none detected.

Substrate and ecology: usually on soil, sometimes on soil over acidic rocks, occasionally in calcareous areas; **World distribution:** North America, Europe, southern Africa and Australasia; **Sonoran distribution:** broadly distributed in the study area, Arizona, California, Baja California, Baja California Sur and Sonora.



Note: In general *H. lutosa* has a more northerly distribution (to areas well north of the Sonoran Desert) than the other species.

HETERODERMIA

by R. Moberg and T. H. Nash III

Heterodermia Trevis., Atti Soc. Ital. Sc. Nat. Milano 11: 613 (1868) *emend* Poelt, Nova Hedwigia 9: 31 (1965).

Family: Physciaceae; Type: *Heterodermia speciosa* (Wulf.) Trevis.; Species No.: *c.* 92 world-wide; Selected lit.: Kurokawa (1962, 1973 & 1998), Poelt (1965), Poelt and Wunder (1970), Esslinger and Bratt (1998), and Moberg and Nash (1999).

Thallus: foliose to subfruticose, small to medium sized, moderately to very loosely attached, sometimes combining to form extensive, radiating mats, lobate; **lobes:** linear to sublinear, elongate to shorter, discrete or contiguous; tips rounded or flabellate, sometimes ascending, with or without marginal cilia; cilia: black or pale; **upper surface:** white, ivory white or gray to dark greenish brown, with or without pruina, with or without soredia or isidia; **upper cortex:** prosoplectenchymatous, composed of periclinal hyphae; **medulla:** white or sometimes yellow pigmented; **photobiont:** primary one a trebouxioid alga, secondary photobiont absent; **lower cortex:** lacking or prosoplectenchymatous, but sometimes only weakly organized and poorly differentiated from the medulla; **lower surface:** surface pale or darkening; sparsely to rather densely rhizinate; rhizines: pale or darkening, simple or branched, sometimes protruding beyond the margin as seen from above; **Apothecia***:* present or absent, with a thalline exciple; subhymenium: hyaline; **asci:** cylindrical, subclavate to clavate, *Lecanora*-type, 8-spored; **ascospores:**, smooth, brown, thick walled, 1-septate, 15-54 x 7-25 µm; **Pycnidia:** blackened and immersed; **conidia:** bacilliform to short-cylindrical, 4-6 x ± 1 µm; **Secondary metabolites:** terpenoids; β-orcinol depsides and β-orcinol depsidones and various pigments; **Geography:** pri-

marily pantropical with a few species extending into temperate areas, North America, Europe, Australasia, Asia and Africa**; Substrate:** bark or wood, rock or rarely soil.

Notes: Kurokawa (1962) published a definitive world monograph of the genus *Anaptychia* in which 72 predominately tropical species were treated. Subsequently, that genus was recognized as heterogeneous by Poelt (1965), who separated the genus *Heterodermia* with smooth, thick-walled spores and the constant occurrence of atranorin in the upper cortex from *Anaptychia*, all species of which have *Physconia*-type spores and lack atranorin in the upper cortex. All but nine of Kurokawa's originally recognized species have been transferred to *Heterodermia.* This delimitation is now widely accepted, and also by Kurokawa (1998).

Key to the species of ***Heterodermia*** from the Sonoran region:

1. Thallus dichotomously branched, lobes long and narrow, with marginal cilia 2
1. Thallus irregularly branched, lobes broad, with or without cilia 4

2. Thallus without soralia ..... ***H. linearis***
2. Thallus with soralia 3

3. Lobe-tips upturned; discrete soralia present on lower surface ..... ***H. appalachensis***
3. Lobe-tips flat; soralia more diffuse on lower surface ..... ***H. leucomela*** ..... (ssp. ***boryi*** extremely narrow)

4. Lobes with cilia along the margin and sometimes on the lobe surface 5
4. Lobes without marginal cilia (but may have rhizines projecting beyond the margin) 10

5. Lobes erect or suberect 6
5. Lobes along the substrate 10

6. Lobes with cilia on upper side, lobes erect and paddle-shaped ..... ***H. comosa***
6. Lobes without cilia on upper side, lobes not paddle-shaped 7

7. Thallus sorediate, soredia on lower side ***H. namaquana***
7. Thallus not sorediate 8

8. Apothecia with prominent lobules ..... ***H. podocarpa***
8. Apothecia without lobules 9

9. Saxicolous, apothecia ciliate ..... ***H. ciliatomarginata***
9. Corticolous, apothecia not ciliate ..... ***H. erinacea***.

10. Lobes without lower cortex; with marginal rhizines 11
10. Lobes with lower cortex; with few or no marginal rhizines 13

11. Thallus without soralia ..... ***H. hypoleuca***
11. Thallus with soralia 12

12. Lower side with yellow to rusty-brown pigment (K+ violet) ..... ***H. obscurata***
12. Lower side without or with orange to bluish or black pigment (K-) ..... ***H. japonica***

13. Thallus with isidia ..... ***H. granulifera***
13. Thallus without isidia 14

14. Thallus with soralia 15
14. Thallus without soralia 18

15. Soralia mainly marginal; medulla with salazinic or norstictic acid 16
15. Soralia mainly apical; medulla without salazinic or norstictic acid 17

16. Soralia mainly continous along lobe-margin, salazinic acid present (K+ yellow →red) .... ***H. albicans***
16. Soralia from knob-like, marginal structures, norstictic acid present (K+ yellow →orange) ..... ***H. pseudospeciosa***

17. Soralia few, but prominent, spathulate, thallus with "spathulin" ..... ***H. spathulifera***
17. Soralia more abundant, lip-shaped, thallus without "spathulin" ..... ***H. speciosa***

18. Thallus distinctly pruinose, mostly with patches of pigment in the medulla, salazinic acid absent ..... ***H. rugulosa***
18. Thallus not or weakly pruinose, without medullary pigment, salazinic acid present (K+ yellow →red) .. ***H. tropica***

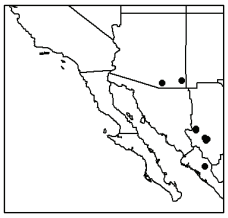
The Species

Heterodermia albicans (Pers.) Swinscow & Krog, Lichenologist 8: 113 (1976).

Basionym: *Parmelia albicans* Pers., Annaln Wetter Ges. 2: 17 (1811) *non Anaptychia albicans* Kurok.; Synonym: *Physcia albicans* (Pers.) J. W. Thoms.; Illustrations: Hale (1979), p. 105; Moberg and Purvis (1997), p. 190; Brodo et al. (2001), p. 334.

Thallus: foliose, orbicular to irregular, small, less than 4 cm diam., firmly adnate, dichotomously lobate; **lobes:** linear, elongate, narrow, 0.5-1 mm broad, up to 3 mm long, usually richly branched, weakly convex, widening, tips without soralia, not ascending, eciliate; **upper surface:** gray to brownish gray, darker at lobe-tips, sometimes weakly pruinose, sorediate; **soredia:** white to bluish gray, in soralia arising from small lateral knob-like structures forming small, ± continous marginal soralia towards the thallus center; **upper cortex:** prosoplectenchymatous; **medulla:** white; **lower surface:** whitish to pale brownish, rarely dark gray, ± canaliculate; rhizines: weakly developed, usually short (*c.* 1 mm), pale to dark brown or black; **lower cortex:** prosoplectenchymatous, together with upper one occupying more than 2/3 of the thallus thickness; **Apothecia:** rare (not seen in Sonoran material), up to 2.5 mm in diam., margin becoming sorediate; disc: dark brown; **asci:** clavate, 8-spored; **ascospores:** brown, l-septate, narrowly ellipsoid, 21-32 x 7-14 µm; **Pycnidia:** ± common, inserted with black weakly protruding tips; **conidia:** bacilliform, 4-6 x 1 µm; **Spot tests:** cortex K+ yellow C-, KC-, P+ yellow; medulla K+ yellow during deep red, C-, KC-, P+ orange; **Secondary metabolites:** cortex with atranorin and chloroatranorin; medulla with atranorin and zeorin and salazinic acid (major) and ± unidentified terpenes.

Substrate and ecology: growing on trees or rocks or over mosses on rocks in open situations; **World distribution:** North and South America, the Azores, and East Africa; **Sonoran distribution:** relatively common at intermediate elevations in SE Arizona, Chihuahua, and Sinaloa.



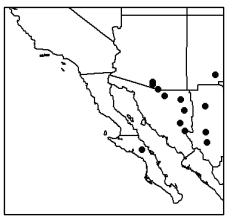
Notes: *Heterodermia albicans* is characterized and distinguished by the narrow, convex, short lobes, corticate on the lower surface. The soralia arise from marginal knob-like structures forming small, ± continous marginal soralia towards the thallus center. *Heterodermia speciosa* also has a lower cortex but has larger, ± flat lobes and lacks salazininc acid. *Heterodermia albicans* differs from *H. pseudospeciosa* by more adpressed thallus, less delimited soralia and the absence of norstictic acid. TLC is recommended to separate the two species.

Heterodermia appalachensis (Kurok.) W. L. Culb., Bryologist 69: 479 (1966).

Basionym: *Anaptychia appalachensis* Kurok. Beih. Nova Hedwigia 6: 83 (1962); Illustration: Kurokawa (1962), Pl 8, Fig. 48 as *Anaptychia appalachensis.*

Thallus: foliose, irregular, up to 6 cm diam. with ± narrow, radiating, dichotomously to subpalmately lobate; **lobes:** linear, elongate, ± narrow, 0.5-1 (-2) mm wide, subimbricate centrally, ciliate; cilia: prominent, marginal, pale at the base and blackened towards the branched apices; **upper surface:** gray to dark gray without or with a weak pruina, sometimes with laminal cilia; sorediate; **soredia:** in soralia on the underside near the tips, bending the tips upwards and thus appearing labriform (designated capitate by Kurokawa [1962]); **upper cortex:** prosoplectenchymatous; **medulla:** white above and salmon below; **lower cortex:** lacking; **lower surface:** white but mostly overlaid by a yellow to salmon-colored pigment (K-), arachnoid, rhizinate; rhizines: marginal, simple; **Apothecia** and **Pycnidia:** not seen; **Spot tests:** cortex K+ yellow, C-, KC-, P+ yellow; medulla K+ yellow, C-, KC-, P-; **Secondary metabolites:** cortex with atranorin and chloroatranorin; medulla with atranorin, zeorin and leucotylin.

Substrate and ecology: growing on tree trunks in open situations in humid places; **World distribution:** North America from the southern Appalachian Mountains; **Sonoran distribution:** relatively rare in SE



Arizona and Baja California Sure, more common in the Sierra Madre Occidental region of Sonora and Chihuahua.

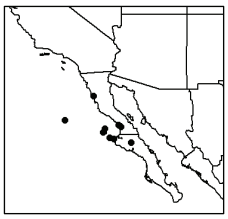
Notes: *Heterodermia appalachensis* is recognized by its dichotomously divided lobes, sorediate, upwardly curved lobe tips and its ecorticate lower side mostly overlaid with a yellow to salmon-colored pigment (K-). *Heterodermia leucomela* lacks the pigment and its soralia are more irregular on the underside. *Heterodermia appalachensis* might be regarded as the sorediate counterpart of *H. linearis*.

Heterodermia ciliatomarginata (Linder) Essl., Lich. Thomsonia 34 (1998).

Basionym: *Anaptychia ciliatomarginata* Linder, Proc. Calif. Acad. Sci., 4th ser. 21: 217 (1934); Synonym: *Anaptychia erinacea* f. *ciliatomarginata* (Linder) Kurok.; Illustration: Esslinger and Bratt (1998), p. 28.

Thallus: foliose, orbicular, up to 7 cm diam., but usually smaller, loosely adnate with radiating, distinctly discrete, dichotomously or somewhat irregularly lobate; **lobes:** linear, elongate, up to 1.5 mm broad, but mostly around 1 mm, ± convex, weakly ascending at the tips, ciliate; cilia: marginal, white below and darkening above, up to 6 mm long; **upper surface:** gray to very dark gray, usually minutely bullate, with stout cilia; soralia and isidia absent; **upper cortex:** prosoplectenchymatous; **medulla:** white, lowermost part often containing agglutinate hyphae that may appear like a cortex; **lower cortex:** absent; **lower surface:** white, shiny, agglutinated hyphae giving a false impression of a cortex, erhizinate; **Apothecia:** abundant, very variable in size, short stipitate, up to 4 mm diam. with ciliate margins; disc: plane, black, often pruinose; **asci:** subclavate to clavate, 8-spored; **ascospores:** brown, l-septate, ellipsoid, *Physcia*-type, (15-) 16.5-19.7 (-22.5) x (6.5-) 7.5-9 (-9.5); **Pycnidia:** abundant and large, inserted, but distinctly protruding above lobe surface; **conidia:** ellipsoid to bacilliform, 3-4 x 1 µm; **Spot tests:** cortex K+ yellow, C-, KC-, P+ yellow; medulla K-, C-, KC-, P-; **Secondary metabolites:** cortex with atranorin and chloroatranorin; medulla without any detected secondary products.

Substrate and ecology: growing on rocks in sun-exposed, ± coastal habitats (see Esslinger and Bratt 1998); **World and Sonoran distribution:** only known on the Pacific Ocean side of Baja California and Baja California Sur.



Notes: It is distinguished by its robust, orbicular thallus with elongate, discrete and ciliate lobes having abundant, ciliate apothecia. Its agglutinated medulla is also distinctive. In comparison with *H. erinacea* and *H. namaquana*, *H. ciliatomarginata* lacks zeorin and has more prominent pycnidia (up to 0.5 mm wide).

Heterodermia comosa (Eschw.) Follmann & Redón, Willdenowia 6: 446. (1972).

Basionym: *Parmelia comosa* Eschw., in Martius Icon. Pl. Crypt. Brasil. 1: 26 (1828); Synonym: *Physcia comosa* (Eschw.) Nyl.; Illustrations: Swinscow and Krog (1988), p. 91; Moberg and Nash (1999), p. 4.

Thallus: foliose to subfruticose, usually forming small tufts of ascending lobes, up to 7 cm across, irregularly lobate; **lobes:** linear spathulate or paddle-shaped, rarely branched, suberect, partially imbricate, up to 5 mm wide, convex, ciliate; cilia: prominent, usually simple, marginal whitish, up to 4 mm long; **upper surface:** white to grayish white, mostly with cilia if not densely covered by pycnidia; soredia and isidia absent; **upper cortex:** prosoplectenchymatous; **medulla:** white; **lower cortex:** absent; **lower surface:** white or variegated ochraceous, apically sorediose, erhizinate; **Apothecia:** common in epitype, terminal to subterminal, substipitate, 1-5 (-10) mm diam., lobulate, ciliate, situated at the end of the ascending lobes; disc: dark brown, densely pruinose; **asci:** cylindrical to subclavate, 8-spored; **ascospores:** brown, l-septate, narrowly ellipsoid to fusiform, *Pachysporaria*-type, without sporoblastidia, 31-34 x 13-15.5 µm; **Spot tests:** cortex K+ yellow C-, KC-, P+ yellow; medulla K+ yellow, C-, KC-, P-; **Secondary metabolites:** cortex with atranorin and chloroatranorin; medulla with atranorin, zeorin and an unknown ochraceous pigment.

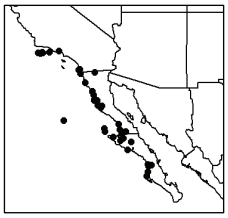
Substrate and ecology: growing on tree trunks and branches in fairly open but moist situations; **World distribution:** known from Central and South America, Africa and Asia; **Sonoran distribution:** not known from the Sonoran Desert region, but present in other parts of Mexico and might eventually be found in the Sonoran Desert area.

Notes: *Heterodermia comosa* is recognized by its helmet-shaped lobes with cilia both on the margins and upper surface and the absence of soralia. Apothecia and pycnidia were not seen in Mexican material.

Heterodermia erinacea (Ach.) W. A. Weber, Bryologist 90: 163 (1987).

Basionym: *Borrera erinacea* Ach., Lich. Univ.: 499 (1810); Synonyms: *Anaptychia erinacea* (Ach.) Trevis., *Physcia erinacea* (Ach.) Tuck., *Physcia ciliaris* var. *erinacea* (Ach.) Nyl.; Illustrations: Esslinger and Bratt (1998), p. 28; Hale and Cole (1988), p. 48; Brodo et al. (2001), p. 337.

Thallus: foliose to caespitose-subfruticose, irregular, very loosely adnate, up to 7 cm in diam., ± dichotomously lobate; **lobes:** linear, elongate, up to 2 mm broad, but usually around 1 mm, 10-20 mm long, ± plane, sometimes prostrate but more often ascending, sometimes minutely bullate, ciliate; cilia: marginal, simple, black tipped, up to 7 mm long; **upper surface:** gray to dark gray, usually with black spots from the abundant pycnidia; soredia and isidia absent; **upper cortex:** prosoplectenchymatous; **medulla:** white, lax, usually well developed; **lower cortex:** lacking throughout; **lower surface:** white, without a cortex, uneven, arachnoid, erhizinate; **Apothecia:** ± abundant, very variable in size, short stipitate, up to 5 mm diam., without cilia on the margin; disc: black, plane, often pruinose; **asci:** subclavate to clavate, 8-spored; **ascospores:** brown, l-septate, ellipsoid, *Physcia*-type, (16-) 18-20.5 (-21.5) x (7.5-) 8-9.5 (-11) µm; **Pycnidia:** ± abundant, inserted in thallus with black openings on the lobes; **conidia:** bacilliform, 3.5-5 x 1µm; **Spot tests:** cortex K+ yellow C-, KC-, P+ yellow; medulla K+ yellow, C-, KC-, P-; **Secondary metabolites:** cortex with atranorin and chloroatranorin; medulla with atranorin and zeorin.



Substrate and ecology: growing on tree trunks, shrubs and cacti in open situations; **World** and **Sonoran distribution:** known from ± coastal parts of Baja California, Baja California Sur and southern California.

Notes: The ± flat lobes with marginal cilia and abundant apothecia makes this common, coastal species easy to recognize.

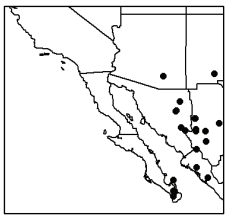
Heterodermia granulifera (Ach.) W. L. Culb**.,** Bryologist 69: 482 (1966).

Basionym: *Parmelia granulifera* Ach., Syn. Lich.: 212 (1814); Synonyms: *Anaptychia granulifera* (Ach.) A. Massal. and *Physcia speciosa* var. *granulifera* (Ach.) Tuck.; Illustrations: Hale (1979), pp. 109 & 110.

Thallus: foliose, irregular, sometimes orbicular, to 3 cm. diam., firmly adnate, repeatedly irregularly lobate; **lobes:** radiating, up to 1.5 mm broad, adnate to the tips, ± sinuous, short and overlapping or discrete, flat to convex, minutely notched, eciliate; **upper surface:** whitish gray to gray, mostly distinctly pruinose particularly at lobe-tips; isidiate; **isidia:** marginal and/or laminal, very variable in length from the usual 0.1 mm and knob-like but also rarely up to 0.5 cm long and then becoming lobulate; soredia: sometimes present and may develop from broken isidia or wartlike projections; **upper cortex:** prosoplectenchymatous; **medulla:** white, lax; **lower cortex:** prosoplectenchymatous; **lower surface:** white or pale to medium brown; rhizines: simple, gray to brown; **Apothecia:** ± common, short stipitate, up to 3 mm diam.; margin: scabrous, minutely crenate, isidiose or lobulate; disc: dark brown, epruinose; **asci:** subclavate to clavate, 8-spored; **ascospores:** brown, l-septate, ellipsoid, *Pachysporaria*-type, without sporoblastidia, (20.5-) 21-27 (-30) x (8.5-) 10.5-14 µm; **Pycnidia:** ± common, inserted in the thallus, visible only as black warts on the surface; **conidia:** bacilliform, 4-5 x 1 µm; **Spot tests:** cortex K+ yellow, C-,

KC-, P+ yellow; medulla K+ yellow to red, C-, KC-, P+ orange; **Secondary metabolites:** cortex with atranorin and chloroatranorin; medulla with atranorin, zeorin and salazinic acid (major).

Substrate and ecology: mainly growing on bark of various deciduous trees in moist, but open conditions from the thorn forest into adjacent montane areas; **World distribution:** both eastern and SW North America (including Mexico); **Sonoran distribution:** relatively common in mesquite, riparian areas, thorn forests and deciduous forests at low to intermediate elevations in southern Arizona, Sonora, Sinaloa and Baja California Sur.



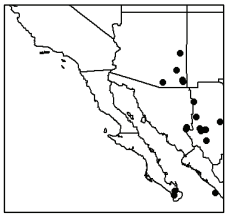
Notes: *Heterodermia granulifera* is recognized by the isidia on the lobe margins and/or the upper surface which sometimes develop soralia in the openings after the isidia are broken.

Heterodermia hypoleuca (Ach.) Trevis., Atti Soc. Ital. Sci. Nat. 11: 615 (1869).

Basionym: *Parmelia speciosa* β *hypoleuca* Ach., Syn. Lich.: 211 (1814); Synonym: *Anaptychia hypoleuca* (Ach.) A. Massal.; Illustrations: Hale (1979), p. 112; Swinscow and Krog (1988), p. 94; Brodo et al. (2001), p. 338.

Thallus: foliose, irregular to orbicular, up to 5 cm diam. (forming colonies up to 15 cm diam.), loosely adnate with discrete, repeatedly dichotomously or irregularly lobate; **lobes:** up to 2 mm broad, usually around 1 mm, irregularly or dichotomously branched; tips: not ascending, with small adventive lateral lobules, eciliate; **upper surface:** greenish white or gray to dark gray or brownish, not or very weakly pruinose; soredia and isidia absent; **upper cortex:** prosoplectenchymatous; **medulla:** white; **lower cortex:** absent; **lower surface:** white to purple or almost black; rhizines: marginal, pale to black, ± abundantly branched; **Apothecia:** ± common, variable in size, substipitate, up to 5 (-10) mm diam., sometimes cupshaped, shortly stipitate or sessile with lobulate margin; disc: brown to dark brown; **asci:** cylindrical to subclavate, 8-spored; **ascospores:** brown, l-septate, ellipsoid, *Pachysporaria* type, with or without sporoblastidia, (22.5-) 23.5-30.5 (-35.5) x (11-) 12.5-16 (-17) µm; **Pycnidia:** ± common; **conidia:** bacilliform, 4-5 x 1 µm [but Kurokawa (1962) reports 1-2 x 0.3-0.5 µm]; **Spot tests:** cortex K+ yellow C-, KC-, P+ yellow; medulla K+ yellow or K+ yellow to orange, C-, KC-, P- or P+ yellow to orange; **Secondary metabolites:** cortex with atranorin and chloroatranorin; medulla with atranorin, zeorin, leucotylin and ± norstictic acid.

Substrate and ecology: growing on bark in fairly moist but open conditions; **World distribution:** southern North America, Africa and eastern Asia; **Sonoran distribution:** relatively common in SE Arizona and the Sierra Madre Occidental region of Chihuahua, Sonora and Sinaloa and on the mountains of the southern tip of Baja California Sur.



Notes: The "wooly" upper lobe-tips, the ecorticate lower side, discrete lobes with small adventive lobes and lobulate apothecia identify the species. It could be characterized as the fertile counterpart of *H. japonica*.

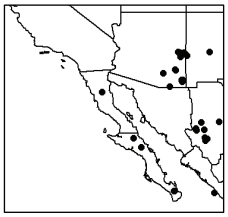
Heterodermia japonica (Satô) Swinscow & Krog, Lichenologist 8: 122 (1976).

Basionym: *Heterodermia dendritica* var. *japonica* Satô, J. Jap. Bot. 12: 427 (1936); Synonyms: *Anaptychia japonica* (Satô) Kurok., *Anaptychia dendritica* var. *propagulifera* Vain., *Heterodermia dendritica* var. *propagulifera* (Vain.) Poelt, *Heterodermia propagulifera* (Vain.) J. P. Dey in Parker & Roane; Illustration: Yoshimura (1974), Pl. 3, Fig. 10 as *Anaptychia japonica.*

Thallus: foliose, very variable, irregular, rarely orbicular, up to 5 cm diam. (often forming colonies up to 15 cm or more in diam.), loosely adnate, dichotomously lobate; **lobes:** sublinear, elongate, radiating, the lobe-tips ascending, usually widening towards apices, *c.* 2-3 (-4) mm at the tips, usually discrete, sometimes dissected with lobules along the margin developing small soralia; **upper**

surface: greenish white, whitish to cream-colored, rarely brownish, sometimes pruinose at tips especially when young, sorediate; **soredia:** farinose to granular, in labriform to capitate soralia, on lateral or terminal lobes, sometimes spreading along lobe margin; **upper cortex:** prosoplectenchymatous; **medulla:** white; **lower cortex:** absent; **lower surface:** white to brownish or bluish black, arachnoid, often sparsely spotted with a brownish orange-red pigment towards lobe apices, rhizinate; rhizines: marginal, simple, black, 1-3 (-7) mm long; **Apothecia:** extremely rare, laminal, substipitate, 1-8 mm in diam.; margin: lacinulate; disc: concave, dark brown to blackish brown, lightly pruinose; **asci:** cylindrical to subclavate, 8-spored; **ascospores:** brown, l-septate, ellipsoid, *Pachysporaria*-type, 40-45 x 20-22 µm; **Pycnidia:** rare, immersed; **conidia:** bacilliform, 4-5 x 1 µm; **Spot tests:** cortex K+ yellow C-, KC-, P+ yellow; medulla K+ yellow or K+ yellow to orange, C-, KC-, P- or P+ yellow to orange; **Secondary metabolites:** cortex with atranorin and chloroatranorin; medulla with atranorin, zeorin, ± norstictic acid, ± salazinic acid and unidentified terpenes.

Substrate and ecology: growing on tree trunks or over mosses on rocks in both open and shady situations; **World distribution:** pantropical to subtropical species extending to warm temperate regions; **Sonoran distribution:** probably the most common *Heterodermia* in the region, occurring in the mountains of Arizona and the Sierra Madre Occidental region of Chihuahua and Sinaloa and in the higher mountains of Baja California and Baja California Sur.



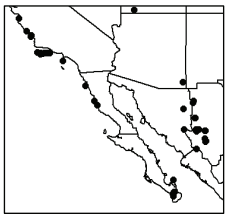
Notes: It is characterized by the dull upper surface, ± fan-like lobe apices, the absence of a lower cortex and by having a white to blackish-violet lower surface. This is however an exceedingly variable species in both morphology and chemistry. The lobes may become more elongate in shady habitats when they may have distinct long, black marginal rhizines (to 7 mm). The soredia may vary from farinose to granular or may be virtually lacking. Swinscow and Krog (1976a) document a similar variation in East Africa. The sparse brownish orange-red pigment pr esent on the lower lobe apices should not be confused with the more distinct, continuous pigmented lower surface of *H. obscurata. Heterodermia dendritica* var. *propagulifera* was already discussed and regarded as a modification of *H. japonica* by Swinscow and Krog (1976a, p. 133) and they have examined the holotype in TUR and the isotype in BM. We fully agree with their conclusions and thus formalize the synonymization.

Heterodermia leucomela (L.) Poelt, Nova Hedwigia 9: 31 (1965).

Basionym: *Lichen leucomelos* L., Sp. Plant., Ed. 2, 2: 1613 (1763); Synonyms: *Anaptychia leucomela* (L.) A. Massal., *Anaptychia hypochrocodes* Vain. and see Kurokawa (1962), p. 74; Illustrations: Hale (1979), p. 103; Swinscow and Krog (1988), p. 96; Brodo et al. (2001), p. 339.

Thallus: foliose but may appear fruticose, composed of interwoven, dichotomously lobate; **lobes:** irregular, narrow, sometimes several cm long, (0.5-) 1-1.5 (-4) mm wide, parallel-sided, not widening towards apices, with long mostly dichotomously branched sometimes squarrose cilia along the margins; **upper surface:** whitish to cream-colored, shiny, without pruina;.sorediate; **soredia:** in irregular soralia formed on the underside causing the lobes to widen; **upper cortex:** prosoplectenchymatous, around half of the lobe thickness; **medulla:** white, very thin; **lower cortex:** absent; **lower surface:** white throughout or partially pinkish brown (paricularly in the herbarium) or rarely purple, margin corticate and prominent (e.g. becoming canaliculate), erhizinate; **Apothecia:** rather rare, subterminal, 2-3 (-5) mm diam., stipitate; disc: dark brown to black, ± pruinose, margin crenulate to lobulate, lobes up to 10 mm; **asci:** cylindrical to subclavate, 8-spored; **ascospores:** brown, l-septate, ellipsoid, *Pachysporaria*-type, (31-) 34.5-42.5 (-49.5) x (15-) 16-20 (-23.5) µm; **Pycnidia:** rare, immersed; **conidia:** bacilliform, 4-5 x 1 µm; **Spot tests:** cortex K+ yellow C-, KC-, P+ yellow; medulla K- or K+ yellow to red, C-, KC-, P- or P+ orange; **Secondary metabolites:** cortex with atranorin and chloroatranorin, medulla with atranorin, zeorin and ± salazinic acid.

Substrate and ecology*:* growing both on trees and over mosses on rocks in both moist and fairly dry situations; **World distribution:** one of the most widespread and abundant species throughout tropical and subtropical regions, extending to warm temperate areas; **Sonoran distribution:** known from coastal localities in southern California and Baja California, the mountains in the southern tip of Baja California Sur and the Sierra Madre Occidental region of Chihuahua, Sonora and Sinaloa; the subsp. *boryi* occurs in Arizona, southern California, Chihuahua, Sonora and Baja California Sur.



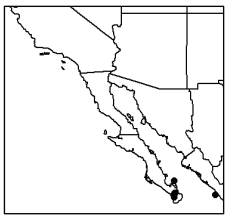
Notes: *Heterodermia leucomela* is easily characterized by the entangled mats of elongate, linear lobes bearing long black cilia and the ecorticate lower surface with ± thick corticate margins. The epithet *lecuomelos* (*leucomelas*), in the feminine should be *leucomelaena,* or it could be abbreviated as *leucomela*. Although Poelt in his combination correctly used *leucomelaena,* we prefer to use the abbreviated form *leucomela* as several publications since Poelt's combination have used this form. It differs from *H. linearis* by the presence of soralia and when apothecia rarely are present they have long lobes on the margins. *Heterodermia leucomela* ssp. *boryi* (*H. boryi*) is included in the treatment.

Heterodermia linearis Moberg & Nash, Bryologist 102: (1999).

Illustration: Moberg and Nash (1999), p. 8.

Thallus: irregular to orbicular, up to 10 cm diam., dichotomously lobate; **lobes:** long, linear, distinctly separate and spreading, up to 1 mm broad, ciliate; cilia: prominent, marginal, up to 7 mm long, giving the margin a comblike appearance; **upper surface:** gray to whitish gray; soredia and isidia absent; **upper cortex:** prosoplectenchymatous; **medulla:** white, forming lowermost part of lobes; **lower cortex:** absent; **lower surface:** white, sometimes bluish, erhizinate; **Apothecia:** laminal and/or terminal, short stipitate, up to 5 mm in diam. with shortly lobulate margin often folded over the hymenium; **asci:** subclavate to clavate, 8-spored; **ascospores:** brown, l-septate, ellipsoid, *Pachysporaria*-type, sometimes with sporoblastidia, (29-) 32.5-38.5 (-42) x (14-) 15-18 (-21.5) µm; **Pycnidia:** common, immersed, appearing as distinct, black warts on the upper side; **conidia:** bacilliform, 4-6 x 1 µm; **Spot tests:** cortex K+ yellow C-, KC-, P+ yellow; medulla K+ yellow, C-, KC-, P-; **Secondary metabolites:** cortex with atranorin and chloroatranorin; medulla with atranorin and zeorin.

Substrate and ecology: grows abundantly on tree trunks in oak woodland and seems to prefer open localities in fairly humid areas; **World** and **Sonoran distribution:** Sinaloa and mountains in southern Baja California Sur between 1200 and 1800 m.



Notes: The publication of this species as *H. lineare* was orthographically incorrect and is hereby emended to *H. linearis. Heterodermia linearis* is a robust species recognized by the linear lobes with regularly ciliate margins and abundant apothecia and pycnidia. It differs from *H. leucomela* by the absence of soralia and from fertile *H. leucomela* by the abundant pycnidia and entire or only shortly lobulate apothecial margins.

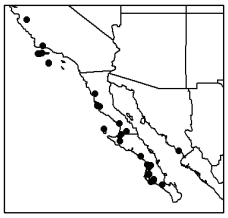
Heterodermia namaquana Brusse, Bothalia 22: 183 (1992).

Illustration: Esslinger and Bratt (1998), p. 28.

Thallus: foliose to caespitose-subfruticose, rarely exceeding 3 cm in diam., very loosely adnate, irregularly lobate; **lobes:** mostly paddle-shaped, up to 3 mm broad, broadest near the tips, simple or weakly branched, often ascending apically, sometimes elongate and linear but tips sometimes helmet-like, ciliate; cilia: marginal and laminal, up to 6 mm long; **upper surface:** whitish gray, uneven, ± pruinose, sometimes minutely bullate, sorediate; **soredia:** farinose, in soralia on the underside of the whole lobes or sometimes on recurved lobe-tips or breaking through the upper cortex; **upper cortex:** prosoplectenchymatous; **medulla:** white, lower part often agglutinate and appearing

like a cortex; **lower cortex:** absent; **lower surface:** white, sorediate, often vein-like due to downward extension of the upper cortex, erhizinate (although cilia may be misleading); **Apothecia:** occasional, up to 3 mm diam., short stipitate, margin mostly ciliate; disc: black, plane, often pruinose; **asci:** subclavate to clavate, 8-spored; **ascospores:** brown, l-septate, ellipsoid, *Physcia*-type (15-) 15.5-18 (-19.5) x (6.5-) 7- 8.5 (-9.5) µm; **Pycnidia:** ± common; **conidia:** usually bacilliform (but sometimes pointed at one end), 4-5 x <1µm; **Spot tests:** cortex K+ yellow C-, KC-, P+ yellow; medulla K+ yellow, C-, KC-, P-; **Secondary metabolites:** cortex with atranorin and chloroatranorin; medulla with atranorin and zeorin (minor to ± accessory).

Substrate and ecology: on shrubs, seems to prefer coastal sites in the Sonoran Desert area; **World distribution:** SW North America and South Africa; **Sonoran distribution:** Channel Islands of California and coastal areas of Baja California, Baja California Sur and southern Sonora.



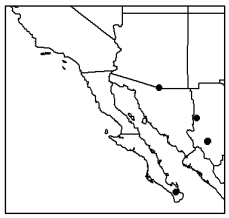
Notes: The species is recognized by the ± helmet-shaped lobes with soredia on the underside, its ciliate lobes and its small size. The presence of soredia readily separates it from *H. erinacea*. See Essinger and Bratt (1998) for a discussion of other, subtle morphological differences.

Heterodermia obscurata (Nyl.) Trevis., Nuovo Giorn. Bot. Ital. 1: 114 (1869).

Basionym: *Physcia obscurata* Nyl., Annals Sci. Nat. Bot., ser. 4, 19: 310 (1863); Synonyms: *Anaptychia obscurata* (Nyl.) Vain. and see Kurokawa (1962), p. 49 as *Anaptychia obscurata*; Illustrations: Hale (1979), p. 104; Swinscow and Krog (1988), p. 98; Brodo et al. (2001), p. 340.

Thallus: foliose, forming ± orbicular rosettes or irregularly spreading, robust, 2-4 (-10) cm diam., ± firmly adnate, dichotomously to irregularly lobate; **lobes:** *c.* 1-2 mm, radiating, sparsely divided, ± discrete, flat to slightly convex, minutely notched, eciliate; **upper surface:** gray-white to rarely dark gray in center, shiny, not or rarely pruinose, sorediate; **soredia:** granular, often rusty brown, in labriform to capitate soralia on lateral and terminal lobes, sometimes confluent and forming marginal soralia; **upper cortex:** prosoplectenchymatous; **medulla:** white above, rusty brown below; **lower cortex:** absent; **lower surface:** felted with rust-colored or yellowish-brown pigment, K+ purple, not to be confused with the bluish-black underside present in *H. japonica,* arachnoid, rhizinate; rhizines: black, marginal, simple to squarrosely branched; **Apothecia:** rare (not seen in Sonoran material), substipitate, 1-5 mm in diam., margin becoming sorediate; disc: blackish brown, epruinose; **asci:** cylindrical to subclavate, 8-spored; **ascospores:** brown, l-septate, ellipsoid, 29-35 x 15-19; **Pycnidia:** not seen; **Spot tests:** cortex K+ yellow C-, KC-, P+ yellow; medulla K-, C-, KC-, P-; **Secondary metabolites:** cortex with atranorin and chloroatranorin; medulla with atranorin, zeorin, an unidentified terpene and a rusty brown pigment.

Substrate and ecology: growing on trunks of deciduous trees and mossy rocks in open but humid conditions; **World distribution:** common and widespread in tropical and subtropical areas, extending to warm temperate region in Europe and SE North America; **Sonoran distribution:** the mountains of SE Arizona, the Sierra Madre Occidental region of Chihuahua and mountains in the southern tip of Baja California Sur.



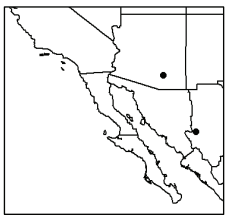
Notes: It is characterized by its robust appearance, the distinct labiate soredia and the rusty-brown pigmented (K+ purple) lower surface. Similar species include *H. japonica*, which differs in having a K+ yellow-red medullary reaction and is not pigmented or with only sparse rusty brown pigment (K–) on its lower surface. Another similar species, *H. speciosa*, is distinguished by having a lower cortex and lacks any rusty brown pigmentation. *Heterodermia obscurata* is regarded as the sorediate counterpart of *H. flabellata*.

Heterodermia podocarpa (Bél.) Awasthi, Geophytology 3: 114 (1973).

Basionym: *Parmelia podocarpa* Bél., Voy. Ind. Or. Bot., II, Crypt.: 122, Pl. 13, Fig. 1 (1834); Synonyms: *Anaptychia podocarpa* (Bél.) A. Massal. and see Kurokawa (1962), p. 86; Illustration: Moberg and Nash (1999), p. 10.

Thallus: foliose to subfruticose, up to 5 cm broad but usually smaller, irregularly lobate; **lobes:** ± convex, variable in width, up to 2 (-3) mm, often ascending, sometimes imbricate with whitish cilia along margins; **upper surface:** grayish white to gray, sometimes reddish in herbarium caused by poor drying; soredia and isidia absent; **upper cortex:** prosoplectenchymatous; **medulla:** white; **lower cortex:** absent; **lower surface:** white, ± canaliculated, arachnoid, appearing sorediate, rhizinate; rhizines, marginal, simple to irregularly branched; **Apothecia:** ± abundant, 1-2 (-5) mm wide, subterminal and substipitate to stipitate and thus appearing terminal, with ± well developed squamules on margin; disc: brown to dark brown, ± pruinose; **asci:** subclavate to clavate, 8-spored; **ascospores:** brown, l-septate, ellipsoid, *Pachysporaria* type with sporoblastidia (26-) 29.5-35 (-35.5) x (13-) 13.5-16 (-17) µm; **Pycnidia:** ± abundant; **conidia:** bacilliform, 4-5 x 1 µm; **Spot tests:** cortex K+ yellow, C-, KC-, P+ yellow; medulla K+ yellow to red, C-, KC-, P+ orange; **Secondary metabolites:** cortex with atranorin and chloroatranorin; medulla with atranorin, zeorin and salazinic acid (major) and norstictic acid (trace or accessory).

Substrate and ecology: on twigs and small branches in oak and pine forests; **World distribution:** widespread but not common species known from southern USA, Central and South America, Africa and Asia; **Sonoran distribution:** SE Arizona and the Sierra Madre Occidental region of Chihuahua.



Notes: No material, from which Bélanger's figures were made, seems to be left. We have seen no material from Réunion, but among the material seen from Africa, that from the Usambara Mountains is the most similar to the figure description. The species usually is fairly small and consequently the epitype is also small. Additional material from the Usambara Mountains. (*Moberg 1484f* and *Santesson 23335a*, UPS) show the variation of the species. *H. podocarpa* is the only species present in the area belonging to the group *Podocarpae.* The spores are a bit smaller than in the material from East Africa. A similar species, but one with soralia, is *H. galactophylla*, that is known from southeastern North America, and Central and South America.

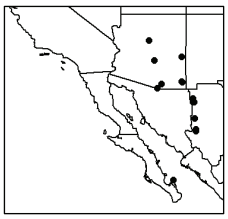
Heterodermia pseudospeciosa (Kurok.) W. L. Culb**.,** Bryologist 69: 484 (1966).

Basionym: *Anaptychia pseudospeciosa* Kurok., J. Jap. Bot. 34: 176 (1959).

Thallus: foliose, orbicular to irregular, small, usually less than 4 cm diam., loosely adnate, densely dichotomously lobate; **lobes:** long and narrow, up to 1 (-1.5)mm broad, repeatedly branched, weakly convex, widening, the tips not ascending, minutely notched, eciliate; **upper surface:** grayish white to gray to brownish gray, darker at lobe tips, sometimes weakly pruinose; sorediate; **soredia:** white to bluish gray, in semi-capitate soralia, sometimes at lobe-tips but mainly arising from small lateral knob-like structures; **upper cortex:** prosoplectenchymatous; **medulla:** white; **lower cortex:** prosoplectenchymatous; **lower surface:** whitish to pale brown, rarely dark gray; rhizines: weakly developed, usually short (*c.* 1 mm), pale to dark brown or black; **Apothecia:** rare (not seen in Sonoran material), subsessile, 1-3 mm in diam., margin sorediate; disc: brown to blackish brown, epruinose; **asci:** cylindrical to subclavate, 8-spored; **ascospores:** brown, l-septate, ellipsoid, 26-32 x 12-14; **Pycnidia:** ± common, immersed; **conidia:** bacilliform, 4-5 x 1 µm; **Spot tests:** cortex K+ yellow C-, KC-, P+ yellow; medulla K+ yellow to orange, C-, KC-, P+ yellow to orange; **Secondary metabolites:** cortex with atranorin and chloroatranorin; medulla with atranorin, zeorin and an unidentified terpenes (accessory) and norstictic acid (major) and connorstictic acid (minor).

Substrate and ecology: growing mainly on rocks, more rarely on trees in open but humid situations; **World distribution:** eastern North America and scattered lo-

calities on all continents; **Sonoran distribution:** Arizona and several in Chihuahua in the Sierra Madre Occidental.



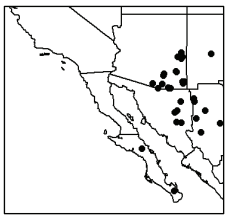
Notes: This species is characterized by the narrow, convex, long lobes, corticate on the lower surface. The soralia arise mainly from marginal knob-like structures forming small, semi-capitate soralia. The records of salazinic acid are probably misinterpretations of connorstictic acid which seems to be regularly present. The type material does not contain salazinic acid (Swinscow and Krog 1976), and our collections from southeastern U.S.A. also lack salazinic acid, which agrees with Culberson (1966). The K+ reaction is similar to that of *H. albicans* (with salazinic acid), which also has similar soralia. However, the soralia of *H. albicans* are ± continuously marginal, and it is more firmly adnate and does not contain norstictic acid. *Heterodermia speciosa* is usually larger, has ± flat lobes and lacks both norstictic and salazinic acid.

Heterodermia rugulosa (Kurok.) Trass, Folia Cryptogr. Estonica 29: 19 (1992).

Basionym: *Anaptychia rugulosa* Kurok., Nova Hedwigia, Beih. 6: 41 (1962); Illustrations: Kurokawa (1962), Pl 5, Fig. 31 as *Anaptychia rugulosa*; Hale (1979), p. 114; Brodo et al. (2001), p. 336 as *H. diademata*.

Thallus: foliose, irregular to orbicular, to 5 cm or up to 10 cm when confluent with other thalli, firmly adnate with distinct lobes and patchily pigmented medulla, dichotomously to subpalmately lobate; **lobes:** linear, elongate, usually overlapping, sometimes discrete, flat, ± sinuose, 1-2 mm broard, usually with peculiar knobs along margins, eciliate; **upper surface:** grayish white, gray to dark gray, often rugulose, usually with a distinct white pruina; soredia and isidia absent; **upper cortex:** prosoplectenchymatous; **medulla:** white, mostly but not always with patches of yellow to yellow-brown pigment (K+ purple); **lower cortex:** prosoplectenchymatous; **lower surface:** pinkish to pale brown or brown, rhizinate; rhizines: scattered, pale to dark, simple; **Apothecia:** ± common, up to 6 mm diam., substipitate, but usually smaller, often with a rough pruina; margins: white pruinose, sometimes lobulate; disc: blackish brown, epruinose; **asci:** subclavate to clavate, 8-spored; **ascospores:** brown, l-septate, ellipsoid, *Pachysporaria*-type, (19.5-) 21-26 (-29) x (9.5-) 10.5-12 (-13) µm; **Pycnidia:** ± common, visible as black dots and often concentrated to lobe margins; **conidia:** bacilliform, 4-5 x 1 µm; **Spot tests:** cortex K+ yellow C-, KC-, P+ yellow; medulla K+ purple (where pigmented), C-, KC-, P-; **Secondary metabolites:** cortex with atranorin and chloroatranorin; medulla with atranorin, zeorin, leucotylin and an unknown yellow to brownish pigment (K+ purple).

Substrate and ecology: growing on trunks, twigs and rocks and seems to prefer open, but humid conditions; **World distribution:** SW USA and extensively in Mexico; **Sonoran distribution:** very common in oak and pine forests of SE Arizona and adjacent Sierra Madre Occidental region of Chihuahua and Sonora and in the mountains in the southern part of Baja California Sur.



Notes: *Heterodermia rugulosa* is an extremely variable species with very different appearances on different substrates. On bark it is usually broad-lobed with overlapping lobes; while on twigs, short-lobed with ± fingerlike lobes and on rocks it has discrete, distinctly effigurate lobes. It may be difficult to identify if the pigment in the medulla is sparse, but the lobe primordia along lobe margins are typical for the species. This is similar to *H. diademata*, that has been erroneously reported from the Sonoran region. Also it is similar to *H. tropica*, which is probably closely related but it lacks the pigment in the medulla.

Heterodermia spathulifera Moberg & Purvis, Symb. Bot. Ups. 32: 192 (1997).

Illustration: Moberg and Purvis (1997), p. 192.

Thallus: foliose, irregular to orbicular, up to 3 cm diam., discretely lobate; **lobes:** narrow, up to 1 mm, usually flat, not distinctly widening at tips, eciliate; **upper surface:**

white to cream-colored, shiny and without pruina, sorediate; **soredia:** in labriform soralia, sometimes becoming very big (up to 5 mm tall) and spathulate; **upper cortex:** thick, prosoplectenchymatous; **medulla:** white; **lower cortex:** absent; **lower surface:** white on outer parts of lobes, pale brown in inner parts (appearing corticate, but in sections this proves to be medulla incrusted by soil particles); rhizines: sparse, marginal, *c.* 1 (-2) mm long, simple, sometimes projecting beyond the margin; **Apothecia:** rare; **asci:** subclavate to clavate, 8-spored; **ascospores:** brown, l-septate, narrowly ellipsoid to ellipsoid, *Pachysporaria*-type, 36-43 x 15-18 µm; **Pycnidia:** not seen; **Spot tests:** cortex K+ yellow C-, KC-, P+ yellow; medulla K+ yellow, C-, KC-, P-; **Secondary metabolites:** cortex with atranorin and chloroatranorin, medulla with atranorin, zeorin and an unidentified substance, UV+ red after charring rf 4-5 (G) [‘spathulin’].

Substrate and ecology: growing on both rocks and tree trunks in open but humid conditions; **World distribution:** earlier known only from the Azores (Moberg and Purvis 1997); **Sonoran distribution:** not present in˝the Sonoran Desert area, but just outside the region and thus suspected to be found.

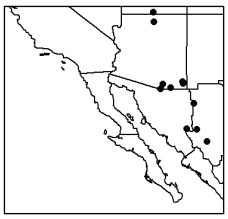
Notes: This species is distinguished by its narrow, shiny, firmly adnate lobes with pale marginal rhizinae and unique chemistry, containing an unknown substance, ‘spathulin’, appearing reddish in UV above zeorin after treatment with sulfuric acid. If soralia are present they are usually big and spathulate. Another *Heterodermia* with small adnate lobes is *H. albicans*, which differs in having, darker lobes with small marginal knob-like projections developing into soralia and a very distinct lower cortex. In moist and shaded habitats the soredia of *H. spathulifera* tend to develop into squamules, that sometimes may cover inner parts of the thallus.

Heterodermia speciosa (Wulfen) Trevis., Atti Soc. Ital. Sci. Nat. 11: 614 (1869).

Basionym: *Lichen speciosus* Wulfen in Jacq., Coll. Bot. 3: 119 (1789); Synonyms: *Anaptychia speciosa* (Wulf.) A. Massal., and see Kurokawa (1962), p. 24; Illustrations: Swinscow and Krog (1988), p. 100; Wirth (1995), p. 419; Brodo et al. (2001), p. 340.

Thallus: foliose, orbicular to irregular, 2-3 (-4) cm diam., often coalescing with other thalli forming colonies up to 15 cm diam., ± firmly adnate, repeatedly dichotomously lobate; **lobes:** linear, elongate, narrow, *c.* (0.5-) 1-2 mm, flat to convex, end-lobes without soralia, slightly widening towards apices, minutely notched, eciliate; **upper surface:** white to cream-colored or brownish to bluish gray, ± shiny, the lobe-tips sometimes darkening, very rarely pruinose, not ascending, sorediate; **soredia:** abundant, farinose to ± granular, gray to bluish gray, in labiate soralia, on lateral lobes, sometimes semi-capitate, starting from lateral lobules; **upper cortex:** prosoplectenchymatous; **medulla:** white; **lower cortex:** prosoplectenchymatous; **lower surface:** pale to dark brown, rhizinate; rhizines: few, scattered, short and robust, sometimes irregularly branched, usually black; **Apothecia:** rare (not seen in Sonoran material), substipitate, 3-8 mm in diam., margin: crenate or lacinulate; disc: brown to blackish brown; **asci:** cylindrical to clavate, 8-spored; **ascospores:** brown, l-septate, ellipsoid, 30-37 x 14-18; **Pycnidia:** not seen; **Spot tests:** cortex K+ yellow C-, KC-, P+ yellow; medulla K+ yellow, C-, KC-, P-; **Secondary metabolites:** cortex with atranorin and chloroatranorin; medulla with atranorin, zeorin and an unidentified triterpene.

Substrate and ecology: growing on sunny, but moist rocks or on tree trunks in humid conditions; **World distribution:** widely distributed in subtropical to temperate areas, extending to northern Scandinavia (Moberg & Holmåsen 1992); **Sonoran distribution:** mountains of SE Arizona and the Sierra Madre Occidental region of Chihuahua and Sonora.



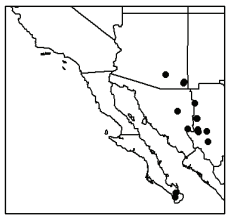
Notes: It is characterized by the striking contrast between the blue-gray soralia and the paler thallus and the presence of lower cortex. The lower surface of *H. obscurata* lacks a cortex and has a rusty orange pigment. *Heterodermia albicans* is much smaller and contains salazinic acid (K+ yellow-red).

Heterodermia tropica (Kurok.) Kurok., Folia Crypt. Estonica 32: 24 (1998).

Basionym: *Anaptychia tropica* Kurok., Beih. Nova Hedwigia 6: 36 (1962); Illustration: Kurokawa (1962), Pl 5, Fig. 29 as *Anaptychia tropica*.

Thallus: foliose, orbicular, up to 5 cm diam. or irregular and confluent with other thalli, ± closely adnate, dichotomously to subirregularly lobate; **lobes:** linear, ± elongated, 0.5-1.5 mm broad, with ± lobulate margins, eciliate; **upper surface:** whitish gray, gray to dark gray often with darker margins and tips, sometimes with a weak pruina; soredia. and isidia absent; **upper cortex:** prosoplectenchymatous; **medulla:** white; **lower cortex:** prosoplectenchymatous; **lower surface:** white to pale gray or brownish, rhizinate; rhizines: abundant, pale gray to black, sparsely branched; **Apothecia:** common, up to 5 mm diam. with abundant lobules along margins on older apothecia; disc: brown to blackish brown, epruinose; **asci:** subclavate to clavate, 8-spored; **ascospores:** brown, l-septate, *Pachysporaria*-type, (25-) 27-32 (-37.5) x (12-) 13-17 (-19.5) µm; **Pycnidia:** ± abundant; **conidia:** bacilliform, 4-5 x 1µm; **Spot tests:** cortex K+ yellow, C-, KC-, P+ yellow; medulla K+ yellow to red, C-, KC-, P+ orange; **Secondary metabolites:** cortex with atranorin and chloroatranorin; medulla with atranorin, zeorin and salazinic acid (major).

Substrate and ecology: on bark of various trees, rarely on rock; **World distribution:** has a limited distribution in SE Arizona, Mexico and Central America; **Sonoran distribution:** mountains of SE Arizona, adjacent Sierra Madre Occidental regions of Chihuahua and Sonora and the mountains of southern Baja California Sur.



Notes: *Heterodermia tropica* is very similar to *H. diademata* and the major difference is presence of salazinic acid. The relation between *H. tropica* and *H. albicans* is probably the same as the relation between *H. diademata* and *H. speciosa*.

HUBBSIA

by A. Tehler

Hubbsia W. A. Weber, Svensk Bot. Tidskr. 59: 61 (1965).

Family: Roccellaceae; Type: *Hubbsia californica* (Räsänen) W. A. Weber; No. species: two world-wide; Selected lit.: Follmann (1997), Tehler et al. (1997).

Life habit: lichenized; **Thallus:** subfruticose to subfoliose, fragile, smooth, pruinose, 5-15 cm in diam., up to 2 cm thick; **lobe surface:** creamy-white to ivory white, with or without soredia; **cortex:** predominantly of interwoven, in parts somewhat anticlinally arranged, branched hyphae; **medulla:** white above, byssoid to chalky with brown plectenchyma in basal parts; **photobiont**: primary one a *Trentepohlia*, secondary photobiont absent; **prothallus:** not seen; **Ascomata:** in synascomata but sometimes solitary, sessile or immersed, lirelliform with branched lirellae, 4-5 x 0.1-0.2 mm; disc: hidden, epruinose; thalline exciple: thin and slightly elevated, with algae and cortex; proper exciple: parathecial; epithecium: 20-25 µm thick with paraphysoids reticulate and richly branched in a brown gel, 1-2 µm diam.; hymenium: 60 µm thick; paraphysoids: reticulate and richly branched, conglutinated, hyaline, 1 µm diam.; hypothecium: distinct, dark-brown (carbonaceous), extending down and gradually disappearing into the medulla; **asci:** clavate, *c.* 75 x 13 µm, 8-spored; **ascospores:** bluntly fusiform to ellipsoid, straight, smooth, 3-4 septate, hyaline, 15-18 x 4-5 µm; **Conidiomata:** pycnidial, numerous, solitary, lateral, immersed or slightly elevated, pale brown, when elevated 0.6 mm, when immersed 0.2 mm diam.; **conidia:** filiform, curved, hyaline, 12-14 x <1 µm; **Secondary metabolites:** orcinol depsides; three other minor substances are probably hydrolysis or methanolysis products; **Geography:** coastal

regions with Mediterranean climates in SW North America; **Substrate**: on acidic rocks.

Key to the species of ***Hubbsia*** from the Sonoran region:

1. Thallus lobes solid; soredia absent ..... ***H. californica***
1. Thallus lobes hollow; soredia present ..... ***H. parishii***

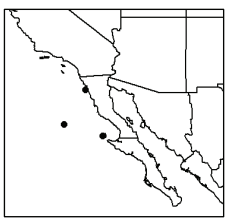
The Species

Hubbsia californica (Räsänen) W. A. Weber in Egan, Bryologist, 90: 110 (1987).

Basionym: *Reinkella californica* Räsänen, Arch. Soc. Zool.-Bot. Fenn. 'Vanamo' 3: 186 (1949); Synonym: *Hubbsia lumbricoides* W. A. Weber (1965); Illustrations: Weber (1965), p. 60 & plates I & II.

Thallus: subfruticose to subfoliose, solid; **lobes:** marginal parts *c.* globular; central parts often with ± terete but *c.* dorsivental towards the tips, lumbricoid (worm-like), appressed branches; **lobe surface:** creamy-white to ivory white, smooth; soredia absent; **medulla:** white with lowermost parts brown or yellowish brown; **"Apothecia":** numerous, lirelliform with branched lirellae; hymenium: 60 µm high; paraphysoids: reticulately and richly branched, conglutinated, hyaline, *c.* 1 µm in diam.; **asci:** clavate, *c.* 75 x 13 µm, 8-spored; **ascospores:** fusiform, 3-4 septate, hyaline, 15-18 x 4-5 µm; **Spot tests:** cortex K-, C+ red, KC+ red, P-; medulla K-, C+ red, KC+ red, P-; **Secondary metabolites:** erythrin and lecanoric acid (both major); montagnetol and orsellinic acid (both minor); three other minor substances are probably hydrolysis or methanolysis products.

Substrate and ecology: on vertical rocks and cliffs near the ocean; individuals often growing in masses covering several square meters; **World** and **Sonoran distribution:** only known from a few localities on the Baja California mainland and on Guadalupe Island.



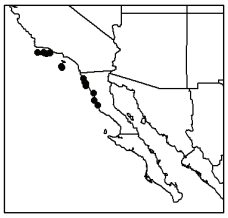
Notes: *Hubbsia californica* is characterized by its solid thallus with lumbricoid lobes in the central parts and the complete absence of soredia.

Hubbsia parishii (Hasse) Follmann, Bibl. Lichenol. 67: 17 (1997).

Basionym: *Reinkella parishii* Hasse Bryologist 17: 45 (1920); Synonym: *Reinkella subcrustacea* Räsänen; Illustrations: Tehler et al. (1997), pp. 259, 261 & 262; Brodo et al. (2001), p. 341.

Thallus: subfruticose to subfoliose, hollow, approximately globular also in central parts; **lobe surface:** creamy white to ivory white, **soredia:** coarse in maculiform soralia, becoming confluent in the central parts of thallus; **medulla:** white with lowermost parts brown; **"Apothecia":** absent or sparse, lirelliform with branched lirellae; hymenium: 60 µm high; paraphysoids: reticulately and richly branched, conglutinated, hyaline, *c.* 1 µm in diam.; **asci:** clavate, c. 75 x 13 µm, 8-spored; **ascospores:** fusiform, 3-4 septate, hyaline, 16-17 x 4-5 µm; **Spot tests:** cortex K-, C+ red, KC+ red, P-; medulla K-, C+ red, KC+ red, P-; **Secondary metabolites:** erythrin and lecanoric acid (major), montagnetol and orsellinic acid (minor) and three other minor unknowns that are probably hydrolysis or methanolysis products.

Substrate and ecology: on vertical rocks and cliffs near the ocean; individuals occasionally growing in masses covering several square meters but near the ocean preferring sheltered crevices and often beneath overhangs; **World** and **Sonoran distribution:** the Channel Islands of southern California south to central Baja California.



Notes: *Hubbsia parishii* is characterized by its hollow thallus lobes and usual presence of soredia.

HYPERPHYSCIA

by R. Moberg

Hyperphyscia Müll. Arg., Bull. Herb. Boissier 2, App. 1: 10 (1894).

Family: Physciaceae; Type: *Hyperphyscia adglutinata*; No. species: eight world-wide; Selected lit.: Hafellner et al. (1979), and Moberg (1987).

Thallus: foliose, small (up to 2 cm diam.), very closely adnate; **upper surface:** pale gray brown to dark brown, usually epruinose; with or without soredia or isidia; **upper cortex:** paraplectenchymatous, cells with lumina µm 3-7 diam.; **medulla:** white or orange or orange-red, composed of loosely interwoven hyphae; **photobiont:** primary one a trebouxioid alga, secondary photobiont absent; **lower surface:** if evident, then black centrally and paler towards the margin; erhizinate or with sparsely developed, simple ones **lower cortex:** prosoplectenchymatous or rudimentary (integrating with the substrate); **Ascomata:** apothecia, lecanorine (with thalline exciple), sessile; disc: brown to blackish, epruinose; epihymenium: pale brown; hymenium: hyaline, I+ blue; paraphyses: simple or weakly branched; hypothecium: colorless or red to orange; **asci:** cylindrical, *Lecanora* type, 8-spored; **ascospores:** *Pachysporia* to *Physcia*-type, brown, 1-3 septate, rarely submuriform, thick walled; **Conidiomata:** pycnidia, wall colorless below but brown round the ostiole, immersed; **conidia:** colorless, filiform, usually longer than 15 µm; **Secondary metabolites:** none detected or pigments (skyrin); **Geography:** pantropical and pantemperate; **Substrate:** common on bark or wood, rarely on mosses over rocks.

Notes: *Hyperphyscia* is separated from other genera of the Physciaceae by its pycnoconidia, very tightly adnate thallus, sparse development of or complete lack of rhizines and rudimentary (at best) lower cortex. An undescribed species occurring on rock just north of the Sonoran region may also belong to this genus, although it also has affinities to *Caloplaca demissa*.

Key to the species of ***Hyperphyscia*** occurring in the Sonoran region:

1. Thallus sorediate 2
1. Thallus not sorediate ..... ***H. syncolla***
   2. Medulla orange ..... ***H. pandani***
   2. Medulla white ..... ***H. adglutinata***

The Species

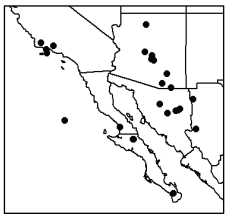
Hyperphyscia adglutinata (Flörke) H. Mayrhofer & Poelt, Herzogia 5: 62 (1979).

Basionym: *Lecanora adglutinata* Flörke, Deutsch. Lich. Gessam. Anmerk. 7 (1819); Synonym: *Physciopsis adglutinata* (Flörke) M. Choisy; Illustrations: Moberg (19 87), p. 720; Brodo et al. (2001), p. 343.

Thallus: foliose, orbicular to irregular (adjacent thalli becoming confluent), small, less than 2 cm diam., very tightly adnate, densely lobate; **lobes:** narrow, 0.3-0.7 (-2) mm wide, radiating, usually plane, margins occasionally black, tips sometimes ascending; **upper surface:** gray-brown to brown or dark brown, darker at lobe-tips, epruinose or weakly pruinose, sorediate; **soredia:** sparse or abundant, granular, laminal in soralia that sometimes arise from small protrusions or lobules on the lobe surface, in maculiform or capitate soralia; isidia absent; **medulla:** white; **lower surface:** blackish centrally, paler marginally whitish to pale brownish, rarely dark gray, erhizinate or weakly rhizinate; **Apothecia:** very rare, *c.* 1 mm diam., thalline margin entire; **ascospores:** brown, ellipsoid, 1-septate, *Pachysporaria* to *Physcia* type, 15-23 x 7-11 µm; **Pycnidia:** ± common, inserted with black weakly protruding tips; **conidia:** filiform, 15–20 x 0..5-1 µm; **Spot tests:** cortex and medulla K- C-, KC-, P-; **Secondary metabolites:** none detected.

Substrate and ecology: growing on nutrient rich, riparian trees, such as *Prosopis*, at low to intermediate elevations;

World distribution: North America, Europe, East Africa and South America; **Sonoran distribution:** relatively common in Arizona, southern California and Sonora; less common in Chihuahua, Baja California and Baja California Sur.

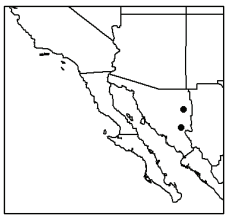


Notes: Traces of skyrin are reported in East African populations (Moberg 1987), but it has not been observed in Sonoran specimens. It needs to be carefully distinguished from adnate *Phaeophyscia* species that have better developed rhizines and a more clearly developed lower cortex.

Hyperphyscia pandani (Magn.) Moberg, Nord. J. Bot. 7: 722 (1987).

Basionym: *Physcia pandani* Magn., Arkiv Bot. 32: 65 (1945); Illustration: Moberg (1987), p. 722.

Thallus: foliose, orbicular but sometimes irregular, small, less than 3 cm diam., very tightly adnate, densely lobate; **lobes:** narrow, 0.3-0.6 (-1.0) mm wide, radiating, partially imbricate, usually plane, tips adnate; **upper surface:** gray brown to dark brown, paler at lobe-tips, rarely white pruinose, sorediate; **soredia:** sparse or abundant, often red-orange, granular, laminal in maculiform, capitate to crateriform soralia; isidia absent; **medulla:** orange to red or red-brown; **lower surface:** blackish centrally, grayish at lobe tips, erhizinate or rarely a few rhizines present; **Apothecia:** uncommon, *c.* 1 mm diam., thalline margin entire or sorediate; hypothecium: reddish; **ascospores:** brown, ellipsoid, 1-septate, *Pachysporaria* type, 16-18 x 8-10 µm; **Pycnidia:** ± common, inserted with black weakly protruding tips; **conidia:** filiform, 15–20 x 0.5-1 µm; **Spot tests:** cortex and medulla K-C-, KC-, P-; **Secondary metabolites:** skyrin.

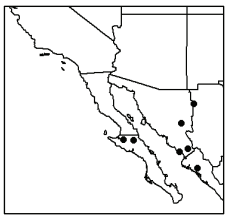


Substrate and ecology: growing on nutrient rich, riparian trees, such as *Prosopis*, at low to intermediate elevations; **World distribution:** Hawaii (type) and East Africa; **Sonoran distribution:** thus far only known from several localities in Sonora.

Hyperphyscia syncolla (Nyl.) Kalb, Lich. Neotropici, Fasc. 6: 11 (1983).

Basionym: *Physcia syncolla* Tuck *ex* Nyl., Acta Soc. Sci. Fenn. 7: 441 (1863); Synonym: *Physciopsis syncolla* (Nyl.) Poelt; Illustrations: Moberg (1987), p. 724; Swinscow and Krog (1988), plate 9; Brodo et al. (2001), p. 344.

Thallus: foliose, orbicular, rarely irregular, small, less than 2 cm diam., very tightly adnate, often verrucose in center, densely lobate; **lobes:** narrow, 0.3-1.0 (-2.0) mm wide, radiating, usually plane, margins occasionally black, tips sometimes ascending; **upper surface:** gray brown to dark brown, darker at lobe-tips, epruinose or very faintly developed pruina, soredia and isidia absent; **medulla:** white; **lower surface:** dark brown to black centrally, paler to whitish at tips, erhizinate or weakly rhizinate; **Apothecia:** common, up to 2 mm diam., thalline margin entire to crenulate; **ascospores:** brown, ellipsoid, 1-septate, *Pachysporaria* type, 15-21 x 7-11 µm; **Pycnidia:** ± common, inserted with black weakly protruding tips; **conidia:** filiform, 15–20 x 0.5-1 µm; **Spot tests:** cortex and medulla K- C-, KC-, P-; **Secondary metabolites:** none detected.



Substrate and ecology: growing on nutrient rich, riparian trees, such as *Prosopis*, at low to intermediate elevations; **World distribution:** North America and East Africa; **Sonoran distribution:** occasional in Sonora, Chihuahua, Sinaloa and Baja California Sur.

Notes: Its verrucose thallus center, tightly adnate thallus and essential absence of rhizines should separate this species from *Phaeophyscia* species, that are usually more robust.

HYPOCENOMYCE

by E. Timdal

Hypocenomyce M. Choisy, Bull. Mens. Soc. Linn. Lyon 20: 133 (1951).

Family: Bacidiaceae?; Type: *Hypocenomyce scalaris* (Ach.) M. Choisy; No. species: 13 world-wide; Selected lit.: Timdal (1984b & 2001).

Life Habit: lichenized, not lichenicolous; **Thallus:** crustose or squamulose, attached by the whole lower surface or basal end of squamule; **areoles/squamules:** dispersed or adjacent or imbricate, up to 2 mm wide, rounded, lobed or with incised margins, soralia present or absent; **upper surface:** grayish green to dark brown, dull or shiny, smooth, not pruinose; **upper cortex:** varying from 10 to 130 µm thick, containing remnants of algae (chlor-zinc-iodine!), consisting of an upper epinecral layer and a lower stainable layer, the latter composed of irregularly to anticlinally oriented hyphae and in most species containing secondary metabolites; **medulla:** white, of intricately interwoven hyphae, I-; algal layer: 40-100 µm thick, horizontally continuous; **photobiont:** primary one a chlorococcoid alga, secondary photobiont absent; algal cells: 10-15 µm in diam.; **lower cortex:** absent or poorly developed; **lower surface:** white to pale brown; **Ascomata:** apothecial, laminal, marginal, or attached to the lower side of upturned squamules, sessile, with a constricted base, persistently flattened and marginate or becoming convex and immarginate, up to 1 (-2.5) mm in diam.; disc: brown or black, sometimes with bluish white pruina, sometimes gyrose; exciple: colorless to brown in the inner part, brown or green in the rim, sometimes containing crystals of secondary metabolites; hypothecium: hyaline to dark brown, lacking crystals; epithecium: green, light brown, or brownish black; hymenium: hyaline, I+ blue, 40-70 µm high; paraphyses: simple or sparingly branched, weakly conglutinated, apical cell swollen or not, with or without pigment cap; **asci:** clavate to rhombic, thin-walled, with a poorly to well developed amyloid tholus containing either a deeper amyloid tube, a deeper amyloid flank, a small non-amyloid axial body, or no visible internal structures, 8-spored; **ascospores:** colorless, simple or 1 (-3)-septate, ellipsoid to fusiform; **Conidiomata:** pycnidial, sessile, globose to ovate, black, wall brown or dirty green; **conidia:** formed acrogenously or pleurogenously, subglobose, ellipsoid, bacilliform, or filiform; **Secondary metabolites:** depsides, depsidones, or benzyl esters in medulla, upper cortex and rarely in exciple and epithecium; **Geography:** temperate regions of the world, especially in boreal conifer forests; **Substrate:** bark and wood, mainly of conifers, many species mainly on charred substrates.

Notes: The genus may be heterogeneous. Timdal (1984b) placed the species in four species groups, based mainly on differences in ascus type, exciple, conidia, and secondary chemistry. In some species, e.g. the type species, mature asci are unknown, and the position of the genus within the Lecanorales is still unsettled.

Key to the species of ***Hypocenomyce*** in the Sonoran region:

1. Thallus crustose 2
1. Thallus squamulose 3

2. Areoles sorediate ..... ***H. sorophora***
2. Areoles not sorediate ..... ***H. praestabilis***

3. Squamules more or less ascending and imbricate, usually with labriform soralia 4
3. Squamules adnate, without soralia 7

4. Squamules C+ red and/or K+ yellow; apothecia black, flattened to weakly convex 5
4. Squamules C- and K-; apothecia brown, soon becoming moderately to strongly convex 6

5. Squamules K-, P- (lecanoric acid), with a more or less entire margin ..... ***H. scalaris***
5. Squamules K+ yellow, P+ yellow (thamnolic acid and often alectorialic acid), with a crenulate margin ..... ***H. sierrae***

6. Squamules P+ orange/red (fumarprotocetraric acid and colensoic acid complex), grayish green to medium brown, with a pale brown to white margin; soredia gray ..... ***H. anthracophila***
6. Squamules P- (colensoic acid complex only), greenish brown to dark brown, with a concolorous margin; soredia brown ..... ***H. castaneocinerea***

7. Squamules K-, P- (unidentified compound); apothecial disc often gyrose; asci becoming mature, with a small, amyloid tholus; conidia ellipsoid to shortly bacilliform, 2.5-5 µm long ..... ***H. friesii***
7. Squamules K+ yellow, P+ yellow (alectorialic and/or thamnolic acid); apothecial disc not gyrose; asci usually remaining immature and without tholus; conidia bacilliform, 7-9 µm long ..... ***H. oligospora***

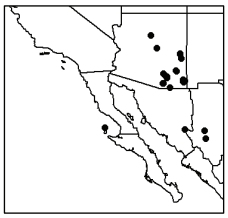
The Species

Hypocenomyce anthracophila (Nyl.) P. James & Gotth. Schneid., in G. Schneider, Biblioth. Lichenol. 13: 81 (1980).

Basionym: *Lecidea anthracophila* Nyl., Flora, Jena 48: 603 (1865); Synonyms: *Lecidea cladonioides* Th. Fr., *Biatora anthracophila* (Nyl.) Hafellner, *Psora cladonioides* var. *albocervina* Räsänen, Illustrations: Brodo et al. (2001), p. 344; Timdal (1984b), p. 94.

Thallus: squamulose; **squamules:** up to 0.8 (-1.3) mm diam., normally ascending and geotropically oriented, concave or plane when young, later weakly to strongly convex; **upper surface:** grayish green to greenish or medium brown, shiny; margin: entire, not or slightly upturned, lighter than upper side or white; **soredia:** gray, farinose to granular, in labriborm soralia; **upper cortex:** up to 100 (-130) µm thick, composed of thick-walled hyphae; **Apothecia:** up to 0.8 (-1.3) mm diam., marginal or on the underside of ascending squamules; disc: reddish to dark brown, convex, epruinose, egyrose; margin: more or less prominent when young, later excluding, entire; exciple: composed of closely conglutinated hyphae, colorless to pale brown, not containing crystals, K-, N-; hypothecium: colorless; epithecium: light brown, not containing crystals, K-, N-; paraphyses: with swelling and pigment cap in apical cell; **asci:** with a well developed tholus containing an amyloid tube; **ascospores:** narrowly ellipsoid to fusiform, simple or more rarely 1-septate, 7-13 x 1.5-2.5 µm; **Pycnidia:** sessile, black, attached marginally or to the underside of the squamule; **conidia:** filiform, 6.5-12.5 x *c.* 1 µm; **Spot tests:** upper cortex and soralia K-, C-, KC-, P+ orange/ red, medulla K-, C-, KC+ purple, P-; **Secondary metabolites:** colensoic acid and related secondary products, fumarprotocetraric acid, and protocetraric acid.

Substrate and ecology: on bark and wood of conifers, usually charred, in conifer forests at 530-3050 m alt.; **World distribution:** North America, Australia, Europe and Asia; **Sonoran distribution:** fairly common in Arizona, Baja California, Sonora and Chihuahua.



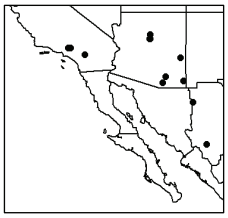
Hypocenomyce castaneocinerea (Räsänen) Timdal, Nordic J. Bot. 4: 97 (1984).

Basionym: *Psora cladonioides* var. *castaneocinerea* Räsänen, Lich. Fenn. Exsicc. No. 282 (1936); Illustration: Timdal (1984b), p. 97.

Thallus: squamulose; **squamules:** up to 0.8 (-1.3) mm diam., normally ascending and geotropically oriented, weakly convex when young, later strongly convex to bullate, with labriform brown soralia (often lacking); **upper surface:** greenish brown to castaneous or dark brown, shiny; margin: crenulate, not or slightly upturned, concolorous with upper side; **soredia:** if present, brown, farinose to granular, in labriform soralia; **upper cortex:** up to 110 µm thick, composed of thick-walled hyphae; **Apothecia:** up to 0.5 (-0.7) mm diam., marginal or on the underside of ascending squamules; disc: reddish to dark brown, convex, epruinose, egyrose; margin: not prominent even when young, entire; exciple: composed of closely conglutinated hyphae, colorless to pale brown, not containing crystals, K-, N-; hypothecium: colorless; epithecium: light brown, not containing crystals, K-, N-; paraphyses: with swelling and pigment cap in apical cell; **asci:** with a well developed tholus containing an amyloid tube; **ascospores:** narrowly ellipsoid to fusiform, simple,

7-13 x 2-2.5 µm; **Pycnidia:** sessile, black, attached marginally or to the underside of the squamule; **conidia:** filiform, 7-11 x *c.* 1 µm; **Spot tests:** upper cortex K-, C-, KC-, P-; medulla K-, C-, KC+ purple, P-; **Secondary metabolites:** colensoic acid and related secondary products.

Substrate and ecology: on charred bark and wood of conifers in conifer forests at 1480-2640 m alt.; **World distribution:** Africa, Europe, and North America; **Sonoran distribution:** Arizona, California, and Chihuahua; uncommon.



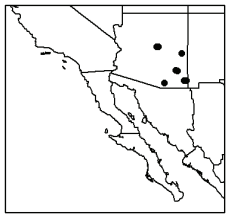
Notes: The species differs from *H. anthracophila* in forming darker, more convex or agglomerate squamules with a brown margin and brown soralia, and in lacking fumarprotocetraric and protocetraric acids (cortex P-).

Hypocenomyce friesii (Ach.) P. James & Gotth. Schneid., in G. Schneider, Biblioth. Lichenol. 13: 84 (1980).

Basionym: *Lecidea friesii* Ach., in Liljeblad, Utkast svensk Fl., Ed. 3: 610 (1816); Illustration: Timdal (1984b), p. 100.

Thallus: squamulose; **squamules:** up to 1.0 (-1.5) mm diam., adnate, concave, plane or weakly convex; **upper surface:** grayish green or greenish to dark brown, dull or shiny; margin: entire, crenulate or incised, not upturned, concolorous with upper side; soredia absent; **upper cortex:** up to 50 µm thick, composed of thin-walled hyphae; **Apothecia:** up to 1.0 (-1.4) mm diam., marginal or laminal, plane; disc: black, epruinose, often gyrose; margin: remaining prominent, more or less flexuose; exciple: composed of closely conglutinated hyphae, brown in inner part, brownish black in the rim, not containing crystals, K+ brown, N-; hypothecium: dark brown; epithecium: dark brown, not containing crystals, K+ brown, N-; paraphyses: without swelling or pigment cap in apical cell; **asci:** with a poorly developed tholus containing a small axial body; **ascospores:** broadly to narrowly ellipsoid, simple, 4.5-7.5 x 2.5-3.5 µm; **Pycnidia:** black, sessile, attached laminally or marginally to the squamule or apparently directly to the substrate; **conidia:** narrowly ellipsoid to shortly bacilliform, 2.5-5 x *c.* 1 µm; **Spot tests:** upper cortex and medulla K-, C-, KC-, P-; **Secondary metabolite:** an unidentified secondary product.

Substrate and ecology: on bark and wood of conifers, usually charred, in conifer forests at 1890-2960 m alt.; **World distribution:** Asia, Europe, and North America; **Sonoran distribution:** Arizona, uncommon.



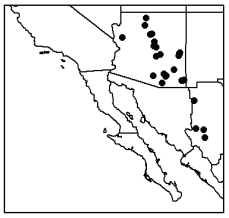
Notes: The species has been much confused with *H. oligospora* in North America, see that species for discussion. The unidentified compound belongs in R_F-classes 2-3:3-4:2-3, is UV+ white, and turns orange with H_2SO_4 and heat.

Hypocenomyce oligospora Timdal, Mycotaxon 77: 446 (2001).

Illustration: Timdal (2001), p. 446.

Thallus: squamulose; **squamules:** up to 1.0 mm diam., adnate or irregularly ascending, concave, plane or weakly convex; **upper surface:** grayish green or greenish to dark brown, dull or shiny; margin: entire, crenulate or incised, not upturned, concolorous with upper side; soredia absent; **upper cortex:** up to 30 µm thick, composed of thin-walled hyphae; **Apothecia:** up to 1.0 mm diam., marginal or laminal, plane; disc: black, epruinose, egyrose; margin: remaining prominent, entire or flexuose; exciple: composed of closely conglutinated hyphae, olivaceous in inner part, brownish black in the rim, not containing crystals, K+ brown, N- or N+ violet; hypothecium: dark brown; epithecium: dark brown, not containing crystals, K+ brown, N-; paraphyses: without swelling or pigment cap in apical cell; **asci:** with a poorly developed tholus not containing visible structures, or remaining immature; **ascospores:** rare, broadly to narrowly ellipsoid, simple, 6-8 x 3-4 µm; **Pycnidia:** sessile, black, attached marginally to the squamule; **conidia:** bacilliform, 7-9 x *c.* 1 µm; **Spot tests:** upper cortex K+ yellow, C+ red (rarely C-), KC+ red (rarely KC-), P+ yellow; **Secondary metabolites:**

alectorialic acid and usually thamnolic acid, rarely thamnolic acid only.



Substrate and ecology: on bark and wood of conifers, usually charred, in conifer forests at 1720-2950 m alt.; **World distribution:** Asia and North America; **Sonoran distribution:** Arizona and Chihuahua, fairly common.

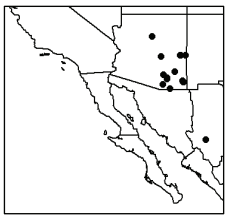
Notes: The species is morphologically very similar to *H. friesii*. It differs in forming mainly immature asci, having longer conidia, and in the chemistry. In *H. friesii* the apothecial disc is often gyrose, but never in *H.oligospora*.

Hypocenomyce praestabilis (Nyl.) Timdal, Nordic J. Bot. 4: 101 (1984).

Basionym: *Lecidea praestabilis* Nyl., Flora, Jena 57: 13 (1874); Illustrations: Timdal (1984b), pp. 101 & 102.

Thallus: crustose; **areoles:** up to 1.0 (-1.5) mm diam., adnate, weakly convex; **upper surface:** light gray or yellowish brown, dull; soredia: absent; **upper cortex:** up to 15 µm thick, composed of thin-walled hyphae; **Apothecia:** up to 0.8 (-1.1) mm diam., marginal or laminal, plane; disc: black, epruinose, egyrose; margin: remaining prominent, entire or flexuose; exciple: composed of closely conglutinated hyphae, brown in inner part, brownish black in the rim, not containing crystals, K+ violet, N-; hypothecium: dark brown; epithecium: dark brown, not containing crystals, K+ violet, N-; paraphyses: without swelling and pigment cap in apical cell; **asci:** with a well developed tholus containing an amyloid flank; **ascospores:** common, broadly to narrowly ellipsoid, simple, 7-11.5 x 3-4.5 µm; **Pycnidia:** sessile, black, attached to the areole or apparently directly to the substrate; **conidia:** ellipsoid, 3-5.5 x 1.5-2.5 µm; **Spot tests:** upper cortex and medulla K+ yellow, C+ red, KC+ red, P+ yellow; **Secondary metabolite:** alectorialic acid.

Substrate and ecology: on wood, more rarely bark, of conifers, in conifer forests at 1970-3400 m alt., not on charred substrates; **World distribution:** Europe and North America; **Sonoran distribution:** Arizona and Chihuahua, uncommon.



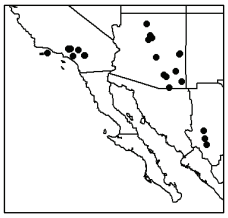
Notes: The closely related boreal species *H. xanthococca* (Sommerf.) P. James & Gotth. Schneid. has subglobose conidia, 2.5-4 x 1.5-3 µm (see Timdal 1984b: 102, fig. 19). There are no reliable reports of *H. xanthococca* from North America.

Hypocenomyce scalaris (Ach.) M. Choisy, Bull. mens. Soc. Linn. Lyon 20: 133 (1951).

Basionym: *Lichen scalaris* Ach., K. Vetensk.Acad. nya Handl. 16: 127, Tab. 5, Fig. 1a-f (1795); Synonym: *Lecidea ostreata* (Hoffm.) Schaer.; Illustrations: Timdal (1984), p. 104; Brodo et al. (2001), p. 345.

Thallus: squamulose; **squamules:** up to 1.2 (-2.0) mm diam., normally ascending and geotropically oriented, weakly convex or strongly convex; **upper surface:** grayish green or yellowish to dark brown, dull; margin: entire or slightly crenulate, not or slightly upturned, concolorous with upper side; **soredia:** greenish brown, farinose to granular, in labriform soralia; **upper cortex:** up to 40 µm thick, composed of thin-walled hyphae; **Apothecia:** up to 1.5 (-2.5) mm diam., marginal, plane; disc: black, bluish white pruinose, egyrose; margin: remaining prominent, entire or flexuose; exciple: composed of loosely conglutinated hyphae, containing crystals (C+ red), colorless in inner part, green in the rim, K-, N+ violet; hypothecium: light brown or dark brown; epithecium: olivaceous green, containing crystals (C+ red), K-, N+ violet; paraphyses: without swelling or pigment cap in apical cell; **asci:** remaining immature; **ascospores:** unknown; **Pycnidia:** sessile, black, attached marginally or laminally to the upper or lower surface or apparently directly to the substrate; **conidia:** bacilliform, 5-7.5 x *c.* 1 µm; **Spot tests:** upper cortex and medulla K-, C+ red, KC+ red, P-; **Secondary metabolite:** lecanoric acid.

Substrate and ecology: on bark and wood, often charred, mainly on conifers in conifers forests, at 290-3000 m alt.; **World distribution:** Africa, Asia, Australia, Europe, and North America; **Sonoran distribution:** Arizona, California, and Chihuahua, fairly common.

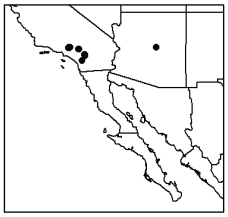


Hypocenomyce sierrae Timdal, Mycotaxon 77: 449 (2001).

Illustration: Timdal (2001), p. 447.

Thallus: squamulose; **squamules:** up to 0.7 mm diam., normally ascending and geotropically oriented, weakly to strongly convex; **upper surface:** grayish green or greenish brown, dull; margin: crenulate, not upturned, concolorous with upper side; **soredia:** green, farinose to granular, in labriform soralia; **upper cortex:** up to 25 µm thick, composed of thin-walled hyphae; **Apothecia:** up to 0.5 mm diam., marginal, plane; disc: black, epruinose, egyrose; margin: remaining prominent, entire or flexuose; exciple: composed of closely conglutinated hyphae, olivaceous in inner part, brownish black in the rim, not containing crystals, K+ brown, N- or N+ violet; hypothecium: dark brown; epithecium: dark brown, not containing crystals, K+ brown, N-; paraphyses: without swelling and pigment cap in apical cell; **asci:** with a poorly developed tholus not containing visible structures, or remaining immature; **ascospores:** broadly to narrowly ellipsoid, simple, 8-11.5 x 3-4.5 µm; **Pycnidia:** sessile, black, attached marginally to the squamule; **conidia:** bacilliform, 7-10 x *c.* 1 µm; **Spot tests:** upper cortex K+ yellow, C+ red or C-, KC+ red or KC-, P+ yellow; **Secondary metabolites:** thamnolic acid and often alectorialic acid.

Substrate and ecology: on bark and wood of conifers (especially bark of *Libocedrus* and *Sequoiadendron*), often charred, in conifer forests at 1380-2160 m alt; **World and Sonoran distribution:** North America, locally common in southern California and rare in Arizona.

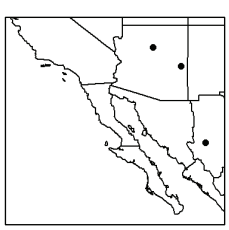


Notes: The species resembles *H. scalaris* morphologically, and the two species often grow in mosaics. *Hypocenomyce sierrae* differs in forming smaller, more green, and more crenulate squamules, in the secondary chemistry (thallus K+ yellow, P+ yellow), and in forming smaller, epruinose apothecia which often contain mature asci and spores. It is apparently more closely related to *H. oligospora*, but differs from that species in forming ascending, sorediate squamules.

Hypocenomyce sorophora (Vain.) P. James & Poelt, in Poelt & Vězda, Biblioth. Lichenol. 16: 364 (1981).

Basionym: *Lecidea xanthococca* ssp. *sorophora* Vain., Acta Soc. Fauna Fl. Fenn. 57, 2: 237 (1934); Illustration: Timdal (1984b), p. 106.

Thallus: crustose; **areoles:** up to 0.5 (-1.0) mm diam., adnate, weakly convex; **upper surface:** light gray or yellowish brown, dull; **soredia:** yellowish brown, diffuse; **upper cortex:** up to 15 µm thick, composed of thin-walled hyphae; **Apothecia:** up to 0.6 (-0.8) mm diam., marginal or laminal, plane; disc: black, epruinose, egyrose; margin: remaining prominent, entire or flexuose; exciple: composed of closely conglutinated hyphae, brown in inner part, brownish black in the rim, not containing crystals, K+ violet, N-; hypothecium: dark brown; epithecium: dark brown, not containing crystals, K+ violet, N-; paraphyses: without swelling or pigment cap in apical cell; **asci:** with a well developed tholus containing an amyloid flank; **ascospores:** broadly to narrowly ellipsoid, simple, 6-9 x 2.5-4.5 µm; **Pycnidia:** sessile, black, attached to the areole or apparently directly to the substrate; **conidia:** ellipsoid to shortly bacilliform, 3.5-5 x 1.5-2.5 µm; **Spot tests:** upper cortex and medulla K+ yellow, C+ red, KC+ red, P+ yellow; **Secondary metabolite:** alectorialic acid.



Substrate and ecology: on wood (elsewhere also bark) of conifers, not charred, in conifer forests at

2750-3400 m alt.; **World distribution:** Europe and North America; **Sonoran distribution:** Arizona and Chihuahua, rare.

Notes: The species may be regarded as the sorediate counterpart of *H. praestabilis*.

HYPOGYMNIA

by B. McCune

Hypogymnia (Nyl.) Nyl., Lichen. Env. Paris 39 (1896).

Family: Parmeliaceae; Type: *Hypogymnia physodes* (L.) Nyl.; No. species: *c.* 80 species world-wide; Selected lit.: Goward (1988), Goward and McCune (1993), McCune and Goward (1995), and Pike and Hale (1982).

Life habit: lichenized; **Thallus:** foliose, small to medium sized, to over 30 cm or more wide, lobate; **lobes:** hollow or rarely solid, short and irregular to linear and elongate, contiguous or free, erect, appressed, imbricate, or pendulous, tips pointed to rounded, perforate in some species; cilia lacking; **upper surface:** whitish, pale gray, greenish gray, black-mottled in some species, often browning or blackening in exposed sites, smooth to rugose or verrucose; pseudocyphellae lacking; soredia, schizidia, isidia (non-Sonoran species only), and lobules present or absent; **upper cortex:** ± columnar paraplectenchymatous; **medulla:** white or dark or with a white ceiling and dark floor, loosely packed or matted around the lobe cavity; **photobiont**: primary one a *Trebouxia*, secondary photobiont absent; **lower cortex:** paraplectenchymatous; **lower surface:** black, usually brown toward the lobe tips, sometimes brown throughout, moderately to extremely wrinkled, attachment by scattered or basal holdfasts; rhizines lacking; cyphellae; pseudocyphellae, and tomentum absent but some species with roundish perforations into the lobe cavity, **Ascomata:** absent or present, apothecial, imperforate, laminal on thallus, orbicular, cup-shaped, sessile to substipitate or stipitate, the stipe swollen or collapsed and funnel-form, margin prominent as a thin, thalloid, eciliate rim; exciple: gray or hyaline; hypothecium: hyaline; epithecium: brown; **asci:** *Lecanora*-type, apex amyloid, with wide, axial body divergent towards apex, 8-spored; **ascospores:** simple, subspherical to ellipsoid, 3.5-10 µm x 3-6 µm, wall thin, hyaline, smooth; **Conidiomata:** pycnidial, laminal, immersed to slightly protruding, black, punctiform; **conidia:** rod-shaped to weakly bifusiform, 4.5-8 x 0.5-1 µm; **Secondary metabolites:** upper cortex with atranorin and chloroatranorin (or usnic acid in some Asian species); medulla with a combination of orcinol or ß-orcinol depsidones and ß-orcinol depsides; **Geography:** temperate, montane, and subalpine forests and woodlands to shrub steppe and arctic-alpine tundra; **Substrate:** mostly bark and wood, less often on acidic rock, mossy rock, or alpine sod.

By TLC unknown C7 has the following characteristics: fluoresces reddish or orange in long-wave UV light, is colorless before and after charring, has Rf classes A:4-5 and C:5-6, usually separating into two adjacent spots in C. Unknown C8 is UV-, colorless before charring, light brown after charring, and falls in Rf classes A1-2, B2, and C2. It is most easily seen in solvent C, often being hidden by other spots in solvent A.

Notes: Many species of *Hypogymnia* occur just north of the area covered by this flora, most commonly *H. apinnata, H. enteromorpha, H. inactiva,* and *H. rugosa*. These and other species of the cool temperate to montane west are covered by McCune and Geiser (1997). South of the study area, high mountain areas in Mexico support *H. bitteri*, a species distributed sporadically along the Cordillera. In their typical forms, all of the *Hypogymnia* species in western North America are morphologically distinct. Chemical tests (especially the P test) are, however, extremely useful in identifying small, depauperate, or otherwise morphologically ambiguous specimens. Pigmentation of the lobe cavity is a very useful character, but it must be checked well back (1 cm or more) from the lobe tips. The interior of the lobe tips is often white, even in species that develop dark cavities.

Key to the species of ***Hypogymnia*** from the Sonoran region:

1. Thallus with soredia or with upper surface flaking off (schizidia) 2
1. Thallus lacking soredia 8

2. Schizidia present; soredia absent or present on the edges of schizidia ..... ***H. schizidiata***
2. Schizidia absent; soredia present, laminal, powdery 3

3. Soredia laminal 4
3. Soredia at least partly terminal 6

4. Soredia developing from rugosities of the upper surface that then crack and develop soredia along the edges of the cracks ..... ***H. farinacea***
4. Soredia developing from gradual dissolution of the cortex or bud-like eruptions from the cortex 5

5. Soredia powdery; thallus white to pale greenish gray; coastal ..... ***H. mollis***
5. Soredia coarsely granular though sometimes disintegrating into powdery masses; thallus pale greenish gray to dark brown; Rocky Mountains ..... ***H. austerodes***

6. Soredia formed within the bursting lobe tips; medulla P+ orange ..... ***H. physodes***
6. Soredia external on the lobes; medulla P- 7

7. Lobes separating, partly free from the substrate; soredia terminal on the main lobes; thallus white to pale greenish gray, the lobe tips sometimes brownish before soredia appear ..... ***H. tubulosa***
7. Lobes contiguous, appressed throughout; soredia terminal on either the main lobes or side lobes or both, but lobes often bearing laminal soredia; thallus pale greenish gray to dark brown ..... ***H. bitteri***

8. Lobe interiors completely white or developing a brownish layer of hyphae over a white background. 9
8. Lobe interiors darkening to gray, brownish, dark brown, or black (the interior of the lobe tips may be white) 11

9. Lobe tips and axils rarely perforate; lobe interiors completely snow white, hollow, semi-solid, or solid; widespread ..... ***H. imshaugii***
9. Lobe tips and axils commonly perforate; lobe interiors whitish, developing a brownish layer of hyphae over a white background, always hollow 10

10. Medulla P+ orange-red; thallus never developing soredia or schizidia ..... ***H. gracilis***
10. Medulla P-; thallus usually developing soredia and schizidia ..... ***H. schizidiata***

11. Medulla P+ orange (physodalic and protocetraric acids present); narrow adventitious lobes usually present. 12
11. Medulla P-; narrow adventitious lobes present or not 13

12. Lobe interiors dark brown; lobes commonly > 1.5 mm wide; thallus commonly > 5 cm diameter ..... ***H. heterophylla***
12. Lobe interiors whitish to light brownish or dusky; lobes seldom > 1.5 mm wide.. ; thallus rarely > 5 cm diameter ..... ***H. gracilis***

13. Lobes appressed and contiguous to somewhat separate and slightly trailing; adventitious lobes mostly bulbous (appearing puffy); 3-hydroxyphysodic acid lacking .... ***H. occidentalis***
13. Lobes suberect or trailing and separate at least in part; adventitious lobes, if present, narrow or bulbous; 3-hydroxyphysodic acid present or not 14

14. Adventitious lobes present, usually abundant; 3-hydroxyphysodic acid present; UV+ unknown C7 present. Guadalupe Island ..... ***H. guadalupensis***
14. Adventitious lobes rare; 3-hydroxyphysodic acid absent; UV+ unknown C7 absent; coastal states north of Santa Cruz ..... [***H. inactiva***]

The Species

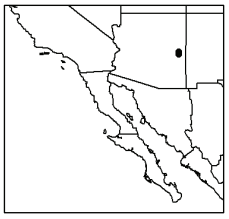
Hypogymnia austerodes (Nyl.) Räsänen, Ann. Bot. Soc. Zool.-Bot. Fenn. Vanamo 18 (1): 13. (1943).

Basionym: *Parmelia austerodes* Nyl. Flora 64 (33): 537 (1881); Illustrations: McCune and Geiser (1997), p. 121; McCune and Goward (1995), p. 106; St. Clair (1999), p. 86; Brodo et al. (2001), p. 347.

Thallus: appressed, up to 5 (-8) cm broad; texture: cartilaginous; branching: variable, budding present; **lobes:** contiguous, 0.5-2 (-2.5) mm wide, sometimes black bor-

dered; profile: pinched and swollen; width/height ratio: 1-15; tips and axils: rarely perforate; **upper surface:** greenish gray to brown, dark mottles often present, smooth; **soredia:** almost always present, mainly laminal, developing from subisidiate granules with a deteriorating cortex, sometimes diffuse and powdery on older parts of the thallus; isidia: lacking; lobules: often present; **medulla:** hollow; ceiling of cavity: white; floor of cavity: dark to grayish; **lower surface:** black, entire; **Apothecia** not seen in local material; **Pycnidia:** rare; **conidia:** not seen; **Spot tests:** cortex K+ yellow, C-, KC-, P+ pale yellow, UV-; medulla K-, C-, KC+ orange-red, P-; **Secondary metabolites:** upper cortex with atranorin and chloroatranorin; medulla with physodic acid (major), 3-hydroxyphysodic acid (accessory, frequency about 75%), 2'-*O*-methylphysodic acid, unknown (C8) with physodic acid (all accessory).

Substrate and ecology: typically on bark or wood, especially conifers in montane and subalpine forests, also on mosses or detritus over rock or alpine sod; **World distribution:** circumpolar arctic, boreal, and montane in continental climates in Europe, Asia, and North America; **Sonoran distribution:** southern Rocky Mountains.

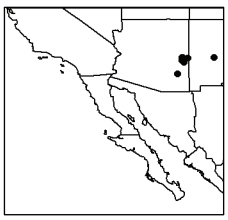


Notes: In most places in the northern hemisphere *H. austerodes* and *H. bitteri* are easily distinguished. The central and southern Rocky Mountains, however, host intermediate populations. The best diagnostic character for *H. bitteri* is the presence of short, narrow, upturned lateral lobes tipped with small soralia. These occur with or without larger terminal soralia or laminal soralia. In contrast, *H. austerodes* typically has only laminal soralia. Occasionally, however, *H. austerodes* has terminal soralia, but usually these are restricted to the larger lobe tips and they are accompanied by extensive laminal soredia. Specimens from the Rockies may contain thalli at several points along the gradation. Although introgression among predominantly asexual species of lichenized fungi has not been demonstrated, this case suggests just that. Confusion between *H. austerodes* and *H. farinacea* is also possible, because both have laminal soredia on a rosette-like thallus. *Hypogymnia farinacea* does not become melanized in exposed environments, unlike the rich brownish thalli of *H. austerodes* and *H. bitteri* when they grow in the sun. Shade forms must be distinguished by the form and development of soredia. In *H. farinacea* the soredia arise from rugosities of the upper surface, which then crack and form soredia along the edges of the cracks. Although this form of soredia can be found rarely in *H. austerodes*, it is accompanied by the typical compound granules budding from the lobe surface.

Hypogymnia bitteri (Lynge) Ahti, Ann. Bot. Fenn. 1: 20 (1964).

Basionym: *Parmelia bitteri* Lynge Stud. Lich. Flora Norway 138 (1921); Illustrations: McCune and Goward (1995), p. 107; Goward et al. (1994), p. 59; Swinscow and Krog (1988), p. 106; Brodo et al. (2001), p. 348.

Thallus: appressed, up to 9 (-12) cm broad; texture: cartilaginous; branching: variable; budding: present; **lobes:** contiguous, 0.5-4 mm broad, sometimes black bordered; profile: pinched and swollen; width/height ratio: 1-15; tips and axils: often minutely perforate; **soredia:** predominantly terminal, both on the main lobes and short, upturned, lateral lobes, sometimes with secondarily diffuse laminal soredia; isidia absent, lobules sparse or none; **upper surface:** greenish gray to brown, dark mottled, becoming rugose; isidia: absent; lobules: sparse or none; **medulla** hollow; ceiling of cavity: white or dark; floor of cavity: dark; **lower surface:** black, entire; **Apothecia:** not seen in local material; **Pycnidia:** rare**; conidia:** not seen; **Spot tests:** cortex K+ yellow, C-, KC-, P+ pale yellow, UV-; medulla K-, C-, KC+ orange-red, P-; **Secondary metabolites:** upper cortex with atranorin and chloroatranorin; medulla with physodic acid (major), 3-hydroxyphysodic acid (accessory, frequency about 20%), 2'-*O*-methylphysodic acid (minor accessory), unknown C8 (minor accessory).



Substrate and ecology: typically on bark or wood, especially conifers in montane and subalpine forests, also on mosses or detritus

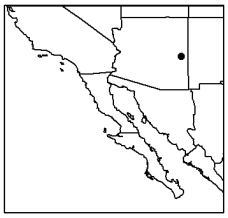
over rock or alpine sod; **World distribution:** circumpolar arctic, boreal, and montane in continental climates in Europe, Asia, and North America, south through Mexico along the cordillera well into South America; high mountains in Africa; **Sonoran distribution:** southern Rocky Mountains.

Notes: See discussion under *H. austerodes*.

Hypogymnia farinacea Zopf, Flechtenstoffe 419 (1907).

Synonym: *Hypogymnia bitteriana* (Zahlbr.) Räsänen; Illustrations: Wirth (1995), p. 429; McCune and Goward (1995), p. 106.

Thallus: appressed, up to 7 (-10) cm broad; texture: cartilaginous; branching: variable; budding: present; **lobes:** contiguous to ± separate, 0.5-3 (-4) mm broad; black border: not visible; profile: even to nodulose; width/ height ratio: 0.7-3, tips and axils: entire; **upper surface:** white to greenish gray, dark mottled or not, becoming rugose; **soredia:** laminal, arising from rugosity on the upper surface which then cracks and develop soredia along the edges of the cracks; isidia and lobules lacking; **medulla:** hollow, ceiling of cavity white, floor of cavity grayish or brownish; **lower surface:** black, entire; **Apothecia:** rare, substipitate to stipitate, up to 5 (-10) mm in diam; stipe funnel shaped, hollow; disc: brown to reddish brown; **ascospores:** subglobose, 5-6 x 4-5 µm; **Pycnidia:** rare; **conidia:** rod-shaped to weakly bifusiform, 2-2.5 x 0.6-0.9 µm; **Spot tests:** cortex K+ yellow, C-, KC-, P+ pale yellow, UV-; medulla K-, C-, KC+ orange-red, P-; **Secondary metabolites:** upper cortex with atranorin and chloroatranorin; medulla with physodic acid (major), 3-hydroxyphysodic acid (accessory, frequency about 80%), 2'-*O*-methylphysodic acid (minor accessory), unknown C8 (minor accessory).



Substrate and ecology: on bark or wood, especially conifers in montane forests; **World distribution:** boreal and montane forests in continental climates of Europe, more rarely in North America; **Sonoran distribution:** southern Rocky Mountains.

Notes: *Hypogymnia farinacea* is distinguished by close-set, imperforate, appressed lobes, pale color, and soredia arising at the edges of cracks in rugosities of the upper cortex. This kind of soredia is occasionally seen in *H. bitteri, H. austerodes*, and *H. mollis*, but in those cases it is never the predominant form of the soredia. *Hypogymnia farinacea* and *H. mollis* do not melanize in exposed environments, while *H. bitteri* and *H. austerodes* become light to dark brown in the sun. See further discussion under *H. austerodes*.

Hypogymnia gracilis McCune, **sp. nov.**

Diagnosis: *Thallus suberectus, corticolus, ad 6 cm latus; lobi linearibi, liber, cinereo-albicans vel subviridi-grisea, 0.5-2.0 (-3.0) mm lata; medulla alba vel albida; soredia isidia desunt; subtus niger, foraminibus subapicalibus et axillaribus; apothecia numerosa; sporae 5.5-8.5 x 4.5-5.0 µm. Cortex K+ flavescens; medulla K-, C-, KC+ rosea, P+ rubra.*

Type: U.S.A.: California, San Luis Obispo County, Los Osos State Reserve, Los Osos Valley Road, 30 m, on *Adenostoma*, Bratt 3879, January 1984 (OSC; isotype US).

Illustration: Fig. 51 on next page.

Thallus: suberect, up to 3 (-5) cm broad; lobe tips: often upturned; texture: cartilaginous; branching: variable; budding and adventitious lobes: usually present; **lobes:** separate, occasionally centrally contiguous, (0.5-) 1.0-1.5 (2.5) mm wide; black border: sometimes visible from above; profile: ± even; width/height ratio: (0.6-) 1-2 (-4); tips and axils: perforate below (perforations always present but not all lobe tips and axils are perforate); **upper surface:** white to greenish gray, usually dark mottled, smooth to rugose; soredia and isidia: lacking; lobules: sparse or lacking; **medulla:** hollow but sometimes partially collapsed, ceiling of cavity white or dusky, floor white or dirty white; **lower surface:** black, sparsely perforate; **Apothecia:** common, substipitate to stipitate, up to 4 (-7) mm in diam; stipe: urn- or funnel-shaped, hollow,

disc: brown to dark brown; **ascospores:** subglobose, 7.0-7.5 x 4.5-5.0 µm; **Pycnidia:** common; **conidia:** weakly bifusiform, 5.5-8.5 x 0.6-0.7 µm; **Spot tests:** cortex K+ yellow, C-, KC-, P+ pale yellow, UV-; medulla K-, C-, KC+ orange-red, P+ orange-red; **Secondary metabolites:** upper cortex with atranorin and chloroatranorin; medulla with physodic acid (major), physodalic acid (major), protocetraric acid (minor), and unknown C7 (UV+, minor but constant), rarely with 3-hydroxyphysodic acid.

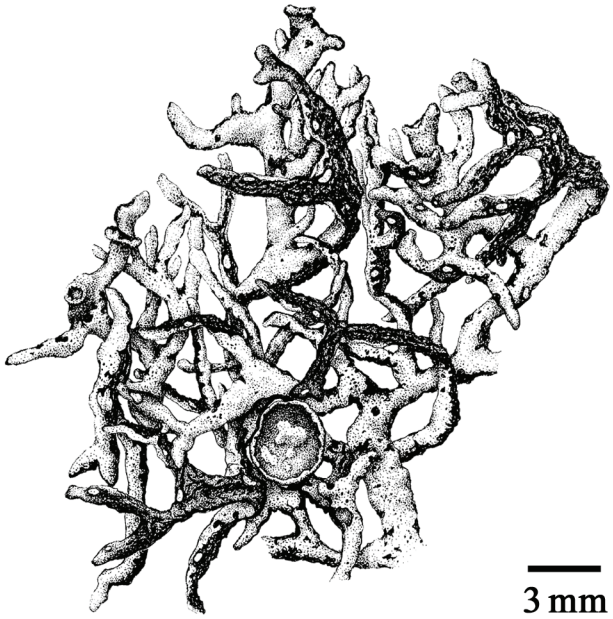
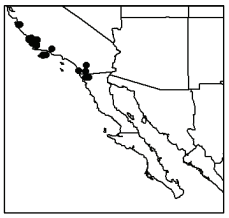


Fig. 51. Type of *Hypogymnia gracilis*, drawing by A. Mikulin.

Substrate and ecology: on bark of shrubs, conifers, and hardwoods, mainly near the coast in chaparral and open woodlands; **World** and **Sonoran distribution:** endemic to southern California, adjoining Mexico, and offshore islands, common in coastal chaparral in Santa Barbara and San Luis Obispo Counties. Mainland populations are mostly within 10 km of the coast, with scattered records farther inland.



Notes: This species is easily recognized by its whitish cavity, slender suberect separate lobes, and small holes below the tips and axils. Most collections were previously identified as *H. imshaugii*. However, typical *H. imshaugii* is imperforate and has a snow white medullary cavity. In contrast, *H. gracilis* typically has 20% or more of the lobe axils and tips perforate below and the lobe cavity varies from white to light brownish or light grayish. The cavity of *H. imshaugii* darkens only when the thallus is damaged; likewise, the rare perforations seen in the lower surface and lobe tips of *H. imshaugii* appear to result from herbivory. However, one of the forms of *H. imshaugii*, almost certain to be separated as a distinct taxon in the future, has occasional perforations, but it has collapsed or semisolid, rugose, non-mottled lobes. Despite the resemblance of *H. gracilis* to *H. imshaugii*, it is more closely related to *H. heterophylla*. They share the frequent presence of adventitious lobes and the presence of unknown C7 (actually a pair of UV+ spots with TLC, constant in both *H. heterophylla* and *H. gracilis*). *Hypogymnia heterophylla*, however, always has a dark brown to blackish medullary cavity. Furthermore, it is often much larger than *H. gracilis* and has slightly narrower spores. *Hypogymnia gracilis* can be distinguished from *H. guadalupensis* by the former's smaller size, P+ medulla, broader spores, and more erect thallus.

Hypogymnia guadalupensis McCune, **sp. nov.**

Diagnosis: *Thallus laxe adnatus, corticolus, ad 6 cm latus; lobis linearibus, libris, cinereus-albus vel subviridibus-griseus, 0.5-2.0 (-3.0) mm latis; medulla fuscata; soredia isidia desunt; subtus niger, foraminibus subapicalibus et axillaribus; apothecia numerosa; sporae 5.5-7.5 x 3-3.5 µm. Cortex K+ flavescens; medulla K-, C-, KC+ rosea, P-.*

Type: MEXICO: Baja California, Guadalupe Island, pine forest, Howell 11, November 1931 (CAS).

Other specimen examined: MEXICO: Baja California, Guadalupe Island, pine forest, Howell 14 and 15, November 1931 (CAS).

Illustration: Fig. 52 on next page.

Thallus: appressed to suberect or trailing, up to 4 (-6) cm broad or long; texture: cartilaginous; branching: variable; budding and adventitious lobes: present; **lobes:** separate to imbricate, 0.5-2 (-3) mm broad, sometimes black bordered; profile: even to ± nodulose; width/height ratio: 1-2; tips and axils: sparsely perforate;

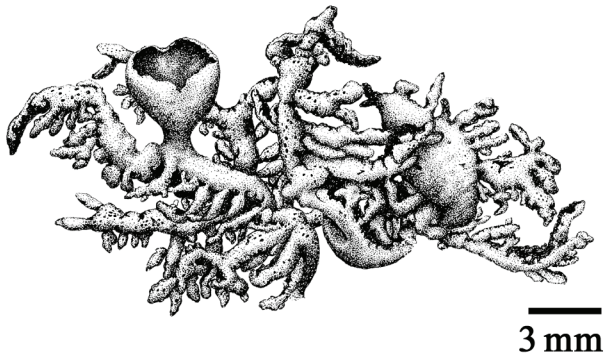


Fig. 52. Type of *Hypogymnia guadalupensis*, drawing by A. Mikulin.

upper surface: white to greenish gray, sometimes dark mottled, smooth to weakly rugose; soredia and isidia: absent; lobules: often present; **medulla:** hollow, ceiling of cavity dark, floor of cavity dark; **lower surface:** black, sparsely perforate; **Apothecia:** common, substipitate to stipitate, up to 7 (-9) mm in diam; stipe: urn- or funnel-shaped, hollow; disc: reddish brown to dark brown; **ascospores:** ellipsoid to broadly ellipsoid, 5-7.5 x 3-3.5 µm; **Pycnidia:** common**; conidia:** rod-shaped to weakly bifusiform, 5.5-8 x 0.5-0.7 µm; **Spot tests:** cortex K+ yellow, C-, KC-, P+ pale yellow, UV-; medulla K-, C-, KC+ orange-red, P-; **Secondary metabolites:** upper cortex with atranorin and chloroatranorin; medulla with physodic acid (major), 3-hydroxyphysodic acid, and unknown C7 (UV+, minor).

Substrate and ecology: on bark of conifers; **World** and **Sonoran distributions:** endemic to Guadalupe Island, Mexico.

Notes: Closely related to *H. heterophylla*, *H. guadalupensis* is distinguished by its P- medulla (physodalic acid absent) and the presence of 3-hydroxyphysodic acid. The habit is also somewhat different with *H. heterophylla* usually having semi-erect to erect lobes, while the specimens of *H. guadalupensis* known so far have a more drooping, lax habit. *H. guadalupensis* is also similar to *H. inactiva*, but *H. inactiva* usually lacks the adventitious branching, 3-hydroxyphysodic acid, and unknown C7 of *H. guadalupensis*. The only known collections of *H. guadalupensis* were made by Howell in 1931 on Guadalupe Island. The exact location is unknown. More recent collections of *Hypogymnia* from the island are mainly *H. imshaugii*, with a bit of *H. schizidiata*. Island endemics are also known in the genus from the Canary Islands and Madeira [*H. tavaresii* D. Hawksw. & P. James and *H. madeirensis* (Tav.) D. Hawksw.].

Because there are so few specimens, perhaps collected at a single site, could this be considered an aberrant population of *H. heterophylla* or another species? A large population can be inferred from the number of individuals that Howell collected. Few others have collected lichens on Guadalupe Island. Despite the shortage of data and small known range, *H. guadalupensis* is distinct from all the other material on the offshore islands, it is easy to identify, and it does not appear to intergrade with other species. Howell's collections could not be accommodated within existing species without significantly expanding our concept of *H. inactiva* or *H. heterophylla*.

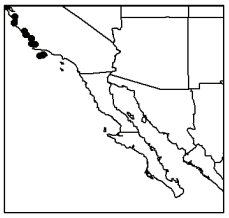
Hypogymnia heterophylla L. H. Pike, Mycotaxon 16: 157 (1982).

Illustrations: McCune and Geiser (1997), p. 124; Pike and Hale (1982), p. 160; Goward et al. (1994), p. 59; Brodo et al. (2001), p. 350.

Thallus: erect or appressed, up to 9 (-15) cm broad; texture: cartilaginous; branching: variable, budding present; **lobes:** separate to centrally contiguous, 1-3 (-4) mm wide, often black bordered; profile: even to ± nodulose; width/height ratio: 0.3-3; tips and axils: often perforate; holes usually developing slowly so that large holes are mainly axillary and the lobe tips have only pinholes; **upper surface:** white to greenish gray, often dark mottled, smooth to rugose; soredia and isidia: lacking; lobules: sparse or lacking; **medulla:** hollow, ceiling of cavity dark, floor of cavity dark; **lower surface:** black, sparsely perforate; **Apothecia:** common, substipitate to stipitate, up to 10 (-15) mm in diam; stipe: urn- or funnel-shaped, hollow;

disc: brown; **ascospores:** ellipsoid, 6-7 x 3.5-4 µm; **Pycnidia:** common**, conidia:** weakly bifusiform, 5-6 x 0.5-0.8 µm; **Spot tests:** cortex K+ yellow, C-, KC-, P+ pale yellow, UV-; medulla K-, C-, KC+ orange-red, P+ orange-red; **Secondary metabolites:** upper cortex with atranorin and chloroatranorin; medulla with physodic acid (major), physodalic acid (major), protocetraric acid (minor), unknown C7 (UV+, minor but constant), occasionally with unknown C10 (minor), rarely with 3-hydroxyphysodic acid.

Substrate and ecology: on bark of conifers, less often on hardwoods; **World distribution:** Pacific coast of North America, southern British Columbia to central California, always near the coast; **Sonoran distribution:** rare disjuncts near the coast, south to Santa Barbara County and Santa Cruz Island.



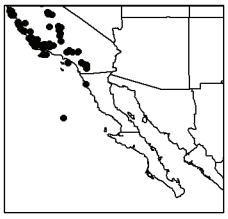
Notes: This species is rare in southern California but becomes common north of San Francisco along the coast. These southern populations usually have relatively small, compact thalli. Some forms with puffy lobes can be confused with *H. enteromorpha*, but the latter has broadly elliptical spores 4.5-6 µm wide versus elliptical spores 3.5-4 µm wide in *H. heterophylla*. They can also be distinguished by TLC, *H. heterophylla* never having diffractaic acid and always with the UV+ reddish unknowns (C7), while *H. enteromorpha* often contains diffractaic acid and never unknown C7.

Hypogymnia imshaugii Krog, Norsk Polarinst. Skrifter 144: 96 (1968).

Illustrations: McCune and Geiser (1997), p. 125; McCune and Goward (1995), p. 107; Goward et al. (1994), p. 60; Hale and Cole (1988), plate 4; Brodo et al. (2001), p. 351.

Thallus: erect to suberect, up to 8 (-13) cm broad or long; texture: cartilaginous; branching: isotomic dichotomous to irregular; budding: absent or rare; **lobes:** separate to centrally contiguous, 0.3-2 (-4) mm broad, sometimes black bordered; profile: even; width/height ratio: 1-3; tips and axils: rarely perforate; **upper surface:** white to greenish gray or brown, sometimes dark mottled, smooth to rugose; soredia and isidia: absent; lobules: sparse or lacking; **medulla:** hollow, semi-solid, or solid; ceiling of cavity white, floor of cavity white; **lower surface:** black, rarely perforate; **Apothecia:** common, substipitate to stipitate, up to 10 (-20) mm in diam; stipe: mainly funnel-shaped, hollow; disc: light brown to dark red brown; **ascospores:** broadly ellipsoid, 6.3-8 x 3.8-5.2 µm; **Pycnidia:** common; **conidia:** rod-shaped, 7-7.5 x 0.5-0.6 µm; **Spot tests:** cortex K+ yellow, C-, KC-, P+ pale yellow, UV-; medulla K-, C-, KC+ orange-red, P- or P+ orange-red, occasionally P+ yellow; **Secondary metabolites:** upper cortex with atranorin and chloroatranorin; medullary chemistry highly variable, containing virtually all combinations of diffractaic acid (minor, accessory), physodic acid (major), physodalic acid (major), protocetraric acid (minor), 3-hydroxyphysodic acid (minor, frequency about 20%), 2'-*O*-methylphysodic (minor accessory), and various accessory unknowns. The most frequent chemotype is P+, with diffractaic, physodic, physodalic, and protocetraric acids. Also common is a P- chemotype with physodic acid as the only major substance in the medulla.

Substrate and ecology: on bark or wood, including both conifers and hardwoods, occurring in a wide range of habitats, including semi-arid suboceanic forest, oceanic woodlands and forests; **World distribution:** western North America, Alaska to northern Baja California, inland to Sierra Nevada, Montana, and Alberta; **Sonoran distribution:** coast ranges and offshore islands of California and northern Baja California.



Notes: *Hypogymnia imshaugii* is extremely variable in morphology and chemistry, probably reflecting multiple closely related species or phenotypic plasticity, or both. The most typical form occurring throughout its range has imperforate lobe tips, hollow lobes, open, dichotomous branching, suberect or erect lobes, and medulla P+ orange. This form is infrequent in southern California. Another form is restricted to southern California and is very compact and appressed, with compressed to folded,

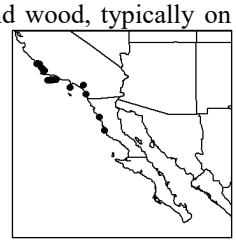
hollow lobes, usually P-, and a distinctive set of unknowns by TLC. A third form, also restricted to southern California, has lobes collapsed and ± channeled on the lower surface, semi-solid to solid, with or without extended lobes that are hollow, not black mottled, the central part of the upper cortex strongly rugose, and medulla P+ orange. This form can have sparse subapical and subaxillary perforations, suggesting a relationship to *H. gracilis*.

Hypogymnia mollis L. H. Pike & Hale, Mycotaxon 16: 161 (1982).

Illustration: Pike and Hale (1982), p. 160.

Thallus: appressed, up to 5 (-6) cm broad; texture: soft; branching: variable; budding: often present; **lobes:** contiguous, 1-4 (-6) mm broad; black border: not visible from above; profile: pinched and swollen; width/height ratio: 1.5-5; tips and axils: perforate; **upper surface:** white to greenish gray, rarely dark mottled, becoming rugose; **soredia:** diffuse, powdery, laminal, generally 15-40 µm in diameter, developing from gradual deterioration of the cortex, rarely arising from the edges of a cracking cortex; isidia absent, lobules rare; **medulla:** hollow; ceiling and floor of cavity: both dark; **lower surface:** black, rarely perforate; **Apothecia:** rare, substipitate to stipitate, up to 4 mm in diam; stipe: urn-shaped, hollow; disc: dark reddish brown; **ascospores:** subglobose to globose, 5-5.5 x 5-5.5 µm; **Pycnidia:** uncommon; **conidia:** rod-shaped to weakly bifusiform, 4.5-5.5 x 0.5-0.7 µm; **Spot tests:** cortex K+ yellow, C-, KC-, P+ pale yellow, UV-; medulla K-, C-, KC+ orange-red, P-; **Secondary metabolites:** upper cortex with atranorin and chloroatranorin; medulla with physodic acid (major), and 3-hydroxyphysodic acid (accessory).

Substrate and ecology: on bark and wood, typically on shrubs (*Salvia, Adenostoma*) and conifers (*Pinus*), most often in coastal chaparral scrub; infrequent; **World** and **Sonoran distribution:** San Luis Obispo County, California, south to at least 31°N in Baja California, including Channel Islands (Santa Catalina, Santa Cruz, and Santa Rosa).



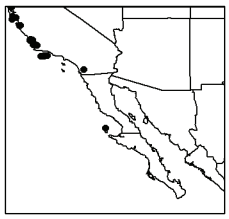
Notes: This distinctive species has soft, puffy, whitish lobes nearly covered by very fine soredia. See notes under *H. austerodes* and *H. farinacea*.

Hypogymnia occidentalis L. H. Pike, Mycotaxon 16: 158 (1982).

Illustrations: McCune and Geiser (1997), p. 128; Pike and Hale (1982), p. 160; McCune and Goward (1995), p. 109; Goward et al. (1994), p. 59; Hale and Cole (1988), p. 54; Brodo et al. (2001), p. 353.

Thallus: appressed rarely pendulous, sometimes imbricate, up to 10 cm broad; texture: cartilaginous; branching: variable; budding: present; **lobes:** contiguous or separate, (1-) 2-4 mm broad, sometimes black bordered; profile: pinched and swollen; width/height ratio: 0.5-2; tips and axils: perforate; **upper surface:** white to greenish gray, sometimes dark mottled, becoming rugose; soredia and isidia: absent, lobules sparse or absent; **medulla:** hollow, ceiling of cavity dark, floor of cavity dark; **lower surface:** black, rarely perforate; **Apothecia:** common, substipitate, up to 10 mm in diam; stipe: urn- or funnel-shaped, hollow; disc: brown; **ascospores:** broadly ellipsoid, 6.5-8 x 5-6.5 µm; **Pycnidia:** common; **conidia:** rod shaped to weakly bifusiform, 5-7 x 0.6-0.8 µm; **Spot tests:** cortex K+ yellow, C-, KC-, P+ pale yellow, UV-; medulla K-, C-, KC+ orange-red, P-; **Secondary metabolites:** upper cortex with atranorin and chloroatranorin; medulla with physodic acid (major), 2'-*O*-methylphysodic acid (minor accessory), 3-hydroxyphysodic acid (rarely accessory), and unknowns C7 and C8 (uncommon minor accessories).

Substrate and ecology: on bark and wood, including both conifers and hardwoods, most frequent in cool, moist, suboceanic conifer forests north of the Sonoran region; **World distribution:** Alaska to northern California with sporadic records south to Santa Barbara County, California, inland to western Montana and Alberta; **Sonoran distribution:** disjuncts in the coast ranges to Pt. Sal Ridge, Santa



Cruz Island, and Santa Rosa Island.

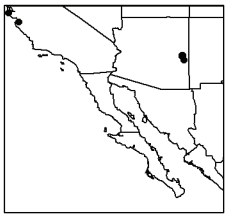
Notes: This species is characterized by esorediate, puffy, swollen lobes with dark interiors and perforate tips; always P-. In the southern end of its range specimens are often depauperate, but no consistent differences from northern populations other than thallus size and lobe size could be found. Spores may be smaller and more elongate in the California populations than in the Pacific Northwest, but more study is needed. An unusual form is common near Los Osos, forming compact masses of narrow (*c.* 1 mm wide), imbricate lobes.

Hypogymnia physodes (L.) Nyl., Lich. Envir. Paris 39 (1896).

Basionym: *Lichen physodes* L. Spec. Plant. p. 1144 (1753); Illustrations: McCune and Geiser (1997), p. 130; McCune and Goward (1995), p. 106; Goward et al. (1994), p. 58; Wirth (1995), p. 429; St. Clair (1999), p. 88; Brodo et al. (2001), p. 354.

Thallus: appressed, up to 6 (-8) cm broad; texture: cartilaginous; branching: isotomic dichotomous, budding occasional; **lobes:** contiguous to imbricate or ± separate, 0.5-2.5 (-4) mm broad; black border: not visible from above; profile: even to irregular; width/height ratio: 1-4; tips and axils: entire or torn; **upper surface:** white, gray to greenish gray, dark mottles none or rare, occasionally rugose; **soredia:** on the inside of the burst lobe tips, appearing as if in labriform soralia; isidia absent, lobules rare; **medulla:** hollow, ceiling of cavity white or dark, floor of cavity dark; **lower surface:** black, rarely perforate; **Apothecia:** rare, substipitate to stipitate, up to 2 (-4) mm in diam; stipe: funnel-shaped, hollow; disc: brown; **ascospores:** ellipsoid, 7-8 x 4.5-5.5 µm; **Pycnidia:** occasional; **conidia:** rod shaped, 5.5-5.8 x 0.5-0.6 µm; **Spot tests:** cortex K+ yellow, C-, KC-, P+ pale yellow, UV-; medulla K-, C-, KC+ orange-red, P+ orange-red.; **Secondary metabolites:** upper cortex with atranorin and chloroatranorin; medulla with physodic acid (major), 2'-*O*-methylphysodic acid (minor or accessory), 3-hydroxyphysodic acid (major), physodalic acid (major), and protocetraric acid (minor).

Substrate and ecology: on bark or wood including conifers and hardwoods, rarely on rock, moss, or alpine sod; **World distribution:** circumpolar arctic, boreal, and montane; northern Asia, North America, and Europe; throughout northern North America, south in California to about Santa Cruz and S throughout the Appalachian and Rocky Mountains; **Sonoran distribution:** southern Rocky Mountains.



Notes: Although this generalist species is widespread and common in the northern hemisphere, in the southwestern U.S. and Mexico it is apparently restricted to the higher mountains in a continental climate. It is remarkably consistent in chemistry considering its wide geographic range and the variability in chemistry of so many *Hypogymnia* species. Occasional small esorediate individuals can be recognized by the P+ medulla and imperforate lobe tips.

Hypogymnia schizidiata McCune, **sp. nov.**

Diagnosis: *Thallus adnatus vel laxe adnatus, corticolus, ad 4 (-8) cm diametro; lobi liber, cinereo-albicans vel subviridus, 1-3 (-4) mm lata; medulla alba vel fuscata; schizidia numerosa, schizidia margine sorediata; isidia desunt; subtus niger, foraminibus subapicalibus et axillaribus; apothecia sparsa; sporae (5.5-) 6.5-7 (-8) x (3.5-) 4-5 µm. Cortex K+ flavescens; medulla K-, C-, KC+ rosea, P-.*

Type: MEXICO: Baja California, Cedros Island, south end, top of hill north of town of Cedros, 28°08'N, 115° 13'W, 1100 m, on *Juniperus californicus*, with *Pachycormus, Ambrosia*, and *Mammillaria*, Marsh 7384, 21 March 1994 (ASU).

Other specimens examined: MEXICO: Baja California, Cedros Island, Marsh 7383, 7388 (ASU), track from town of Cedros, E side of the ridge below Cerro Redondo, 28° 08'N, 115°13.5'W, 1000 m, on *Pachycormus*, Nash 34483; on *Simmondsia*, 34497 (ASU); Cerro Redondo, N-facing slope, 800 m, Marsh 7409 (ASU); N end of island, N-facing slope on NE ridgetop with pines, 28° 22'N, 115°

15'W, 400 m, on *Pinus muricata*, Nash 34257 (ASU); N end of island above mine, 442-488 m, *Pinus muricata* forest, Beauchamp 62444 (COLO); ridge crest to W of Cerro Redondo, 28° 8.5'N, 115° 14'W, on *Juniperus*, Nash 34501 (ASU); NW shoulder of Cedros Mountain, 28°8.5'N, 115°13.25'W, 1050 m, on *Juniperus*, Moran 10647a (ASU, COLO); Guadalupe Island, 1200 m, *Cupressus* forest on ridge, Tretiach 31618b,c (TSB). USA: California, Santa Barbara County, Santa Rosa Island, group of large oaks near Soledad, 33°56.75'N, 120° 7.5'W, 480 m, Ryan 31429 (ASU); pass adjacent to Black Mountain, pine-oak-chaparral mixture, 33°59'N, 120° 4.5'W, 260 m, on *Pinus remorata*, Nash 33051a (ASU).

Illustration: Fig. 53 below.

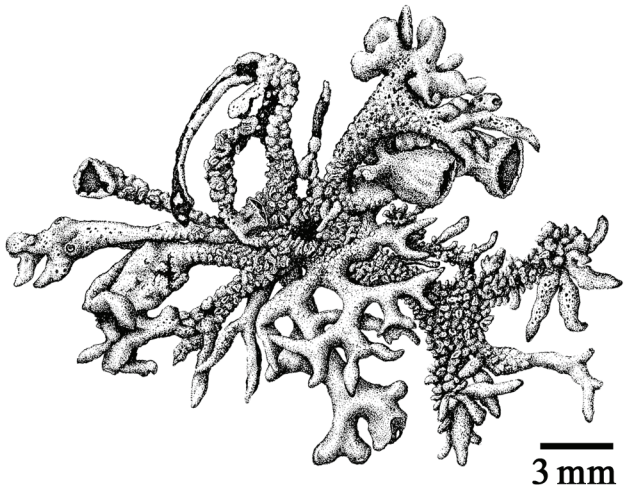
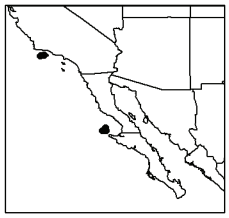


Fig. 53. Type of *Hypogymnia schizidiata*, drawing by A. Mikulin.

Thallus: appressed to suberect, up to 4 (-8) cm in diam.; texture: cartilaginous; branching: isotomic dichotomous; budding: absent or rare; **lobes:** separate to centrally subcontiguous, 1-3 (-4) mm broad; black border: not visible from above; profile: even to ± nodulose; width/height ratio: 1-4; tips and axils: perforate, **upper surface:** greenish gray, greenish, or dark brownish green, often dark mottled, smooth or becoming strongly rugose; **schizidia:** formed as flakes of cortex plus algal layer, developing from either the smooth or rugose areas of the thallus; **soredia:** sometimes developing on the edges of the schizidia, particularly in rugose areas of the upper surface, rarely spreading into diffuse laminal soredia; isidia: absent; lobules: rare; **medulla:** hollow, ceiling of cavity brownish to white, floor of cavity brownish to white; **lower surface:** black, sparsely perforate; **Apothecia:** occasional, substipitate to stipitate, up to 6 mm diam; stipe: urn- to funnel-shaped, hollow; disc: light to dark brown; **ascospores:** ellipsoid, (5.5-) 6.5-7 (-8) x (3.5-) 4-5 µm; **Pycnidia:** common; **conidia:** rod-shaped to weakly bifusiform, 6-7.5 x 0.5-0.7 µm; **Spot tests:** cortex K+ yellow, C-, KC-, P+ pale yellow, UV-; medulla K-, C-, KC+ orange-red, P-; **Secondary metabolites:** upper cortex with atranorin and chloroatranorin; medulla with physodic acid (major), 2'-*O*-methylphysodic acid (minor), 3-hydroxyphysodic acid (accessory, frequency 25%), unknown C7 (minor UV+ accessory), unknown C8 (minor accessory).

Substrate and ecology: on bark and wood of both hardwoods and conifers, including *Juniperus, Pachycormus, Quercus*, *Pinus,* and *Simmondsia* in woodlands, isolated groves, and forests; **World** and **Sonoran distribution:** offshore islands of Baja California (Isla Cedros) and California (Santa Rosa Island).



Notes: Production of asexual propagules is rather variable, but in most specimens the cortex tends flake off from both smooth parts and rugose parts, taking with it the algal layer. The type is not as heavily schizidiate as some specimens, but it is fertile and shows the variation from smooth to rugose lobes. True soredia can be nonexistent to well developed. The species is also unusual in its light brownish lobe cavities. In most specimens it is somewhat variable, having pure white portions, occasional dark brown portions, but the majority of the lobe interiors have a loose mesh of brown hyphae over a white background. This plus the frequently perforate lobe tips separate the species from *H. imshaugii.* The P- medulla is also useful in separating *H. schizidiata* from the P+ chemotype of *H. imshaugii*. The somewhat darkened lobe cavities and perforations suggest *H. inactiva*, another P- species, but that species lacks asexual propagules and differs in accessory seconddary metabolites. Small presored-

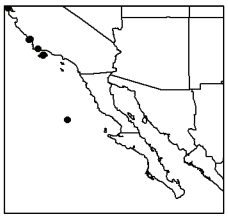
iate specimens can be recognized by their brownish cavities, isotomic dichotomous branching, and perforations in the lobe tips and lower surface.

Hypogymnia tubulosa (Schaer.) Hav., Bergens Mus. Aarbog, Hefte 1, Naturvidensk. Raekke 1917-18 (2): 31 (1918).

Basionym: *Parmelia ceratophylla* var. *tubulosa* Schaer. Lich. Helvet. Spicil. 10:459 (1840); Illustrations: McCune and Geiser (1997), p. 132; Wirth (1995), p. 429; McCune and Goward (1995), p. 107; Goward et al. (1994), p. 58; St. Clair (1999), p. 89; Brodo et al. (2001), p. 356.

Thallus: erect to suberect, up to 6 (-8) cm broad; texture: cartilaginous; branching: isotomic dichotomous; budding: absent or rare; **lobes:** separate to centrally subcontiguous, 1-3 (-4) mm broad; black border: not visible from above; profile: even; width/height ratio: 0.5-2; tips and axils: entire, **upper surface:** white to greenish gray, sometimes dark mottled, becoming rugose; **soredia:** terminal, in capitate soralia; isidia and lobules absent; **medulla:** hollow, ceiling of cavity white or dark, floor of cavity white or dark; **lower surface:** black, sparsely perforate; **Apothecia:** rare, substipitate, up to 2 mm in diam; stipe: urn- or funnel-shaped, loosely filled with hyphae; disc: brown; **ascospores:** subglobose, 6-7 x 5-5.5 µm; **Pycnidia:** sparse; **conidia:** not seen in local material; **Spot tests:** cortex K+ yellow, C-, KC-, P+ pale yellow, UV-; medulla K-, C-, KC+ orange-red, P-, UV-; **Secondary metabolites:** upper cortex with atranorin and chloroatranorin; medulla with physodic acid (major), 3-hydroxyphysodic acid (major), 2'-*O*-methylphysodic acid (accessory, frequency about 50%).

Substrate and ecology: typically on bark or wood, including conifers and deciduous trees, rarely on mossy rock or alpine sod; **World distribution:** circumboreal, montane, and cool temperate areas; northern Asia, North America, and Europe; in North America south to southern California and central Rocky Mountains; **Sonoran distribution:** southern California and Guadalupe Island in Baja California.



Notes: Much more common northward, the species is easily distinguished by its suberect to erect lobes with soredia coating the tips. Young, pre-sorediate specimens might be confused with *H. imshaugii*, but that species has pure white lobe interiors and only rarely contains 3-hydroxyphysodic acid. *Hypogymnia bitteri* has terminal soralia but an appressed, rosette-like thallus with contiguous lobes and often an overall brownish color.

HYPOTRACHYNA

by T. H. Nash III, H. G. M. Sipman and J. A. Elix

Hypotrachyna (Vain.) Hale, Phytologia 28: 340 (1974).

Family: Parmeliaceae; Type: *Hypotrachyna brasiliana* (Nyl.) Hale; No. species: *c.* 165 world wide; Selected lit.: Elix (1993a & 1994e) and Hale (1975).

Life habit: lichenized; **Thallus:** tightly to loosely adnate, foliose, often dichotomously lobate; **lobes:** usually sublinear, sometimes subirregular or linear-elongate, sometimes imbricate; axils: sinuous or V-shaped; lobe tips: usually subtruncate, but sometimes rounded, incised or not, cilia absent or rarely short ciliate; **upper surface:** gray, ivory or yellow green, smooth, plane to rugulose, shiny or dull, sometimes white maculate, usually epruinose, pseudocyphellae absent; **upper cortex:** pored epicortex, palisade paraplectenchymatous; **medulla:** white or rarely partially yellow or orange, cell walls containing isolichenan; **photobiont**: primary one a *Trebouxia*, secondary photobiont absent; **lower surface:** black, sometimes with brown tips, plane to sometimes wrinked, rarely subcanaliculate, attachment by dichotomous rhizoid holdfasts, without cyphellae, pseudocyphellae or tomentum; **Ascomata:** apothecial, imperforate, laminal, orbicular, cup-shaped, sess-

ile or subpedicellate; margin: prominent with thalloid rim; exciple: gray or hyaline; epithecium: brown or brownish yellow; hypothecium: hyaline; **asci:** lecanoral, apex I+ blue, with wide, axial body divergent towards apex, 8-spored; **ascospores:** simple, ellipsoid to broadly ellipsoid; wall: thin, hyaline; **Conidiomata:** pycnidial, laminal to marginal, immersed; **conidia:** bacilliform or weakly bifusiform, 5-8 x 1 µm; **Secondary metabolites:** upper cortex with either atranorin and chloroatranorin (gray), lichexanthone (ivory), or usnic acid (yellow-green); medulla with some combination of orcinol depsides, orcinol depsidones, ß-orcinol depsides, ß-orcinol depsidones, (higher) aliphatic acids, rarely triterpenoids, anthraquinones, xanthones, and dibenzofurans; **Geography:** predominantly tropical, montane to subalpine, but some species also occurring in temperate areas (particularly in maritime influenced regions); **Substrate:** mostly on bark or acidic rocks, rarely on compacted soil.

Notes: Although all the species in the Sonoran region are gray and have atranorin or rarely lichexanthone or isousnic acid in the upper cortex, there are a few yellow species, particularly in the tropics, with usnic acid in the upper cortex. Previously *Hypotrachyna* was treated as a section of *Parmelia* by Vainio (1890) and later raised to a subgenus (Hale and Kurokawa 1964). As it became clear that this large, predominately tropical group of lichens was quite different from the temperate to arctic *Parmelia s.s*, it was finally raised to the genus level (Hale 1974a), a status that is widely recognized today. Key characters for the genus include subtruncate lobe apices, lack of marginal cilia, dichotomously branched rhizines and bifusiform conidia.

Key to the species of ***Hypotrachyna*** from the Sonoran region:

1. Thallus lobulate, isidiate or dactylate 2
1. Thallus not isidiate or dactylate or lobulate 11

2. Thallus lobulate ..... ***H. culbersoniorum***
2. Thallus not lobulate 3

3. Thallus dactylate; medulla with colensoic acid (major) . ..... ***H. dactylifera***
3. Thallus isidiate; medulla lacking colensoic acid series 4

4. Medulla P+ red (protocetraric or echinocarpic acid major) 5
4. Medulla P- 6

5. Thallus on bark; medulla with protocetraric acid major ..... ***H. consimilis***
5. Thallus on rock; medulla with echinocarpic acid major ..... ***H. dentella***

6. Medulla C+ red (gyrophoric or lecanoric acids) 7
6. Medulla C- (lacking gyrophoric or lecanoric acids). 8

7.Thallus shiny white maculate; lower surface not subcanaliculate; medulla with lecanoric and evernic acids .... ***H. bogotensis***
7. Thallus emaculate, lower surface subcanaliculate, medulla with gyrophoric acid complex ..... ***H. neodissecta***

8. Occurring on rocks or detritus over rocks; medulla UV+ white with alectoronic acid (major) .... ***H. meridensis***
8. Occurring on bark; medulla UV- 9

9. Medulla KC+ yellow, with barbatic and 4-*O* demethyl barbaric acids (major) ..... ***H. imbricatula***
9. Medulla KC-, with a series of fatty acids (constipatic, dehydroconstipatic, protopraesorediosic acids and praesorediosic acids) ..... ***H. costaricensis***

10. Thallus sorediate (in soralia or pustulae) 11
10. Thallus not sorediate 22

11. Thallus UV+ bright yellow (lichexanthone in upper cortex); medulla with echinocarpic acid . ***H. adaffinis***
11. Thallus UV- (atranorin in upper cortex); medulla without echinocarpic acid) 12

12. Lobes 0.5-1.0 mm wide (colensoic syndrome present) ..... ***H. subpustulifera***
12. Lobes more than 1.0 mm wide (most but not all species without colensoic syndrome) 13

13. Medulla K+ yellow, turning deep red (salazinic acid [major]) ..... ***H. brevirhiza***
13. Medulla K- (salazinic acid not present) 14

14. Medulla P+ red (protocetraric acid [major]) 15
14. Medulla P- (protocetraric or echinocarpic acid not present) 16

15. Soredia in laminal pustulae; medulla white with orange patches ..... ***H. croceopustulata***

15. Soredia in subterminal, capitate soralia; medulla just white ..... ***H. pseudosinuosa***

16. Medulla C- and KC- (with the fatty acids protolichesterinic and lichesterinic acids) .... ***H. punoensis***
16. Medulla C± and KC+ (fatty acids absent; other secondary products present) 17

17. Medulla C-, KC+ yellow (with barbatic and 4-*O* demethylbarbaric acids [major]) ..... ***H. laevigata***
17. Medulla C+ red, KC+ red (with gyrophoric, lecanoric or olivetoric acids) 18

18. Lobe tips becoming revolute and often subascending; medulla with gyrophoric acid (major) and hiascic acid series (minor) ..... ***H. revoluta***
18. Lobe tips plane to slightly convex (not revolute or subascending); medulla without gyrophoric acid and the hiascic acid series 19

19. Soredia coarse and granular in pustules 20
19. Soredia farinose (at least initially) and in capitate soralia 21

20. Medulla with evernic and lecanoric acids only .... ***H. rockii***
20. Medulla with lividic acid (major) and with colensoic acid series (minor) ..... ***H. pustulifera*** (but see the more common ***H. dactylifera*** above)

21. Lobes usually less than 3 mm wide; medulla C+ red (with olivetoric acid only) ..... ***H. lividescens***
21. Lobes usually more than 3 mm wide; medulla C- [with lividic acid (major) and colensoic acid series] .... ***H. immaculata***

22. Medulla K+ yellow, turning deep red (salazinic acid [major]) 23
22. Medulla K- (salazinic acid not present 24

23. On bark, wide lobes, spores 8-10 µm long .... ***H. sublaevigata***
23. On rocks, narrow lobed, spores 11-15 µm long .... ***H. subsaxatilis***

24. On rocks; lobes strongly convex; medulla UV+ (alectoronic acid [major]) ..... ***H. protenta***
24. On trees; lobes plane or slightly convex; medulla UV- (lacking alectoronic acid) 25

25. Medulla C+ red (lecanoric and evernic acids present) ..... ***H. pulvinata***
25. Medulla C- or C+ yellow-orange (lecanoric and evernic acids not present) 26

26. Medulla KC+ yellow-orange (barbaric and 4-*O* demethylbarbaric acids) ..... ***H. physcioides***
26. Medulla KC+ rose (lividic acid and the colensoic acid series present) ..... ***H. livida***

The Species

Hypotrachyna adaffinis Sipman, Trop. Bot. 6: 16 (1992).

Illustration: Sipman (1992), p. 17.

Thallus: foliose, 2-5 cm in diam., tightly adnate, subdichotomously to irregularly lobate; **lobes:** sublinear, elongate, plane to subconvex, separate, 0.4-2 mm wide; margin: entire but sometimes incised; apices: subtruncate, plane to convex; **upper surface:** light gray, smooth to somewhat rugulose, plane, dull, faintly maculate or emaculate, epruinose; **soredia:** farinose to slightly granular, in laminal, capitate soralia that sometimes become confluent; isidia and dactyls absent; **medulla:** white with continuous algal layer; **lower surface:** black centrally, brown peripherally; rhizines: dense, black, dichotomous; **Apothecia:** rare, laminal, substipitate, 1-2.5 mm diam.; disc: brown; margin: smooth, esorediate; **asci:** clavate, 8-spored; **ascospores:** broadly ellipsoid, 8-11 x 5-7 µm; **Pycnidia:** not seen; **Spot tests:** upper cortex K-, C-, KC-, P+ pale orange, UV+ yellow; medulla K-, C-, KC-, P+ red; **Secondary metabolites:** upper cortex with lichexanthone; medulla with echinocarpic acid (major).

Substrate and ecology: on bark of oak and pine in montane forests; **World distribution:** throughout the neotropics, including the Carribean; **Sonoran distribution:** Sinaloa in the Sierra Madre Occidental.

Notes: Initially Hale (1975, p. 66) inadvertently created confusion about this species by listing the cortex as having usnic acid in the description of the species. However, in the introductory pages Hale (1975, p. 10)

listed the species as having lichexanthone, a fact that we confirm for several specimens in addition to the Sonoran material.

Hypotrachyna bogotensis (Vain.) Hale, Smithson. Contr. Bot. 25: 23 (1975).

Basionym: *Parmelia bogotensis* Vain., Hedwigia 38: 122 (1899); Illustration: Hale (1975), p. 24.

Thallus: foliose, (2-) 5-12 cm in diam., adnate to loosely adnate, dichotomously to subdichotomously lobate; **lobes:** sublinear, elongate, plane to subconvex, separate, becoming crowded and imbricate, 1-6 mm wide; margin: entire or dentate-crenate, sometimes lacinate; apices: subtruncate; **upper surface:** gray, smooth, shiny, white maculate, sometimes marginally pruinose; **isidia:** laminal to marginal, cylindrical, sometimes becoming procumbent, tips, mostly concolourous with thallus surface but tips may become blackened; soralia, pustulae, and dactyls all absent; **medulla:** white with continuous algal layer; **lower surface:** black centrally to margin; rhizines: abundant, black, dichotomous; **Apothecia:** rare, laminal, sessile, 1-5 (-7) mm in diam.; disc: brown; margin: smooth, sometimes isidiate, epruinose; **asci:** clavate, 8-spored; **ascospores:** broardly ellipsoid, 10-12 x 6-8.5 µm; **Pycnidia:** laminal, immersed; **conidia:** bacilliform, 3-4 µm; **Spot tests:** upper cortex K+ yellow, C-, KC-, P+ yellow, UV-; medulla K-, C+ red, KC+ red, P-; **Secondary metabolites:** upper cortex with atranorin and chloroatranorin; medulla with evernic acid (major) and lecanoric acid (major or minor).

Substrate and ecology: on bark of many species, fence posts, rocks and soil in open, montane to subalpine forests; **World distribution:** throughout the neotropics; **Sonoran distribution:** Sinaloa in the Sierra Madre Occidental.

Hypotrachyna brevirhiza (Kurok.) Hale, Smithson. Contr. Bot. 25: 26 (1975).

Basionym: *Parmelia brevirhiza* Kurok., Contr. U.S. Natl. Herb. 36: 166 (1964); Illustration: Hale (1975), p. 24.

Thallus: foliose, 2-6 (-8) cm in diam., tightly adnate to adnate, subdichotomously lobate; **lobes:** sublinear to subirregular, short, often imbricate, irregularly branched; plane to subconvex, 1-5 mm wide; margin: entire, rarely incised; apices: subtruncate to rotund; **upper surface:** light gray, smooth to rugulose, dull, frequently white pruinose (especially marginally), emaculate; **soredia:** initially farinose but becoming coarse and granular, in subcapitate, laminal to subterminal soralia but becoming diffuse; pustulae, isidia and dactyls all absent; **medulla:** white with continuous algal layer; **lower surface:** black centrally, blackish brown tips; rhizines: sparse to dense, black, dichotomous; **Apothecia:** rare, laminal, sessile, 1-5 mm in diam.; disc: brown; margin: smooth, sometimes sorediate; **asci:** clavate, 8-spored; **ascospores:** ellipsoid, 6-8 x 3-4 µm; **Pycnidia:** not seen; **Spot tests:** upper cortex K+ yellow, C-, KC-, P+ yellow, UV-; medulla K+ yellow, turning deep red; C-, KC-, P+ orange; **Secondary metabolites:** upper cortex atranorin and chloroatranorin; medulla with salazinic acid (major), consalazinic acid (minor), norstictic acid (trace).

Substrate and ecology: usually on wood and bark in humid forests, occasionally on rocks, in montane to subalpine forests; **World distribution:** pantropical and extending to temperate parts of Argentina and Chile; **Sonoran distribution:** Sinaloa in the Sierra Madre Occidental.

Hypotrachyna consimilis (Vain.) Hale, Smithson. Contr. Bot. 25: 28 (1975).

Basionym: *Parmelia consimilis* Vain., Acta Soc. Fauna Flora Fenn. 7: 58 (1890); Illustration: Hale (1975), p. 27.

Thallus: foliose, 3-8 cm diam., adnate to loosely adnate, subdichotomously lobate; **lobes:** sublinear, elongate, plane, separate, 1-3 mm wide; margin: entire; apices: subtruncate; **upper surface:** light gray, smooth, dull or shiny; white maculate; **isidia:** laminal, cylindrical to rarely coralloid; soralia, pustulae and dactyls absent; **medulla:** white with continuous algal layer; **lower surface:** black, peripherally brownish black; rhizines: sparse; black, dichotomous; **Apothecia:** rare, laminal, sessile, 2-5 mm in diam.; disc: brown; margin: crenulate, isidiate; **asci:** cla-

vate, 8-spored; **ascospores:** broardly ellipsoid, 8-11 x 5-8 µm; **Pycnidia:** not seen; **Spot tests:** upper cortex K+ yellow, C-, KC-, P+ yellow, UV-; medulla K- or K+ if skyrin present, C-, KC-, P+ orange; **Secondary metabolites:** upper cortex with atranorin and chloroatranorin; medulla with protocetraric acids (major) and skyrin (accessory).

Substrate and ecology: on hardwood or pine bark in upper montane and subalpine forests; **World distribution:** throughout the neotropics, including the Carribean region; **Sonoran distribution:** Sinaloa in the Sierra Madre Occidental.

Hypotrachyna costaricensis (Nyl. in Polakowsky) Hale, Smithson. Contr. Bot. 25: 29 (1975).

Basionym: *Parmelia costaricensis* Nyl. in Polakowsky, 225 (1877); Synonyms: *Parmelia hypotrachyna* Nyl., *Parmelia tropica* Vain., *Parmelia deformis* (Vain.) Vain. and see Hale (1975); Illustration: Hale (1975), p. 27.

Thallus: foliose, 3-10 (-15) cm diam., adnate to loosely adnate, subdichotomously lobate; **lobes:** sublinear to irregular, elongate, plane, often imbricate, 2-6 mm wide; apices: subtruncate to subrotund; **upper surface:** whitish to greenish gray (tan in herbarium with age), smooth, shiny, usually strongly white maculate; **isidia:** laminal to submarginal, dense, cylindrical, simple to coralloid branched, slender, rarely becoming lobulate, concolorous with the thallus but tips sometimes blackened; soralia, pustulae and dactyls absent; **medulla:** white with continuous algal layer; **lower surface:** black, peripherally brownish black, shiny; rhizines: dense, often visible from above, black, dichotomous; **Apothecia:** rare, laminal, sessile, 2-7 mm in diam.; disc: brown; margin: crenulate, without isidia; **asci:** clavate, 8-spored; **ascospores:** ellipsoid, spores 8-10 x 4-6 µm; **Pycnidia:** not seen; **Spot tests:** upper cortex K+ yellow, C-, KC-, P+ yellow, UV-; medulla K-, C-, KC-, P-; **Secondary metabolites:** upper cortex with atranorin and chloroatranorin; medulla with protoconstipatic acid (major), constipatic, dehydroconstipatic, protopraesorediosic acids (all minor), and praesorediosic acid (trace).

Substrate and ecology: usually on hardwood or pine bark and rarely on rock in montane to subalpine forests,; **World distribution:** pantropical and subtropical; **Sonoran distribution:** Chihuahua and Sinaloa in the Sierra Madre Occidental.

Hypotrachyna croceopustulata (Kurok.) Hale, Smithson. Contr. Bot. 25: 30 (1975).

Basionym: *Parmelia croeceopustulata* Kurok., Contr. U. S. Natl. Herb. 36: 169 (1964); Illustration: Hale (1975), p. 32.

Thallus: foliose, 2-8 cm in diam., adnate, subdichotomously lobate; **lobes:** sublinear, elongate, plane to subconvex, separate, 1-3.5 mm wide; margin: entire; apices: subtruncate; **upper surface:** whitish gray, smooth to rugulose, shiny; pruina and maculae absent; **soredia:** granular, not confluent, in laminal, crateriform pustulae; isidia and dactyls absent; **medulla:** white or yellowish ochre with continuous algal layer; **lower surface:** black centrally, brown peripherally; rhizines: sparse, black, dichotomous; **Apothecia:** rare, laminal, sessile, 1-6 mm diam.; disc: brown; margin: smooth, epruinose and without soredia; **ascospores:** not found; **Pycnidia:** not seen; **Spot tests:** upper cortex K+ yellow, C-, KC-, P+ yellow, UV-; medulla K- or + purple, C-, KC-, P+ red; **Secondary metabolites:** upper cortex with atranorin and chloroatranorin; medulla with protocetraric acid (major), succinprotocetraric acid (trace or accessory) and pigmentosin B (accessory).

Substrate and ecology: on pine and hardwood bark in open, but humid oak and pine forests; **World distribution:** throughout the neotropics and in East Africa; **Sonoran distribution:** Sinaloa in the Sierra Madre Occidental, common on pines.

Hypotrachyna culbersoniorum Elix & T. H. Nash, **sp. nov.**

Diagnosis: *Thallus ut Hypotrachyna dentella sed lobis exisidiatis et atranorino absente, acido echinocarpico et acido conechinocarpico continente differt*.

Type: MEXICO, Chihuahua, Parque Nacional Basaseachic, overlook area above Cascade de Basaseachic, 28º 10'05"N, 108º12'25"W, T. H. Nash 37629 (ASU).

Illustration: Fig. 54 below.

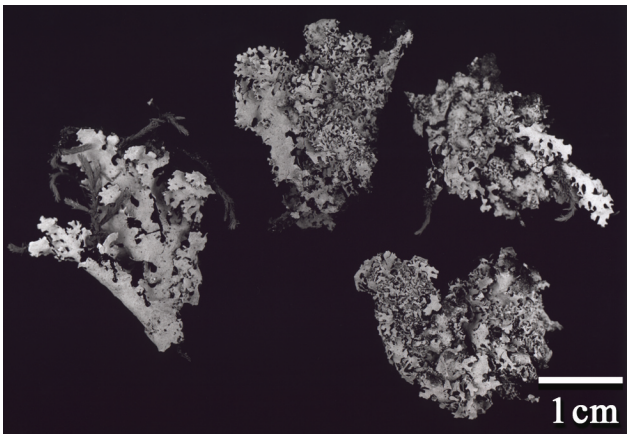


Fig. 54. Part of holotype of *H. culbersoniorum*, photo by F. Bungartz.

Thallus: foliose, 3-6 cm in diam., adnate, rather fragile, subdichotomously lobate; **lobes:** sublinear to subirregular, rather short, plane to subconvex, contiguous or becoming imbricate, 1-2 mm wide; margin: entire or dentate-crenate, sometimes lacinate; apices: subtruncate; **upper surface:** pale gray-green, smooth, dull but shiny at the lobe apices, weakly white maculate, sometimes marginally pruinose; **lobulae:** abundant, laminal and marginal, dorsiventral, tips, simple to forked, procumbent to subascending, with or without isidial inititials; soralia, pustulae and dactyls all absent; **medulla:** white with continuous algal layer; **lower surface:** black centrally to margin; rhizines: moderately abundant, black, richly dichotomous; **Apothecia:** rare, laminal, sessile, up to 3 mm in diam.; disc: pale brown to cinnamon-brown; margin: smooth, sometimes lobulate, epruinose; **asci:** clavate, 8-spored; **ascospores:** subglobose, 5 x 4 µm; **Pycnidia** and **conidia:** not seen; **Spot tests:** upper cortex K-, C-, KC-, P-, UV-; medulla K-, C-, KC-, P-; **Secondary metabolites:** upper cortex with isousnic acid; medulla with echinocarpic acid and conechinocarpic acid (both minor).

Substrate and ecology: on bark, in open pine-oak forests; **World** and **Sonoran distribution:** thus far only known from the type locality in Chihuahua in the Sierra Madre Occidental.

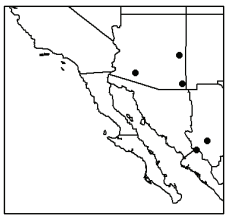
Notes: The new species is named in honor of Drs. C. F. and W. L. Culberson who have contributed considerably to our knowledge of the Parmeliaceae in general and to the Mexican flora in particular. Morphologically this new species resembles *Hypotrachyna bogotenis* (Nyl.) Hale in its habitat, in having broad, sublinear to subirregular lobes with dense, dorsiventral lobulae. However, whereas *H. bogotensis* is coriaceous, gray in color (atranorin and chloroatranorin in the upper cortex) and contains lecanoric acid in the medulla, *H. culbersoniorum* is very fragile, gray-green in color (isousnic acid in the upper cortex) and contains echinocarpic and conechinocarpic acids in the medulla. *Hypotrachyna culbersoniorum* is only the second species of *Hypotrachyna* known to contain isousnic acid in the upper cortex.

Hypotrachyna dactylifera (Vain.) Hale, Smithson. Contr. Bot. 25: 30 (1975).

Basionym: *Parmelia dactylifera* Vain., Acta Soc. Fauna Flor. Fenn. 7: 57 (1890); Illustration: Hale (1975), p. 32.

Thallus: foliose, 3-9 cm in diam., tightly adnate, subdichotomously lobate; **lobes:** sublinear, elongate, plane to subconvex, separate and becoming somewhat imbricate, 1-4 mm wide; apices: subtruncate, plane; **upper surface:** tannish gray, smooth but becoming rugose with age, shiny, pruina and maculae absent; **dactyls:** inflated, tips often breaking open (appearing superficially sorediate or isidiate within); isidia absent; **medulla:** white with continuous algal layer; **lower surface:** black with peripherally brown tips; rhizines: abundant but not at margins, black; dichotomous; **Apothecia:** rare, laminal, substipitate, 1-4 mm in diam.; disc: brown; margin: smooth to crenulate; **asci:** clavate, 8-spored; **ascospores:** ellipsoid, 9-13 x 5-7 µm; **Pycnidia:** not seen; **Spot tests:** upper cortex K+ yellow, C-, KC-, P+ yellow, UV-; medulla K-, C-, KC+ red, P-; **Secondary metabolites:** upper cortex with atranorin and chloroatranorin; medulla with 4-*O*-demethylphysodic and colensoic acids (major), hydroxycolensoic acid, lividic and methoxycolensoic acids (minor), oxyphysodic and physodic acids (trace).

Substrate and ecology: on bark in oak and pine forests of montane regions; **World distribution:** across the neotropics and extending into SW USA; **Sonoran distribution:** SE and E Arizona and south along the Sierra Madre Occidental into Chihuahua and Sinaloa.



Notes: According to Hale (1975), the dactylate tips break open, but are not sorediate. Sonoran collections in contrast certainly appear sorediate within broken dactyls, although the tips are not sorediate. Some dactyls remain unbroken.

Hypotrachyna dentella (Hale & Kurok.) Hale, Smithson. Contr. Bot. 25: 30 (1975).

Basionym: *Parmelia dentella* Hale & Kurok., 172 (1964); Synonym: *Parmelia laevigata* var. *ceratina* Müll. Arg.; Illustrations: Hale and Kurokawa (1964), plate 5 (4) as *Parmelia dentella*; Hale (1975), p. 32.

Thallus: foliose, 3-8 cm diam., adnate to loosely adnate, subdichotomously lobate; **lobes:** linear to subirregular, short, plane, separate, becoming partially imbricate, 2-6 mm wide; apices: subtruncate to subrotund; **upper surface:** whitish gray (tan in herbarium with age), smooth, shiny; usually white maculate; **isidia:** laminal to marginal, dense, cylindrical, simple to coralloid branched, slender, rarely becoming lobulate, concolorous with the thallus but tips sometimes blackened; soralia, pustulae and dactyls absent; **medulla:** white with continuous algal layer; **lower surface:** black, peripherally brownish black, shiny; rhizines: sparse to moderate, black, dichotomous; **Apothecia:** rare, laminal, sessile, 1-2 mm in diam.; disc: brown; margin: crenulate, isidia absent; **asci:** clavate, 8-spored; **ascospores:** ellipsoid, spores 8-10 x 4-6 µm; **Pycnidia:** marginal, immersed; **conidia:** not seen; **Spot tests:** upper cortex K+ yellow, C-, KC-, P+ yellow, UV-; medulla K+ yellow, C- or C+ pale yellow, KC + yellow, P+ orange; **Secondary metabolites:** upper cortex with atranorin, chloroatranorin, and isousnic acid (Eliasaro et al. 1998); medulla with echinocarpic acid, 4-*O*-demethylbarbatic and barbatic acids (all major), norobtusatic, and obtusatic acids (minor to trace).

Substrate and ecology: on rocks in open, but humid oak and pine forests; **World distribution:** SE USA and throughout the neotropics; **Sonoran distribution:** Sinaloa in the Sierra Madre Occidental.

Hypotrachyna imbricatula (Zahlbr.) Hale, Smithson. Contr. Bot. 25: 41 (1975).

Basionym: *Parmelia imbricatula* Zahlbr., Denkschr. Kaiserl. Akad. Wiss., Math.-Naturwiss. Kl. 83: 168 (1909); Illustrations: Hale (1975), p. 43; Elix (1994f), p. 53.

Thallus: foliose, 3-15 cm diam., adnate to loosely adnate, subdichotomously lobate; **lobes:** sublinear, elongate, plane, separate, becoming partially imbricate, 1.5-4 mm wide; apices: subtruncate to truncate; **upper surface:** whitish gray (tan in herbarium with age), smooth, shiny; usually strongly white maculate; **isidia:** laminal to marginal, dense, cylindrical, simple to coralloid branched, slender, rarely becoming lobulate, concolorous with the thallus but tips sometimes blackened; soralia, pustulae and dactyls absent; **medulla:** white with continuous algal layer; **lower surface:** black, peripherally brownish black, shiny; rhizines: dense, black, dichotomous; **Apothecia:** rare, laminal, sessile, 2-10 mm in diam.; disc: brown; margin: crenulate, without isidia; **asci:** clavate, 8-spored; **ascospores:** broadly ellipsoid, 11-16 x 7-10 µm; **Pycnidia:** marginal, immersed; **conidia:** not seen; **Spot tests:** upper cortex K+ yellow, C-, KC-, P+ yellow, UV-; medulla K-, C+ yellow-orange, KC + yellow-orange, P-; **Secondary metabolites:** upper cortex with atranorin and chloroatranorin; medulla with 4-*O*-demethylbarbatic and barbatic acids (both major), obtusatic and norobtusatic acids (both minor to trace).

Substrate and ecology: on bark of many different trees in lower to upper montane forests; **World distribution:** neotropical, Oceania, SE Asia and Australasia; **Sonoran distribution:** Sierra Madre Occidental in Sinaloa.

Hypotrachyna immaculata (Kurok. in Hale & Kurokawa) Hale, Smithson. Contr. Bot. 25: 41 (1975).

Basionym: *Parmelia immaculata* Kurok. in Hale and Kurokawa, Contr. U.S. Natl. Herb. 36: 178 (1964); Illustration: Hale (1975), p. 43.

Thallus: foliose, 2-7 cm in diam., adnate to loosely adnate, subdichotomously lobate; **lobes:** sublinear, elongate, plane or convex, 2-7 mm wide, contiguous; margin: entire; apices: subtruncate, plane to convex; **upper surface:** light gray, smooth, shiny, emaculate; **soredia:** granular, usually in capitate soralia but sometimes in crateriform, slightly excavated soralia; isidia and dactyls absent; **medulla:** predominately white with continuous algal layer but orange-brown below the soralia and intermittently orange-brown adjacent to the lower cortex; **lower surface:** black, shiny; rhizines: sparse, black, dichotomous; **Apothecia:** sparse, laminal, sessile, 2-3 mm in diam.; disc: brown; margin: crenulate, sorediate; **asci:** clavate, 8-spored; **ascospores:** rare, ellipsoid, 11-12 x 6-7 µm; **Pycnidia:** marginal, immersed; **conidia:** not seen; **Spot tests:** upper cortex K+ yellow, C-, KC-, P+ yellow, UV-; medulla K-, C-, KC+ red, P-; **Secondary metabolites:** upper cortex with atranorin and chloroatranorin; medulla with lividic acid and skyrin (both major), pigmentosin A (or B) (major or minor), methoxycolensoic, physodic, oxyphysodic and 4-*O*-methylphysodic (all minor) and colensoic (minor or trace).

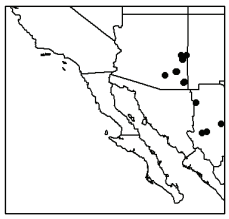
Substrate and ecology: on bark in oak and pine forests of montane regions; **World distribution:** pantropical and extending into some adjacent temperate areas; **Sonoran distribution:** in the southern mountains of Baja California Sur.

Hypotrachyna laevigata (Sm.) Hale, Smithson. Contr. Bot. 25: 44 (1975).

Basionym: *Lichen laevigatus* Sm., Engl. Bot. 26, pl 1852 (1808); Synonym: *Parmelia laevigata* (Sm.) Ach.; Illustration: Hale (1975) p. 43.

Thallus: foliose, 2-10 cm in diam., adnate to loosely adnate, subdichotomously lobate; **lobes:** sublinear to subirregular, elongate, subconcave to plane to subconvex, initially separate, becoming imbricate, 1-6 mm wide; margin: entire to rarely incised; apices: subtruncate to subrotund; **upper surface:** whitish to greenish gray, smooth to rugulose, dull to shiny, usually strongly white maculate; **soredia:** farinose to granular, white but darkening with age, in laminal to subapical, capitate, slightly excavated soralia, not confluent; isidia, pustulae and dactyls all absent; **medulla:** white with algal layer; **lower surface:** black, sometimes with a thin, brown rim, tips brownish black; rhizines: dense, black, dichotomous; **Apothecia:** rarely, sparse, laminal, sessile; disc: brown; margin: crenulate, epruinose and without soredia; **ascospores:** mature spores not found; **Pycnidia:** marginal, immersed; **conidia:** not seen; **Spot tests:** upper cortex K+ yellow, C-, KC-, P+ yellow, UV-; medulla K-, C+ yellow-orange, KC+ yellow-orange, P-; **Secondary metabolites:** upper cortex with atranorin and chloroatranorin; medulla with 4-*O*-demethylbarbatic and barbatic acids (both major), obtusatic and norobtusatic acids (trace).

Substrate and ecology: on hardwood bark and occasionally conifers in lower to upper montane forests; **World distribution:** tropics and extending into some temperate regions in Europe, North and South America and Australasia; **Sonoran distribution:** mountains of SE Arizona southwards through the Sierra Madre Occidental to Durango.



Hypotrachyna livida (Taylor) Hale, Smithson. Contr. Bot. 25: 45 (1975).

Basionym: *Parmelia* livida Taylor, J. Bot., Lond. 6: 171 (1847); Illustrations: Hale (1975), p. 46; Hale (1979), p. 101.

Thallus: foliose, 2-9 cm in diam., somewhat fragile, tightly adnate, subdichotomously lobate; **lobes:** sublinear, elongate, plane to rugulose, 1-2 mm wide, initially separate, becoming contiguous to partly imbricate; margin: entire; apices: subtruncate; **upper surface:** whitish gray, smooth, shiny, emaculate, isidia, soralia, pustulae and dactyls all absent; **medulla:** white with continuous algal

layer; **lower surface:** black, tips brownish black; rhizines: frequent, black, sparsely dichotomous; **Apothecia:** usually present, laminal, sessile, 1-5 mm in diam.; disc: brown, margin crenulate, lacking pruina, soredia or isidia; **asci:** clavate, 8-spored; **ascospores:** ellipsoid, 10-12 x 5-6 µm; **Pycnidia:** peripheral on thallus, semi-immersed; **conidia:** not seen; **Spot tests:** upper cortex K+ yellow, C-, KC-, P+ yellow, UV-; medulla K-, C-, KC+ red, P-; **Secondary metabolites:** upper cortex with atranorin and chloroatranorin; medulla with 4-*O*-methylphysodic and colensoic acids (major), hydroxycolensoic acid, lividic and methoxycolensoic acids (minor), oxyphysodic and physodic acids (trace).

Substrate and ecology: on hardwood bark and rarely acidic rocks in lower montane to montane forests; **World distribution:** neotropics and SE USA; **Sonoran distribution:** Chihuahua in the Sierra Madre Occidental.

Hypotrachyna lividescens (Kurok.) Hale, Phytologia 28: 341 (1974).

Basionym: *Parmelia lividescens* Kurok. in Hale & Kurokawa, Contr. U.S. Natl. Herb. 36: 181 (1964).

Thallus: foliose, 3-10 cm in diam., closely adnate, dichotomously lobate; **lobes:** sublinear, elongate, plane to subconvex, separate to contiguous, 1-3 mm wide; margin: entire to subcrenate; apices: subtruncate to subrotund, plane to convex; **upper surface:** light gray, gray to yellowish gray, smooth to somewhat rugulose, dull but shiny in younger lobes, irregularly cracked in older lobes, emaculate, epruinose; **soredia:** farinose to slightly granular, in mostly subterminal, capitate soralia; isidia, pustules and dactyls absent**; medulla:** white with continuous algal layer; **lower surface:** black centrally, brown peripherally; rhizines: sparse to moderate, black, dichotomous; **Apothecia:** rare, laminal, substipitate, 2-3 mm diam.; disc: dark brown; margin: sorediate; **asci:** clavate, 8-spored; **ascospores:** broadly ellipsoid, 9-11 x 5-7 µm; **Pycnidia:** not seen; **Spot tests:** upper cortex K+ yellow, C-, KC-, P+ yellow, UV-; medulla K-, C+ red, KC+ red, P-; **Secondary metabolites:** upper cortex with atranorin and chloroatranorin; medulla with olivetoric acid (major).

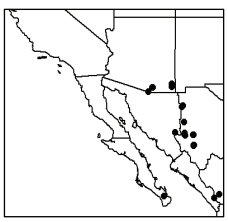
Substrate and ecology: on bark of hardwoods and pines in montane and upper montane forests; **World distribution:** neotropics (Columbia to Mexico), South Africa and Australasia; **Sonoran distribution:** Baja California (Cedros Island).

Hypotrachyna meridensis Hale & López, Bryologist 81: 592 (1978).

Illustration: Hale and López-Figueiras (1978), p. 591.

Thallus: foliose, 2-5 cm in diam., adnate to loosely adnate, subdichotomously lobate; **lobes:** sublinear, elongate, usually convex, initially separate, becoming weakly imbricate, 0.5-2 mm wide, apices subtruncate, revolute to plane; **upper surface:** light to greenish gray, smooth, dull to shiny, emaculate; **isidia:** laminal, cylindrical; tips darker than thallus surface; soralia, pustulae and dactyls absent; **medulla:** white with continuous algal layer; **lower surface:** black with peripherally brown tips; rhizines: abundant but not at margins, black, dichotomous; **Apothecia:** rare, laminal, substipitate, 3-8 mm in diam.; disc: brown; margin: smooth to crenulate, rarely isidiate; **asci:** clavate, 8-spored; **ascospores:** broadly ellipsoid, 14-18 x 8-10 µm; **Pycnidia:** laminal, immersed; **conida:** not seen; **Spot tests:** upper cortex K+ yellow, C-, KC-, P+ yellow, UV-; medulla K-, C-, KC+ rose to red, P-, UV+ white; **Secondary metabolites:** upper cortex with atranorin and chloroatranorin; medulla with alectoronic acid (major), α-collatolic acid (minor), β-alectoronic and β-collatolic acids (trace).

Substrate and ecology: on various acidic rocks, frequently with a layer of detritus between the specimen and the rock in lower montane to montane regions, particularly in sheltered canyons; **World distribution:** neotropics and extending into SW USA; **Sonoran distribution:** in shaded canyons throughout SE Arizona southwards through the Sierra Madre Occidental of Sonora, Chihuahua and Sinaloa and in southern mountains of Baja California Sur.



Notes: Initially these specimens were determined as *H. ensifolia* (Kurok.) Hale and confirmed by Hale. The presence of isidia and similar chemistry was consistent with this evaluation. However, the availability of a wider range of specimens reveals substantial morphological differences between *H. ensifolia* and *H. meridensis*. *H. ensifolia* is a substantially larger speices with more linear, wider lobes, marginal lobulae (or lacinae) and a looser attachment to its substrate. Secondary lobes in *H. ensifolia* are not as well developed as in *H. meridensis* and do not exhibit the typical dichotomous branching of *H. meridensis*.

Hypotrachyna neodissecta (Hale) Hale, Smithson. Contr. Bot. 25: 49 (1975).

Basionym: *Parmelia neodissecta* Hale, Phytologia 22: 94 (1971); Illustrations: Hale (1975), p. 50; Swinscow and Krog (1988), p. 118.

Thallus: foliose, 3-7 cm in diam., rather fragile, loosely adnate, subdichotomously lobate; **lobes:** sublinear to subirregular, elongate, plane to subconvex, 1-3 mm wide; margin: entire; apices: subtruncate to subrotund, subconvex; **upper surface:** gray to greenish gray, smooth, shiny; emaculate; **isidia:** laminal, cylindrical, mostly simple; soralia, pustulae, and dactyls all absent; **medulla:** white with continuous algal layer; **lower surface:** black, tips brown, becoming subcanaliculate; rhizines: dense, black, dichotomous; **Apothecia:** sparse, laminal, substipitate, 2-3 mm in diam.; disc: brown; margin crenulate, isidiate; **asci:** clavate, 8-spored; **ascospores:** ellipsoid, 12-14 x 6-8 µm; **Pycnidia:** not seen; **Spot tests:** upper cortex K+ yellow, C-, KC-, P+ yellow, UV-; medulla K-, C+ red, KC+ red, P-; **Secondary metabolites:** upper cortex with atranorin and chloroatranorin; medulla with gyrophoric and 5-*O*-methylhiascic acids (both major).

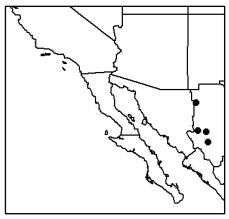
Substrate and ecology: on bark and rocks in open montane forests; **World distribution:** primarily tropical in North and South America and Africa; **Sonoran distribution:** Sierra Madre Occidental of Chihuahua.

Hypotrachyna physcioides (Nyl.) Hale, Smithson. Contr. Bot. 25: 58 (1975).

Basionym: *Parmelia physcioides* Nyl., Synop. meth. lich. 1: 385 (1860); Synonyms: *Hypotrachyna subplumbeata* (Dodge) Hale, *Parmelia subplumbeata* auct. (neotropical records), *Parmelia boliviana* Nyl., *Parmelia digitata* Lynge, and see Hale (1975); Illustration: Hale (1975), p. 53.

Thallus: foliose, 5-15 cm in diam., often coriaceous, loosely adnate, subdichotomously lobate; **lobes:** sublinear, elongate, initially separate, becoming slightly imbricate, 2-6 mm wide; margin: entire; apices: subtruncate, plane to subconvex; **upper surface:** gray, plane to convex, smooth to shallowly rugulose, dull, somewhat pruinose towards tips, strongly white maculate; isidia, soredia, pustulae and dactyls all absent but secondary lacinae sometimes developing centrally; **medulla:** white with continuous algal layer; **lower surface:** black, somewhat shiny; rhizines: dense, black, dichotomous; **Apothecia:** common, laminal, sessile to substipitate, 2-10 mm in diam.; disc: brown; margin: crenulate; **asci:** clavate, 8-spored; **ascospores:** ellipsoid, 12-16 x 6-9 µm; **Pycnidia:** not seen; **Spot tests:** upper cortex K+ yellow, C-, KC-, P+ yellow, UV-; medulla K-, C+ yellow-orange, KC+ yellow-orange, P-; **Secondary metabolites:** upper cortex with atranorin and chloroatranorin; medulla with barbatic and 4-*O* demethylbarbatic acids (major).

Substrate and ecology: on rocks, soil and bark in oak and pine forests; **World distribution:** throughout the neotropics, including the Carribean, and also in SE Asia; **Sonoran distribution:** fairly common in the Sierra Madre Occidental in Chihuahua.



Hypotrachyna protenta Hale, Smithson. Contr. Bot. 25: 58 (1975).

Illustration: Hale (1975), p. 57.

Thallus: foliose, 4-10 cm in diam., adnate to loosely adnate, subdichotomously lobate; **lobes:** sublinear, elon-

gate, convex, 0.5-2 mm wide, contiguous to somewhat imbricate; margin: entire; apices: subtruncate to subrotund, often convex; **upper surface:** whitish gray, smooth, shiny; pruina and maculae absent; isidia, soredia, pustulae and dactyls all absent; **medulla:** white with continuous algal layer; **lower surface:** black, tips brownish black; rhizines: sparse, black, dichotomous; **Apothecia:** usually present, laminal, substipitate, 2-8 mm diam.; disc: blackish brown; margin: smooth to crenulate; **asci:** clavate, 8-spored; **ascospores:** ellipsoid, 11-12 x 5-6 µm; **Pycnidia:** marginal, immersed; **conidia:** not seen; **Spot tests:** upper cortex K+ yellow, C-, KC-, P+ yellow, UV-; medulla K-, C-, KC+ red, P-; **Secondary metabolites:** upper cortex with atranorin and chloroatranorin; medulla with α-collatolic and alectoronic acids (major), ß-alectoronic (minor).

Substrate and ecology: on acidic rocks in open habitats lower montane to montane forests; **World distribution:** throughout the neotropics; **Sonoran distribution:** Sinaloa in the Sierra Madre Occidental.

Hypotrachyna pseudosinuosa (Asah.) Hale, Smithson. Contr. Bot. 25: 58 (1975).

Basionym: *Parmelia pseudosinuosa* Asah., J. Jap. Bot. 26: 329 (1951); Illustration: Hale (1975), p. 57.

Thallus: foliose, 2-9 cm in diam., closely adnate, subdichotomously to irregularly lobate; **lobes:** sublinear, elongate, plane to subconvex, separate, 1-4 mm wide; margin: entire but sometimes incised; apices: subtruncate to subrotund, plane to convex; **upper surface:** light gray, smooth to somewhat rugulose, dull, faintly maculate or emaculate, epruinose; **soredia:** farinose to slightly granular, in laminal to subterminal, capitate soralia that sometimes become confluent; isidia and dactyls absent**; medulla:** white with continuous algal layer; **lower surface:** black centrally, brown peripherally; rhizines: moderately common, black, dichotomous; **Apothecia:** rare, laminal, substipitate, 2-4 mm diam.; disc: brown; margin: smooth, esorediate; **asci:** clavate, 8-spored; **ascospores:** broadly ellipsoid to subglobose, 8-10 x 6-8 µm; **Pycnidia:** not seen; **Spot tests:** upper cortex K+ yellow, C-, KC-, P+ yellow, UV-; medulla K-, C± pink (depending on the concentration of gyrophoric acid), KC± pink, P+ red; **Secondary metabolites:** upper cortex with atranorin and chloroatranorin; medulla with protocetraric acid (major) and gyrophoric acid (trace or absent).

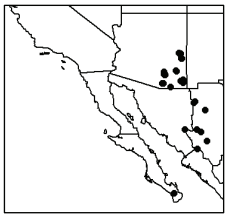
Substrate and ecology: on bark of hardwoods and pines in montane and upper montane forests; **World distribution:** neotropics (and extending to central Chile); **Sonoran distribution:** Sinaloa in the Sierra Madre Occidental.

Hypotrachyna pulvinata (Fée) Hale, Smithson. Contr. Bot. 25: 59 (1975).

Basionym: *Parmelia pulvinata* Fée, Essai crypt. ecor. exot. off. 123 (1824); Illustration: Hale (1975), p. 61.

Thallus: foliose, 4-12 cm in diam., adnate to tightly adnate, subdichotomously lobate; **lobes:** sublinear to subirregular, somewhat elongate, initially separate, becoming slightly imbricate, concave or plane, 1-2 mm wide, margin: entire; apices: subtruncate, plane; **upper surface:** whitish gray, smooth, shiny, white maculate; isidia, soredia, pustulae and dactyls all absent; **medulla:** white with continuous algal layer; **lower surface:** black, rhizines: dense, black, dichotomous; **Apothecia:** abundant, laminal, substipitate, 2-20 mm in diam.; disc: brown; margin: crenulate and white maculate; **asci:** clavate, 8-spored; **ascospores:** ellipsoid, 10-13 x 6-7 µm; **Pycnidia:** marginal or submarginal, immersed; **conidia:** not seen; **Spot tests:** upper cortex K+ yellow, C-, KC-, P+ yellow, UV-; medulla K-, C + red, KC + red, P-; **Secondary metabolites:** upper cortex with atranorin and chloroatranorin; medulla with evernic and lecanoric acids (both major).

Substrate and ecology: on hardwood bark, particularly smooth barked *Quercus* species, in montane and upper montane forests; **World distribution:** neotropics and extending into adjacent temperate areas; **Sonoran distribution:** SE and E Arizona and S along the Sierra Madre Occidental in Sonora, Chihuahua and Sinaloa and the mountains of southern Baja California Sur.



Notes: Particularly in SE Arizona and the northern part of the Sierra Madre Occidental this species is the most common *Hypotrachyna* at mid-elevations.

Hypotrachyna punoensis Kurok. & K. H. Moon, Bull. Bot. Gard. Toyama 5: 19 (2000).

Illustration: Kurokawa and Moon (2000), p. 20.

Thallus: foliose, 2.5-5 cm diam., adnate to loosely adnate, subdichotomously lobate; **lobes:** irregular, relatively short, plane, often imbricate, 2-5 mm wide; apices: subtruncate to subrotund; **upper surface:** medium to dark gray, smooth, shiny, emaculate; **soredia:** coarse, in submarginal to apical pustulae; isidia, and dactyls absent; **medulla:** white with continuous algal layer; **lower surface:** black, peripherally brownish black, shiny, often wrinkled; rhizines: sparsely to moderately dense, black, simple to rarely dichotomous; **Apothecia** and **ascospores:** not seen; **Pycnidia** and **conidia:** not seen; **Spot tests:** upper cortex K+ yellow, C-, KC-, P+ yellow, UV-; medulla K-, C-, KC-, P-; **Secondary metabolites:** upper cortex with atranorin and chloroatranorin; medulla with protolichesterinic acid (major) and lichesterinic acid (minor).

Substrate and ecology: usually on hardwood or pine bark in montane forests; **World distribution:** South and North America in Peru and Arizona; **Sonoran distribution:** southern Arizona.

Notes: Morphologically the species is similar to *H. costaricensis* which has a different fatty acid profile. In addition, the latter species has isidia whereas *H. punoensis* has sorediate pustules. Chemically the species was not originally characterized but is herein determined by J. A. Elix.

Hypotrachyna pustulifera (Hale) Skorepa, Phytologia 53: 445 (1974).

Basionym: *Parmelia pustulifera* Hale, Brittonia 24: 23 (1972); Illustration: Hale (1972), p. 23.

Thallus: foliose, 2-7 cm in diam., adnate to loosely adnate, subdichotomously lobate; **lobes:** sublinear, elongate, plane or convex, 2-7 mm wide; margin: entire; apices: subtruncate, plane to convex; **upper surface:** light gray, smooth, shiny, emaculate; **soredia:** in slightly excavated soralia of pustulae that initially may appear dactylate (but not isidia-like as in *H. dactylifera*); isidia absent; **medulla:** white with continuous algal layer; **lower surface:** black, shiny; rhizines: sparse, black, dichotomous; **Apothecia:** sparse, laminal, substipitate, 1-8 mm in diam.; disc: brown; margin: crenulate, sorediate; **asci:** clavate, 8-spored; **ascospores:** rare, ellipsoid, 11-12 x 6-7 µm; **Pycnidia:** marginal, immersed; **conidia:** not seen; **Spot tests:** upper cortex K+ yellow, C-, KC-, P+ yellow, UV-; medulla K-, C+ red, KC+ red, P-; **Secondary metabolites:** upper cortex with atranorin and chloroatranorin; medulla with lividic acid (major), colensoic, methoxycolensoic, 4-*O*-methylphysodic acids (all submajor), gyrophoric acids (minor), and physodic, oxyphysodic, norcolensoic and 4-*O*-methyllividic acids (all trace).

Substrate and ecology: on hardwood bark in lower montane to montane forests; **World distribution:** neotropics and southern USA; **Sonoran distribution:** in the mountains of SE Arizona.

Notes: In the Sonoran region this species may be confused with the more common *H. dactylifera* but that species has a different chemosyndrome, in which lividic acid is at most a trace as well as development of dactyls. Also the lobes of *H. pustulifera* are usually wider than those of *H. dactylifera*.

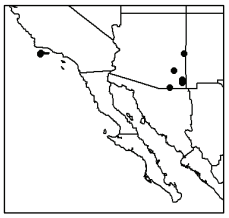
Hypotrachyna revoluta (Flörke) Hale, Smithson. Contr. Bot. 25: 60 (1975).

Basionym: *Parmelia revoluta* Flörke, Deutsche Lichenum 1: 11 (1815); Illustrations: Hale (1975), p. 61; Hale (1979), p. 83.

Thallus: foliose, 2-8 (-10) cm in diam., loosely adnate to adnate, irregularly lobate; **lobes:** sublinear to subirregular, often short, plane to convex, usually separate, rarely slightly imbricate, 1-4 mm wide; axils: often sinuous; margin: entire, rarely somewhat incised; apices subtrun-

cate to rounded, often revolute (especially when sorediate), convex to subascending, often black; **upper surface:** gray to greenish gray, smooth, shiny, faintly white maculate or emaculate; **soredia:** initially farinose, becoming granular, initially in subcapitate, subterminal soralia that become crateriform, excavated pustulae, with age becoming confluent and often eroded, white or greenish white; isidia and dactyls absent; **medulla:** white or off-white with continuous algal layer; **lower surface:** black, brownish towards apices; rhizines: sparse, black, sparsely dichotomous; **Apothecia:** very rare, sessile to substipitate, 2-6 mm in diam.; disc: brown; **asci:** clavate, 8-spored; **ascospores:** ellipsoid to broadly ellipsoid, 10-12 x 6-8 µm; **Pycnidia:** not seen; **Spot tests:** upper cortex K+ yellow, C-, KC-, P+ yellow, UV-; medulla K-, C+ red, KC+ red, P-; **Secondary metabolites:** upper cortex with atranorin and chloroatranorin; medulla with gyrophoric acids (major), 4, 5-di-*O*-methylhiascic acid, 5-*O*-methylhiascic acid (both minor), lecanoric and umbilicaric acids (both trace or absent).

Substrate and ecology: relatively rare, on acidic rock or bark in lower montane and upper montane forests; **World distribution:** neotropical and pantemperate (at least in regions adjacent to the tropics); **Sonoran distribution:** Channel Islands of California and montane areas of SE Arizona.



Note: This widespread species exhibits considerable morphological plasticity that requires further evaluation.

Hypotrachyna rockii (Zahlbr.) Hale, Smithson. Contr. Bot. 25: 62 (1975).

Basionym: *Parmelia rockii* Zahlbr., Annls. Mycol. 10: 379 (1912); Illustrations: Hale (1975), p. 61; Hale (1979), p. 83; Swinscow and Krog (1988), p. 121.

Thallus: foliose, 3-12 cm in diam., tightly adnate to adnate, subdichotomously to irregularly lobate; **lobes:** sublinear to somewhat subirregular, short to elongate, initially separate, becoming slightly imbricate, 1.5-5 mm wide; margin: entire, rarely lobulate; apices: subtruncate to subrotund, plane to subconvex; **upper surface:** whitish gray, smooth to slightly rugulose and occasionally becoming cracked centrally, shiny, often white maculate, becoming pruinose towards apices; **soredia:** initially farinose but soon granular, in laminal, crateriform, slightly excavated pustulae that sometimes become confluent; isidia and dactyls absent; **medulla:** white with continuous algal layer; **lower surface:** black with brownish apices, somewhat shiny; rhizines: sparse, black, dichotomous; **Apothecia:** rare, sparse, laminal, sessile to substipitate, 2-8 mm in diam.; disc: brown; margin: crenulate, sometimes sorediate; **asci:** clavate, 8-spored; **ascospores:** ellipsoid, 11-14 x 5-7 µm; **Pycnidia:** not seen; **Spot tests:** upper cortex K+ yellow, C-, KC-, P+ yellow, UV-; medulla K-, C+ red, KC+ red, P-; **Secondary metabolites:** upper cortex with atranorin and chloroatranorin; medulla with evernic acid (major) and lecanoric acids (minor to major).

Substrate and ecology: on bark (especially pines) in montane forests; **World distribution:** neotropics and East Africa in montane and upper montane forests; **Sonoran distribution:** Sinaloa in the Sierra Madre Occidental.

Hypotrachyna sublaevigata (Nyl.) Hale, Smithson. Contr. Bot. 25: 66 (1975).

Basionym: *Parmelia tiliacea* var. *sublaevigata* Nyl., Synop. meth. lich. 1: 383 (1860); Synonym: *Parmelia sublaevigata* (Nyl.) Nyl.; Illustration: Hale (1975), p. 64.

Thallus: foliose, 3-8 cm in diam., adnate to loosely adnate, subdichotomously lobate; **lobes:** subirregular, somewhat elongate, initially separate, becoming slightly imbricate, 2-5 mm wide; margin: entire; apices: subtruncate, plane to subconvex; **upper surface:** gray, smooth to shallowly rugulose, becoming cracked with age, dull, often white pruinose, emaculate; isidia, soredia, pustulae and dactyls all absent; **medulla:** white with continuous algal layer; **lower surface:** black, somewhat shiny; rhizines: dense, black, dichotomous; **Apothecia:** common, laminal, substipitate, 2-8 mm in diam.; disc: brown; margin: crenulate; **asci:** clavate, 8-spored; **ascospores:** broadly ellipsoid, 8-10 x 5-7 µm; **Pycnidia:** not seen; **Spot tests:** upper cortex K+ yellow, C-, KC-, P+ yellow, UV-; medulla K+ yellow to red, C-, KC-, P+ red; **Secondary meta-**

bolites: upper cortex with atranorin and chloroatranorin, medulla with salazinic acids (major), consalazinic acid (minor) and norstictic acid (trace).

Substrate and ecology: on hardwoods in montane oak and pine forests; **World distribution:** neotropics and ex tending into temperate regions of Chile; **Sonoran distribution:** Sierra Madre Occidental in Chihuahua and Sinaloa.

Hypotrachyna subpustulifera Elix, Mycotaxon 47: 108 (1993).

Illustration: Elix (1993b), p. 109.

Thallus: foliose, 2.5-4.0 cm in diam., tightly adnate to adnate, dichotomously to subirregularly lobate; **lobes:** linear, elongate, plane or convex, 0.5-1.0 mm wide, separate to subimbricate; margin: entire; apices: subtruncate to subrotund, plane to slightly convex; **upper surface:** light gray, smooth, shiny, emaculate; **pustules:** eroding, erumpent, becoming granular sorediate and exposing black lower cortex; dactyls and isidia absent; **medulla:** white with continuous algal layer; **lower surface:** black, shiny; rhizines: sparse, black, dichotomous; **Apothecia:** not observed; **Pycnidia** and **conidia:** not seen; **Spot tests:** upper cortex K+ yellow, C-, KC-, P+ yellow, UV-; medulla K- or K+ pale reddish, C -, KC + rose, P-; **Secondary metabolites:** upper cortex with atranorin and chloroatranorin; medulla with colensoic, 4-*O*-methylphysodic acids (both major), physodic acid (minor), lividic and oxyphysodic acids (both trace).

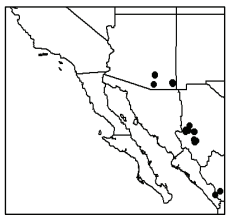
Substrate and ecology: on hardwood bark in lower montane to montane forests; **World distribution:** Australasia, neotropics (Brazil and Mexico) and South Africa; **Sonoran distribution:** Sinaloa, in the Sierra Madre Occidental.

Hypotrachyna subsaxatilis (de Lesd.) Hale, Smithson. Contr. Bot. 25: 68 (1975).

Basionym: *Parmelia subsaxatilis* de Lesd., Lich. Mexiq. 6 (1914); Illustration: Hale (1975), p. 67.

Thallus: foliose, 2-8 cm in diam., tightly adnate to adnate, subdichotomously lobate; **lobes:** sublinear to subirregular, somewhat elongate, plane, (0.5-) 1-3.5 mm wide; margin: entire; apices: subtruncate, plane; **upper surface:** gray to dark gray, smooth to rugose, becoming cracked with age, dull to shiny, epruinose, white maculate; isidia, soredia, pustulae and dactyls all absent; **medulla:** white with continuous algal layer; **lower surface:** black, somewhat shiny; rhizines: sparse, black, dichotomous; **Apothecia:** abundant, laminal, sessile to substipitate, 1.5-5 mm in diam.; disc: brown; margin: crenulate; **asci:** clavate, 8-spored; **ascospores:** broadly ellipsoid, 11-15 x 7-9 µm; **Pycnidia:** marginal, immersed; **conidia:** not seen; **Spot tests:** upper cortex K+ yellow, C-, KC-, P+ yellow, UV-; medulla K+ yellow to red, C-, KC-, P+ red; **Secondary metabolites:** upper cortex with atranorin and chloroatranorin; medulla with salazinic acids (major), consalazinic acid (minor) and norstictic acid (trace).

Substrate and ecology: on acidic rocks or on soil over rocks, frequently in canyons on relatively open boulders and cliff faces in montane and upper montane forests; **World distribution:** Central America north to southern Arizona; **Sonoran distribution:** SE Arizona and S along the Sierra Madre Occidental in Chihuahua and Sinaloa.



Note: In the northern part of its range the species is somewhat more narrow lobed.

IMSHAUGIA

by B. D. Ryan

Imshaugia S. L. F. Meyer, Mycologia 77: 337 (1985).

Family: Parmeliaceae; Type: *Imshaugia aleurites* (Ach.) S. F. Meyer; No. species: three world-wide; Selected lit.: Meyer (1985), Elix (1994f), and Hinds (1999).

Life habit: lichenized; **Thallus:** foliose, adnate to loosely adnate, appressed, 2-8 (-12) cm diam., rosette-forming, lobate; **lobes:** ± radiating, irregular, 0.5-1.5 (-2.5) mm wide, linear to rounded, discrete or contiguous and imbricate; margins wavy to somewhat dissected, apices subrotund, without cilia; **upper surface:** ashy whitish gray (becoming cream-colored in herbarium) to greenish gray, sometimes becoming brownish, dull and slightly arachnoid or pruinose under strong magnification (x 50), becoming smooth and somewhat shiny toward periphery, sometimes wrinkled or shallowly pitted towards center; without pseudocyphellae or maculae; with or without isidia (occasionally also becoming sorediate); **upper cortex:** paraplectenchymatous, 10-20 µm thick, covered by a pored epicortex; **medulla:** white, forming an irregular layer; cell walls containing *Cetraria*-type lichenan (I+ blue); **photobiont:** primary one a chlorococcoid alga (*Trebouxia* or *Myrmecia*), secondary photobiont absent; **lower cortex:** similar in thickness and structure to upper one; **lower surface:** white to light brown; rhizines: scattered and sparse to moderately dense or dense, usually rather short, concolorous with lower surface, simple, tufted or not, extending to the margins but rarely on the margins themselves; **Ascomata:** apothecial, mostly laminal, rather large, to 7 (-12) mm diam., adnate to sessile or short-pedicellate,with a thalline margin concolorous with thallus; disc: round, ± concave, imperforate, light brownish yellow to yellowish brown or dark brown; true exciple: gray or hyaline; epihymenium: brown or ochraceous-yellowish; ostiolar filaments absent; hymenium: hyaline, with simple or rarely branched paraphyses; hypothecium: hyaline or tinted brown; **asci:** clavate, *Lecanora*-type, unitunicate; tholus I+ blue, 8-spored; **ascospores:** ellipsoid, obtuse at the poles, straight, simple, 4-6 (-9) x 3-4 (-6) µm, wall hyaline, thin, smooth, without distinct endospore thickening, I-; **Conidiomata:** pycnidial, laminal and marginal, to 0.2 mm diam., emergent, globose, black; conidiophores *Psora*-type; **conidia:** ampulliform or occasionally bifusiform (3-) 4-5 (-6) x (0.5-) 1 (-1.5) µm; **Secondary metabolites:** cortex atranorin and chloroatranorin; medulla with ß-orcinol depsides or orcinol depside; **Geography:** circumpolar, temperate-boreal in the Northern Hemisphere; also known from Australia; **Substrate:** usually on bark or wood of conifers.

Notes: It is distinguished from most other parmelioid genera by its conidiophore type, and by its narrow, often strap-shaped, and ± appressed lobes. It was segregated from *Parmeliopsis* on the basis of its emergent and partly marginal pycnidia, its short, ellipsoid spores and its short, lageniform to bifusiform conidia; *Imshaugia* is also distinguished from that genus by its consistently pale lower surface, lack of soredia (at least without first developing isidia), content of lichenan rather than isolichenan in the cell walls, and presence of thamnolic acid (P+) rather than divaricatic acid (P-) in the medulla. Nomenclatural and taxonomic history of *Parmeliopsis* (syn. *Foraminella*) and *Imshauga* is complex and has led to incorrect or misleading information in the literature (Hinds 1999). Both of the species occurring in the Sonoran Region exhibit extremes of morphology and color as annotated by Meyer.

Key to species of ***Imshaugia*** in the Sonoran region:

1. Thallus bearing isidia and/or soredia; apothecia usually rare ..... ***I. aleurites***
1. Thallus not bearing isidia or soredia; apothecia common ..... ***I. placorodia***

The Species

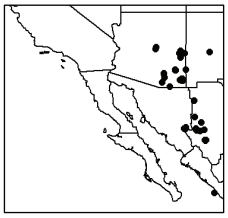
Imshaugia aleurites (Ach.) S. L. F. Meyer, Mycologia 77: 338 (1985).

Basionym: *Lichen aleurites* Ach., Lich.. suec. prodr.: 117 (1798); Synonym: *Parmeliopsis aleurites* (Ach.) Nyl.; Il-

lustrations: Hale (1979), p. 110; Meyer (1982, fig. 9 [conidia]); Thomson (1984), p. 322; Goward et al. (1994), p. 63, Wirth (1995), p. 435; Hinds (1999), figs. 5-6.

Thallus: foliose, adnate to loosely adnate, appressed, orbicular, (2-) 3-8 (-12) cm diam., often rather randomly arranged; **lobes:** usually 1-4 mm long, 0.5-1.5 mm broad, flat, linear to sublinear, divergent to contiguous or crowded and overlapping, sometimes quite dissected, irregularly (± pinnately) branched, tips rounded, often forked; **upper surface:** whitish mineral gray, light gray or bluish gray, or in some thalli becoming darker and distinctly greenish or brownish, sometimes wrinkled or shallowly pitted in older parts, continuous to faintly rimulose; lobe tips shiny, becoming rough with incipient isidia; **isidia:** laminal, abundant, cylindrical, simple to branched, to *c.* 2 mm tall, usually with warty tips, grayish- or yellowish-brown, to brown-black and shiny at tips, often breaking, rarely becoming granulose and coalescing to form a paler gray or greenish sorediate-isidiate mass; **medulla:** white; algal layer with *Trebouxia*; **lower surface:** white to cream-color or pale brownish, somewhat wrinkled; rhizines: sparse to dense, brownish or darkening, simple, *c.* 0.5-1 mm long, sometimes short and wart-like; **Apothecia:** occasional, 2-7 mm diam., flat, saucer-shaped, adnate; disc: pale gray or brownish or reddish brown, dull, epruinose; thalloid margin persistent, entire or breaking up into isidia; **ascospores:** ellipsoid, (5-) 6 (-9) x (3.5-) 4 (-6) µm; **Pycnidia:** rare, small, black, at or near margins of lobes, up to 0.1 mm diam.; **conidia:** 3-4 x 1 µm; **Spot tests:** upper cortex and medulla K+ deep yellow, C-, KC-, P+ deep yellow, orange, or reddish, UV-; **Secondary metabolites:** upper cortex with atranorin and chloroatranorin; medulla with thamnolic acid (major) and decarboxythamnolic acid (trace).

Substrate and ecology: on bark of conifers and on dead stumps in open pine-oak woodlands and mixed conifer forests, sometimes in ravines or near streams, occasionally on broad-leaved trees and shrubs, sometimes on old wood, rarely on rocks; **World distribution:** circumpolar, boreal, montane; in North America, Europe, Asia, Australasia; **Sonoran distribution:** Arizona, Chihuahua, Sonora and Sinaloa, at 1300-3000 m.



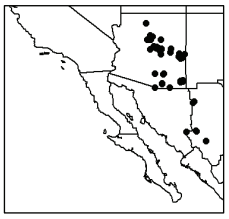
Notes: Somewhat similar species include *Parmelinopsis minarum* and *P. horrescens*, both of which have dark lower surfaces and sparse cilia, *Heterodermia granulifera*, which has a dull, fibrous upper surface, pustular isidia, and a K+ red medulla, and *Myelochroa obsessa,* which has a pale yellowish medulla and sparse cilia. All of these species have different secondary metabolite profiles from either *Imshaugia* species.

Imshaugia placorodia (Ach.) S. L. F. Meyer, Mycologia 77: 338 (1985).

Basionym: *Parmelia placorodia* Ach., Syn. Meth. Lich.: 196 (1814); Synonym: *Parmeliopsis placorodia* (Ach.) Nyl.; Illustrations: Hale (1979), p. 116; Meyer (1982), fig. 7 [ascospores]); Hinds (1999), fig. 7.

Thallus: foliose, adnate throughout or loosely adnate and marginally ascending, 2-4 cm broad; **lobes:** somewhat randomly to ± regularly arranged, contiguous to crowded or overlapping, narrow, 0.5-1 (-1.5) mm wide, strap-shaped to rounded, branched, sometimes quite dissected, margins deeply wavy to pinnate-cleft, tips often forked or dissected; **upper surface:** whitish gray-green or ashy or darkening, smooth or becoming wrinkled toward center, somewhat shiny where smooth; **medulla:** white, algal layer with *Myrmecia*; **lower surface:** whitish to pale brown, somewhat wrinkled; rhizines scattered, brownish to brown; **Apothecia:** usually present and often numerous and almost hiding thallus surface, often much wider than the lobes, 1.5-7 (-12) mm diam., sessile to shortly pedicellate, saucer-shaped; disc: concave to convex, yellowish to pale brown or chestnut brown to dark grayish brown, dull or slightly shiny, concolorous with thallus, or darker and browner next to the disc when young, raised or level, crenulate, persistent; **ascospores:** subspherical to broadly ellipsoid, (5-) 6.5 (-8) x (3.5-) 4.5 (-6) µm; **Pycnidia:** usually common, laminal or marginal; **Spot tests:** cortex K+ yellow, C-, KC-, P-, medulla K+ deep yellow, C-, KC-, P+ deep yellow or orange, UV-; **Secondary metabolites:** upper cortex with atranorin and chloroatranorin; medulla with thamnolic acid (major) and decarboxythamnolic acid (trace).

Substrate and ecology: on conifer (rare on oak) bark, less often dead branches, in oak-pine-cypress and pine-oak woodlands and forests; **World distribution:** eastern North America, central and southern Rocky Mountains, and northern plains; **Sonoran distribution:** widely distributed and common in Arizona, Chihuahua, and Sonora, at 1600-3000 m.



Notes: A somewhat similar species is the larger *Heterodermia hypoleuca*, but that species has a cottony, noncorticate lower surface and lacks thamnolic acid.

JULELLA

by A. Aptroot

Julella Fabre, Ann. Sci. Nat. Bot. ser. 6, 9: 113 (1879).

Family: Xanthopyreniaceae; Type: *Julella buxi* Fabre; No. species: *c.* four world-wide; Selected lit.: Aptroot and van den Boom (1995), Barr (1990), and Harris (1995).

Life habit: non-lichenized, saprophytic, or possibly facultatively lichenized; **Thallus:** superficially absent but within the substrate; **photobiont:** absent or possibly facultatively *Trentepohlia*, secondary photobiont absent; **Ascomata:** perithecial, circular to ellipsoid in outline; **involucrellum:** present, dark, usually laterally spreading, composed of compacted hyphae and bark cells; **ascomatal wall:** greenish or brown, K+ greenish, N-, black, not continuous below the hamathecium; **asci:** bitunicate, clavate, with tholus, non-amyloid, inner wall thickened towards the apex, ± with a shallow, broad ocular chamber; **hamathecium:** richly branched pseudoparaphyses, anastomosing above the asci, non-amyloid; **ascospores:** hyaline, ellipsoid to clavate, muriform with eusepta, 7-22 x 13-65 µm; walls: not ornamented; **Conidiomata:** pycnidial, black; **conidia:** bacilliform, simple, colorless; **Secondary metabolites:** none detected; **Geography:** mostly subtropical; **Substrate:** on bark.

Notes: For the species concept in the genus *Julella* the publication of Aptroot and van den Boom (1995) is followed. The much narrower species concept proposed by Harris (1995) was tested with the specimens from the Sonoran Desert and found not to be adequate. In the latter species concept much emphasis is laid on the ascus shape and the ascospore arrangement, two very variable characters, even within a single ascoma. The genus is characterized by branched pseudoparaphyses, which are anastomosing above the asci and muriform ascospores. All accepted species are either non-lichenized bark saprophytes or possibly facultatively lichenized.

Key to the species of ***Julella*** from the Sonoran region:

1. Ascospores 2-6 per ascus, 22-28 x 9-13 µm; ascocarps usually over 0.5 mm diam; thallus dull, white ***J. lactea***
1. Ascospores 8 per ascus 2
   2. Ascospores usually less than twice as long as broad, 14-18 x 6-9 µm; ascocarps up to 0.5 mm diam; thallus often shiny, silvery ..... ***J. sericea***
   2. Ascospores usually over twice as long as broad, 25-40 x 8-13 µm; ascocarps over 0.5 mm diam; thallus dull, white ..... ***J. vitrispora***

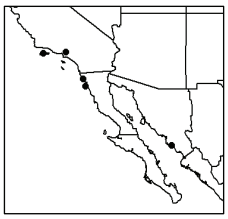
The Species

Julella lactea (A. Massal.) M. E. Barr, Sydowia 38: 13 (1986).

Basionym: *Blastodesmia lactea* Massal., Ric. auton. lich. crost.: 182 (1852); Synonyms: *Polyblastiopsis lactea* (A. Massal.) Zahlbr. and *Pyrenula lactea* (A. Massal) Tuck.; Illustrations: Barr (1990), p. 57; Harris (1973), p. 60 as *Polyblastiopsis lactea*.

Thallus: continuous, immersed in the substrate; **upper surface:** whitish, smooth dull; **photobiont:** absent; **Perithecia:** hemispherical, black, semi-immersed in the thallus, *c.* 0.4-1 mm diam.; **involucrellum:** dark brown; exciple thin, pale brown **ascomatal wall:** black, absent below the hamathecium; **hamathecium:** branched pseudoparaphyses, anastomosing above the asci; filaments: *c.* 1 µm wide, not inspersed with oil droplets; **asci:** cylindrical to clavate, *c.* 70-90 x 20-23 µm, thick-walled, with 2-6, irregularly arranged ascospores; **ascospores:** hyaline, long ellipsoid to clavate, densely muriform, 22-28 x 9-13 µm; walls: not ornamented, with a *c.* 2-4 µm wide gelatinous sheath; **Pycnidia:** not seen; **Spot tests:** all negative, UV negative; **Secondary metabolites:** none detected.

Substrate and ecology: on bark of various woody plants, including *Euphorbia* and *Rhus*; **World distribution:** pantropical or possibly nearly cosmopolitan; **Sonoran distribution:** collected several times in California (including the Channel islands), Baja California and in Sonora.

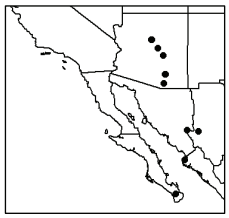


Julella sericea (A. Massal.) Coppins, in Coppins, P. James and D. Hawksw., Lichenologist 24: 367 (1992).

Basionym: *Polyblastia sericea* A. Massal., Symmict. lich.: 99 (1855); Synonym: *Polyblastiopsis fallaciosa* (Stizenb.) R. C. Harris; Illustration: Harris (1973), p. 60 as *Polyblastiopsis fallaciosa*.

Thallus: continuous, effuse, immersed in the substrate; **upper surface:** pale gray or yellowish gray, glossy, smooth; **photobiont:** absent; **Perithecia:** hemispherical, black, semi-immersed in the thallus, *c.* 0.2-0.5 mm diam.; **involucrellum:** dark brown; true exciple: 200-400 µm diam. **ascomatal wall:** black, absent below the hamathecium; **hamathecium:** branched pseudoparaphyses, anastomosing above the asci; filaments: *c.* 1 µm wide, not inspersed with oil droplets; **asci:** clavate, thick-walled, *c.* 70-100 x 17-23 µm, with 8, irregularly arranged ascospores; **ascospores:** hyaline, long ellipsoid to narrowly ovoid, submuriform, 14-20 x 6-10 (15-25 x 10-15 excluding perispore - in Purvis et al. [1992]) µm; walls: not ornamented, without or with a *c.* 2-3 µm wide gelatinous sheath; **Pycnidia:** black; **conidia** bacilliform, 8-10 x 1-1.5 mu; **Spot tests:** all negative, UV negative; **Secondary metabolites:** none detected.

Substrate and ecology: on bark of various woody plants, mostly on *Abies, Acer* and *Quercus*; **World distribution:** pantropical or possibly nearly cosmopolitan; **Sonoran distribution:** common in southern Arizona, furthermore collected in Chihuahua, Sinaloa and Baja California Sur.

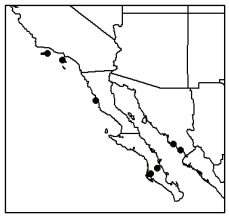


Julella vitrispora (Cooke & Harkness) M. E. Barr, Sydowia 38: 13 (1986).

Basionym: *Pleospora vitrispora* Cooke and Harkness, Grevillea 9: 86 (1881); Synonym: *Julella sublactea* (Nyl.) R. C. Harris; Illustration: Tucker and Harris (1980), p. 11 as *Polyblastiopsis sublactea*.

Thallus: continuous, immersed in the substrate; **upper surface:** whitish, dull, smooth; **photobiont:** absent; **Perithecia:** hemispherical, black, semi-immersed in the thallus, *c.* 0.5-1 mm diam.; **involucrellum:** dark brown; exciple: thin; **Ascomatal wall:** black, absent below the hamathecium; **hamathecium:** branched pseudoparaphyses, anastomosing above the asci; filaments: c. 1 µm wide, not inspersed with oil droplets; **asci:** clavate, *c.* 70-100 x 20-25 µm, thick-walled, with 8, irregularly arranged ascospores; **ascospores:** hyaline, long ellipsoid to broadly fusiform, densely muriform, 25-40 x 8-13 µm; walls: not ornamented, without or with a *c.* 2-4 µm wide gelatinous sheath; **Pycnidia:** not seen; **Spot tests:** all negative, UV negative; **Secondary metabolites:** none detected.

Substrate and ecology: on bark of various woody plants, including *Salvia, Jatropha, Lonicera, Quercus, Bursera*; **World distribution:** pantropical or possibly nearly cosmopolitan; **Sonoran distribution:** rather common; recorded from California (including the Channel



Islands), Baja California Sur and Sonora.

KAERNEFELTIA

by A. Thell

Kaernefeltia Thell & Goward, Bryologist 99: 125 (1996).

Family: Parmeliaceae; Type: *Kaernefeltia californica* (Tuck.) Thell & Goward; No. species: two world-wide; Selected lit.: Thell and Goward (1996) and Kärnefelt (1980 & 1986).

Life habit: lichenized; **Thallus:** terete-foliose, decumbent or caespitose; **lobes:** rather broad to narrow, *c.* 0.5-11.0 mm wide; apices: rounded to fusiform, eciliate; **upper surface:** pale olive brown to greenish black, rather smooth to rough, occasionally ridged or knobby, rather shiny to dull, occasionally pruinose; isida: sometimes present, flattish, with white cortex; soredia and lobules: absent; pseudocyphellae: sparse, indistinct and immersed; **upper cortex:** non-pored epicortex, prosoplectenchymatous; **medulla:** white, loosely packed; **photobiont:** primary one a *Trebouxia*, secondary photobiont absent; **lower cortex**: present or absent; **lower surface:** pale brown, attached by simple black rhizines; cyphellae, pseudocyphellae and tomentum: absent; **Apothecia:** frequent, marginal to laminal, at first concave, later becoming convex, pedicellate; margin: prominent with thalloid rim; disc: imperforate, dark olivaceous brown; exciple: hyaline; epithecium: brown or brownish yellow; hypothecium: hyaline; **asci:** lecanoral, wall layers apex thickened; apex: amyloid, with wide axial body divergent towards apex; 8-spored; **ascospores:** simple, ellipsoid to broadly ellipsoid, 6-10.5 x 2.5-5 µm; walls: thin, hyaline, not amyloid; **Conidiomata:** pycnidial, laminal or marginal, immersed or emergent sessile; **conidia:** bifusiform, 5-7 x 1 µm; **Secondary metabolites:** fatty acids; lichesterinic and protolichesterinic acids and 2-3 other low-Rf fatty acids in the medulla; **Geography:** hypermaritime or temperate /boreal areas of western North America and low to intermediate elevations in Spain; **Substrate:** bark or wood.

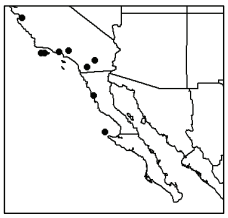
Notes: A lower cortex is only present in *K. merrillii*. Potentially the second species of *Kaernefeltia* may be found in the Sonoran region as it is known from farther north in California.

The Species

Kaernefeltia merrillii (Du Rietz) Thell & Goward, Bryologist 99: 128 (1996).

Basionym: *Cetraria merrillii* Du Rietz; Synonym: *Tuckermannopsis merrillii* (Du Rietz) Hale; Illustrations: Thell and Goward (1996), pp. 127 & 128; McCune and Geiser (1997), p. 53; Brodo et al. (2001), p. 366.

Thallus: foliose, rarely subfruticose, decumbent; **lobes:** rather broad to narrow, *c.* 0.5-11.0 mm wide; apices: rounded to fusiform, eciliate; **upper surface:** olive-brown to greenish black, rough and occasionally ridged or foveolate, usually dull, occasionally pruinose; **cortex:** strongly white, prosoplechtenchymatous; **isidia:** sometimes present, flattened; soralia and lobules: absent; pseudocyphellae: sparse, indistinct, immersed; **medulla:** white, loosely packed; photobiont: a *Trebouxia*; **lower surface:** pale brown, attached by simple, black rhizines; **Apothecia:** frequent, marginal to laminal on thallus, at first concave, later becoming convex, pedicellate; margin: prominent, with thalloid rim; disc: imperforate, dark olivaceous brown; exciple: hyaline; epithecium: brown or brownish yellow; hypothecium: hyaline; **asci:** clavate, lecanoral, 8-spored; **ascospores:** simple, ellipsoid to broadly ellipsoid, 6-10.5 x 2.5-5 µm; walls: thin, hyaline, not amyloid; **Pycnidia:** laminal or marginal, immersed or emergent and sessile; **conidia:** bifusiform, 5-7 x 1 µm; **Spot tests:** all negative; **Secondary metabolites:** cortex



with an unknown pigment, medulla with lichesterinic and protolichesterinic acids and 2-3 other low-R_f fatty acids.

Substrate and ecology: bark or wood; **World distribution:** temperate/boreal areas of western North America from low altitudes to alpine areas and at intermediate altitudes in central Spain; **Sonoran distribution:** chaarral areas of Baja California and southern California.

KIRSCHSTEINIOTHELIA

by A. Aptroot

Kirschsteiniothelia D. Hawksw., Bot. J. Linn. Soc. 91: 182 (1985).

Family: Pleosporaceae; Type: *Kirschsteiniothelia aethiops* (Berk. & M. A. Curtis) D. Hawksw. No. species: *c.* 10 world-wide; Selected lit.: Aptroot (1995b), and Hawksworth (1985a).

Life habit: non-lichenized, saprophytic; **Thallus:** endosubstratic to absent, or a superficial subiculum (a net-like array of hyphae under the perithecia); **photobiont:** absent; **Ascomata:** perithecial, usually arising singly, scattered or loosely aggregated, erumpent, ± superficial when mature, usually with an applanate base; **involucrellum:** absent; **ascomatal wall:** black, conspicuously cellular (pseudoparenchymatous), continuous and built-up of specialized large cells, which are in part radially arranged below the hamathecium (in the corners); **hamathecium:** branched pseudoparaphyses, cellular, anastomosing above the asci, non-amyloid or rarely amyloid; **asci:** bitunicate, fissitunicate, cylindrical, with tholus, non-amyloid, 4 (-8)-spored; **ascospores:** blackish brown, ellipsoid to clavate, 1-septate with one euseptum, 12.5-55 x 5.5-20 µm; walls: sometimes ornamented with tiny warts; **Conidiomata:** hyphal; **conidia:** brown, septate, formed on the subiculum; **Secondary metabolites:** absent; **Geography:** mostly temperate; **Substrate:** mostly on bark but also frequently on wood.

Notes: The genus is characterized by the blackish brown, 1-septate ascospores and the wide, large-cellular exciple. In many respects the genus is similar to *Peridiothelia* (see Table 1, p. 51 in Hawksworth (1985b), but the pseudoparenchyma of the exciple are substantially smaller in *Peridiothelia* and its center is I+ blue (versus I- in *Kirschsteiniothelia*). The hyphomycete anamorphs known for *Kirschsteiniothelia* are not known in *Peridiothelia*.

Key to the species of ***Kirschsteiniothelia*** from the Sonoran region:

1. Ascospores up to 25 µm long; thallus immersed in the bark, only indicated by a shiny area ..... ***K. recessa***
1. Ascospores over 25 µm long; thallus consisting of dark brown to black hyphae with nodular to globose cells, belonging to the *Dendryphiopsis* anamorph 2

2. Ascospores 26-34 x 9-13 µm, ornamented with tiny warts, without a gelatinous sheath ..... ***K. aethiops***
2. Ascospores 35-55 x 12-16 µm, not ornamented, with a 3-5 µm wide gelatinous sheath ..... ***K. thujina***

The Species

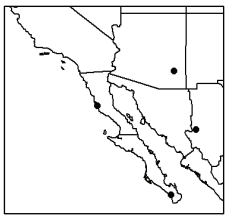
Kirschsteiniothelia aethiops (Berk. & M. A. Curtis) D. Hawksw., Bot. J. Linn. Soc. 91: 185 (1985).

Basionym: *Sphaeria aethiops* Berk. & M.A. Curtis, Grevillea 4: 143 (1876); Synonym: *Microthelia micula* (Flot.) Körb. auct. and see Hawksworth (1985a); Illustrations: Hawksworth (1985a), pp. 186, 188-9 & 191.

Thallus: consisting of superficial hyphae (subiculum), dark brown to black; **photobiont:** absent; **Perithecia:** arising singly or in small groups, hemispherical, black, semi-immersed in the subiculum, 0.2-0.4 mm diam., base slightly or strongly applanate; **ascomatal wall:** black, continuous below the hamathecium, with elongated cells

in the corners (lophiostomoid); **hamathecium:** branched pseudoparaphyses, cellular, persistent, anastomosing above the asci; filaments: *c.* 1 µm wide, not inspersed with oil droplets; **asci:** clavate, *c.* 70-95 x 13-18 µm, with 8, irregularly arranged ascospores; **ascospores:** blackish brown, pyriform, 1-septate with a slightly submedian euseptum, 26-34 x 9-13 µm; walls: ornamented with tiny warts, without a gelatinous sheath; **Spot tests:** all negative, UV negative; **Secondary metabolites***:* none detected.

Substrate and ecology: on bark and wood of various woody plants, e.g. *Alnus* and *Bursera*. Also on *Cactaceae*, from which substrate it was first reported from the Sonoran Desert (Aptroot 1997); **World distribution:** pantropical or possibly nearly cosmopolitan; **Sonoran distribution:** collected in southern Arizona, Baja California, Baja California Sur and Chihuahua.



Kirschsteiniothelia recessa (Cooke & Peck) D. Hawksw., J. Linn. Soc., Bot. 91: 195 (1985).

Basionym: *Sphaeria recessa* Cooke & Peck, New York State Bot. Rep. 29: 61 (1878); Illustrations: Hawksworth (1985a), pp. 194, 196 & 197.

Thallus: continuous, smooth, immersed in the substrate, whitish; **photobiont:** absent; **Perithecia:** arising singly or more often in small groups, hemispherical, black, semi-immersed in the thallus, 0.3-0.5 mm diam, base slightly rounded or applanate; **ascomatal wall:** black, continuous below the hamathecium, with elongated cells in the corners (lophiostomoid); **hamathecium:** branched pseudoparaphyses, cellular, persistent, anastomosing above the asci; filaments: *c.* 2 µm wide, in a gelatinous matrix, not inspersed with oil droplets; **asci:** clavate, *c.* 50-60 x 15-25 µm, with 8, irregularly arranged ascospores; **ascospores:** blackish brown, pyriform, 1-septate with a submedian euseptum, 14-18 x 7-9 µm; walls: not ornamented, with a *c.* 2-3 µm wide gelatinous sheath; **Spot tests:** all negative, UV negative; **Secondary metabolites:** none detected.

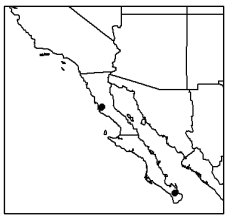
Substrate and ecology: on bark of unknown woody plant; **World distribution:** known from temperate North America, possibly nearly endemic; **Sonoran distribution:** only collected once in southern Arizona.

Kirschsteiniothelia thujina (Peck) D. Hawksw., Bot. J. Linn. Soc. 91: 198 (1985).

Basionym: *Sphaeria thujina* Peck, New York State Bot. Rep. 27: 110 (1875); Illustrations: Hawksworth (1985a), pp. 199 & 200.

Thallus: consisting of superficial hyphae (subiculum), dark brown to black; **photobiont:** absent; **Perithecia:** arising singly or in small groups, hemispherical, black, semi-immersed in the thallus, *c.* 0.3-0.5 mm diam., base applanate; **ascomatal wall:** black, continuous below the hamathecium, with elongated cells in the corners (lophiostomoid); **hamathecium:** branched pseudoparaphyses, cellular, persistent, anastomosing above the asci; filaments: *c.* 1 µm wide, not inspersed with oil droplets; **asci:** clavate, *c.* 90-130 x 15-25 µm, with 8, irregularly arranged ascospores; **ascospores:** hyaline, clavate to narrowly ellipsoid, 1-septate with a supramedian euseptum, 35-55 x 12-16 µm; walls: not ornamented, with a *c.* 3-5 µm wide gelatinous sheath; **Spot tests:** all negative, UV negative; **Secondary metabolites:** none detected.

Substrate and ecology: on bark and wood of various woody plants, including *Idria* and *Quercus*; **World distribution:** so far known from wood in Canada and northern U.S.A.; **Sonoran distribution:** on *Idria* and *Quercus* in Baja California and in Baja California Sur.



KOERBERIA

by R. Schoeninger

Koerberia A. Massal., Geneac.Lich.: 6 (1854).

Family: Placynthiaceae s.l.; Type: *Koerberia biformis* A. Massal.; No. species: two world-wide; Selected lit: Henssen (1963b), Magnusson (1954), and Nimis (1993).

Thallus foliose, rosette-shaped, lobate; **lobes:** stellately radiating, becoming striate; **upper surface:** dark olive green, composed of only one or two discontinuous layers of cells (not a real cortex); with or without isidia or lacinae, soredia absent; **photobiont:** primary one a filiform cyanobacterium (*Scytonema*), commonly with intercalary heterocysts, secondary photobiont absent; **lower surface:** pale olive, pseudoparenchymatous with short celled longitudinally extended hyphae; **Ascomata:** apothecial, usually deep red-brown, sessile, with a thalline margin or proper margin formed by a pseudoexciple; hymenium: generally 50-100 µm, I+ deep blue; paraphyses: simple or sparsely branched, end cells thickened; **ontogeny:** hemiangiocarpic; **asci:** cylindrical or clavate, with apically thickened wall, 8-spored; **ascospores:** simple or once septate at maturity, colorless, ellipsoid, fusiform or acicular; **Conidiomata:** pycnidial, laminal, ostiole brown; **conidia:** rod-shaped, produced laterally and/or terminally; **Secondary metabolites:** none detected; **Geography:** southern and SW Europe, northern Africa as well as SW North America; **Substrate:** on moist siliceous rocks or on the bark of trees in somewhat closed woodland.

Notes: The distinctive olive-green color separates *Koerberia* from small *Collema* or *Leptogium* species.

Key to the species of ***Koerberia*** from the Sonoran region:

1. Thallus isidiate, on bark; spores spirally twisted within asci ..... ***K. biformis***
1. Thallus laciniate, on acidic rocks; spores not twisted within asci ..... ***K. sonomensis***

The Species

Koerberia biformis A. Massal., Genera Lich.: 6 (1854).

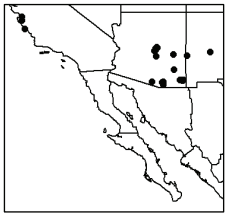
Illustrations: Henssen (1963b) pp.1356 & 1358 and below

Fig. 55. *Koerberia biformis*, photo by R. Schoeninger.

Thallus: small foliose, forming small rosettes, 0.5-2.0 (3.0) cm in diam.; **lobes:** elongate, up to 2 mm long, 0.3-0.5 mm wide, stellately radiating, 0.2-0.8 mm wide at apex (group of lobe tips); **upper surface:** dark olive-green, smooth to slightly grooved; **isidia:** ± developing laminally, cylindrical and erect, up to 1 mm tall and *c.* 0.1 mm thick, present especially in older thalli; **laciniae:** not present; **lower surface:** pale olive, with tuffs of pale rhizines; **Apothecia:** frequent, deep red-brown, soon convex, 0.4-1 (-1.5) mm in diam.; proper margin: formed by a pseudoexciple (35-60 µm wide); hymenium: upper part brown and below hyaline, 65-100 µm high; subhymenium: colorless and partly pseudo-parenchymatous, 40-70 µm thick; **asci:** 32-52 x 6-11.5 µm, 8-spored; **ascospores:** spirally twisted within ascus, acicular to slightly curved, colorless, simple, (32-) 43-55 x 1.5-2 (-3) µm; **Pycnidia:** laminal, pyriform, 0.2-0.3 µm in diam.; ostiole: brown; **conidia:** rod-shaped, 4.5-6 x 1 µm; **Spot**

tests: all negative; **Secondary metabolites:** none detected.

Substrate and ecology: on bark, particularly oak species in moist to open woodlands at intermediate elevations; **World distribution:** western North America (CA, AZ, NM and Mexico) and Mediterranean areas of Europe (Italy); **Sonoran distribution:** common and inconspicuous in eastern and SE Arizona and coastal mountain ranges of California, rarer in the Sierra Madre Occidental region as far south as Durango.



Koerberia sonomensis (Tuck.) Henssen, Canad. J. Bot. 41: 1351 (1963).

Basionym: *Pannaria sonomensis* Tuck., 1877, Proc. Am. Acad. Arts Sci., 12:166-185 (1877); Synonyms: *Placynthium sonomense* (Tuck.) Herre, *Parmeliella sonomensis* (Tuck.) Hasse, *Koerberia orthospora* Couderc, *Koerberia lusitanica* J. P. Samp. and *Tingipsidium pubescens* Werner; Illustrations: Henssen (1963b), pp. 1355-1358; and Fig. 56 to right.

Thallus: small foliose, forming 0.5-1 cm wide rosettes with elongate lobes; **lobes:** up to 2 mm long, *c.* 0.1-0.3 (-0.5) mm wide, stellately radiating, 0.1-0.3 (-1.0) mm wide at apex; **upper surface:** dark olive-green, sometimes becoming striate; isidia absent; **laciniae:** up to 1.5 mm long, up to 0.1 mm wide, usually flattened, prostrate or erect, pale on one side; **lower surface:** pale olive, with tufts of pale rhizines; **Apothecia:** deep red-brown, flat or slightly convex, 0.4-0.6 mm in diam.; pseudoexciple: ± pseudoparenchymatous, 60-160 µm wide; hymenium: upper part brown and below hyaline, 55-100 µm high; subhymenium: colorless and partly pseudoparenchymatous, 70-160 µm thick; **asci:** 9-11.5 x 35-66 µm, 8-spored; **ascospores:** simple and narrowly ellipsoid when young, 1-septate and fusiform when mature, biseriately arranged within the ascus, colorless, 10-17 (-36) x (1.5-) 3.5-4.5 µm; **Pycnidia:** laminal, subglobose, ± 0.2 µm in diam.; ostiole: brown; **conidia:** rod-shaped, 3-6 x 1 µm; **Spot tests:** all negative; **Secondary metabolites:** none detected.

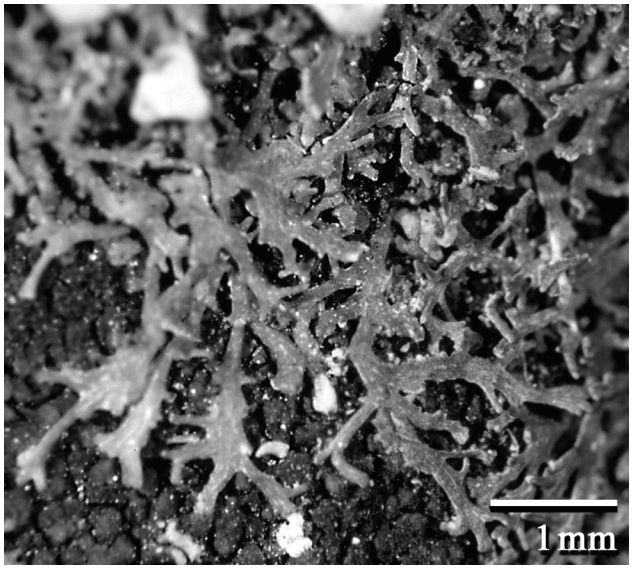
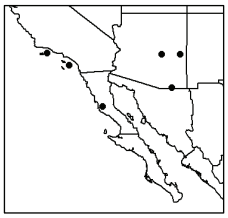


Fig. 56. *Koerberia sonomensis*, photo by R. Schoeninger.

Substrate and ecology: on silicate rocks in relatively moist canyons; **World distribution:** western North America, Mediterranean areas of Europe and northern Africa; **Sonoran distribution:** rare and inconspicuous, only known from a few locations at intermediate elevations, central Arizona, southern California and Baja California.



Note: Sometimes the laciniae may become vertically oriented and thus resemble isidia, but they are still pale on one side (as is the lower thallus surface) and are usually flattened, and consequently can be distinguished from isidia.

LEMMOPSIS

by M. Schultz

Lemmopsis (Vain.) Zahlbr., Natürl. Pflanzenfam., Teil 1: 171 (1906).

Family: Lichinaceae; Type: *Lemmopsis arnoldiana* (Hepp) Zahlbr.; No. species: three world-wide; Selected lit.: Ellis (1981).

Life habit: lichenized; **Thallus:** crustose, granulose, gelatinous when wet; **surface:** blackish, rough; **anatomy:** ecorticate, paraplectenchymatous; **photobiont:** primary one a chroococcoid cyanobacterium, secondary photobiont absent; **Ascomata:** absent or present, apothecial, laminal on thallus, orbicular, sessile; margin: distinct to prominent, with thalloid rim, evanescent with age; **ontogeny:** hemiangiocarpous, ascogonia arising in a tangle of generative hyphae beneath the thallus surface; **anatomy:** exciple: yellow, yellowish brown or hyaline; epithecium: brownish yellow; **asci:** prototunicate; walls: thin, nonamyloid; 8-spored; **ascospores:** simple, ellipsoid to broadly ellipsoid, 10-28 x 7-15 µm; walls: thin, hyaline; **Conidiomata:** pycnidial, laminal, immersed; **conidia:** ellipsoid, *c.* 3 x 1 µm; **Secondary metabolites:** not detected; **Geography:** in arid, semi-arid to warm temperate regions of the Northern Hemisphere; **Substrate:** on limestone, caliche or calcareous soil.

Notes: The genus is most similar to *Psorotichia* which has a distinctly thinner exciple or lacks an exciple completely. In *Porocyphus* the ascomata arise beneath pycnidia and the paraphyses are usually more slender.

The Species

Lemmopsis arnoldiana (Hepp) Zahlbr., Natürl. Pflanzenfam. Teil 1: 171 (1906).

Basionym: *Physma arnoldianum* Hepp, Flora 41: 94 (1858); Synonyms: see Ellis (1981); Illustration: Fig. 57 to right.

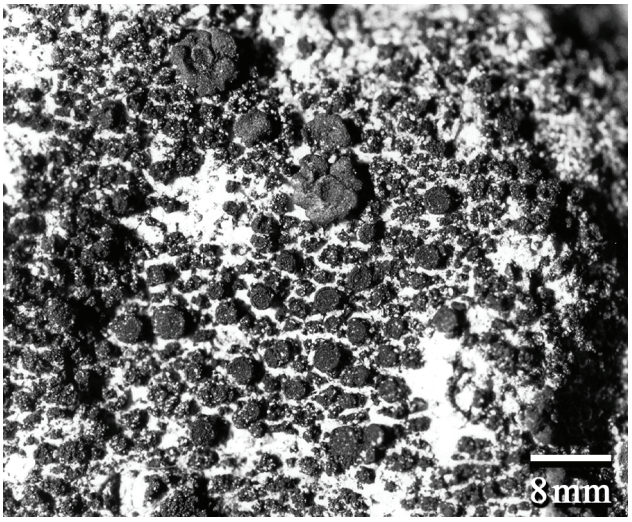


Fig. 57. *Lemmopsis arnoldiana*, with *Peltula obscurans* var. *hassei*, photo by M. Schultz.

Thallus: crustose areolate to granulose, scattered, areolate: **areoles:** 0.25-0.5 mm wide, angular to irregular in outline; **surface:** dull black, rough to granulose; **attachment:** by rhizohyphae; **Apothecia:** sessile, zeorine, small, up to 0.5 mm wide, with thin thalline margin; disc: opening early in development, flat, dark red, receding with age; exciple: distinct (already distinct in juvenile apothecia), often visible as a light ring surrounding the apothecial disc, color faintly yellow to golden, composed of interwoven, gelatinized hyphae; epihymenium: brownish red; hymenium: 100-120 µm high, hyaline, amyloid; paraphyses: distinctly septate, branched and anastomosing, apical cells thickened (3-5 µm) and colored reddish-brown; **asci:** 8-spored; **ascospores:** simple, hyaline, broadly ellipsoid to ellipsoid, (10-) 12.5-17.5 (-22.5) x (7.5-) 10-12.5 (-15) µm; walls: thin; **Pycnidia:** immersed, globose, 0.1-0.125 mm wide, simple; wall: convoluted with age; **conidia:** ellipsoid, 3-4 x 1.5 µm; **Spot tests:** all negative; **Secondary products:** none detected.

Substrate and ecology: on caliche crusts, limestone and rhyolite, and on small pebbles in washes; in sheltered or

rather exposed habitats; montane; **World distribution:** Europe and SW North America; **Sonoran distribution:** south-central Arizona.

Notes: the species is extremely similar to *Psorotichia* and *Porocyphus,* but they lack *L. arnoldiana*'s characteristic yellowish to golden color of the entire excipulum. *Porocyphus* also has a distinct exciple that is sometimes yellowish brown colored, but only in the uppermost parts; it mainly differs from *Lemmopsis* in its type of ascoma development (pycnoascoma) and its slender paraphyses. Furthermore, if *Psorotichia* has an exciple, then it lacks coloration and is very thin. Also the subhymenium of *Psorotichia* usually extends as a stipe deep into the thallus (not found in *Lemmopsis*).

LEPROCAULON

by B. D. Ryan

Leprocaulon Nyl. *ex* Lamy, Bull. Soc. Bot. France 25: 352 (1878).

Family: genus incertae sedis; Type: *Leprocaulon nanum* (Ach.) Nyl.; No. species: eight world-wide; Selected lit.: Lamb and Ward (1974).

Life Habit: lichenized; **Thallus:** crustose to dwarf fruticose; **primary thallus:** ± persistent, densely powdery-leprose or crustose-verrucose-subsquamulose, diffuse, unstructured; **secondary thallus:** subfruticose-dactyliform or dwarf fruticose-caespitose, attached by the whole lower surface or attached basal holdfasts; leprose-sorediate, floccose-tomentose granules or squamule-like structures superficially somewhat similar to phyllocladia of *Stereocaulon*; **pseudopodetia:** small, slender, ± erect, ± terete, branching, interwoven, cartilaginous, fragile; **upper surface:** gray, ochraceous-yellow or white, ecorticate, smooth; isidia and cephalodia absent; **medulla:** white; **photobiont:** primary one a chlorococcoid alga (*Trebouxia*), secondary photobiont absent; **lower surface:** absent or rhizose strands present; hypothallus absent; **Ascomata:** absent; **Conidiomata** absent; **Secondary metabolites:** absent, or orcinol depsides, or orcinol depsidones, or ß-orcinol depsides (including atranorin s. l.), or ß-orcinol depsidones, or aliphatic acids, or dibenzofurans and usnic acids, or triterpenoids; **Geography:** mainly Southern Hemisphere, but also in arctic-alpine to temperate areas of Northern Hemisphere; **Substrate:** on bryophytes, soil, detritus, or non-calciferous, siliceous rock, in ± sheltered and dry areas, often in crevices.

Notes: It is distinguished from *Stereocaulon* by the lack of ascomata, the absence of corticate phyllocladia, cephalodia, and pycnidia, and its different chemistry. The primary thallus, and sometimes the entire thallus, resemble that of some species of *Lepraria*. Although material externally rather similar to *L. subalbicans* (Lamb) Lamb and Ward occurs in at least in southern California (see Riefner et al. 1995), at present it cannot be readily distinguished from various other sterile crusts; in fact, the rather coarsely granular thallus and at best indistinct pseudopodetia make the placement of that species in *Leprocaulon* rather questionable.

Key to species of ***Leprocaulon*** in the Sonoran region:

1. With ill-defined, ± confluent, irregular lumps; pseudopodetia stout and indistinctly developed, central axis absent ..... ***L. cf. subalbicans***
1. With distinctly developed phyllocladial granules; pseudopodetia usually at least partly elongated and slender; central axis well differentiated 2
   2. Pseudopodetia usually greenish to faintly yellowish or aeruginose-yellowish, not distinctly whitish, K-, KC+ yellow or KC-, P-, usually [at least in the Sonoran region] containing usnic acid and lacking atranorin; with zeorin; in herbarium forming mold-like growth of pale crystals within a few years; California, Baja California, Baja California Sur; also rarely in Arizona ..... ***L. microscopicum***
   2. Pseudopodetia white, whitish gray, bluish white, cream-colored, or chalky-whitish, without distinct

yellowish or greenish tinges, K+ or K-, KC-, usually P+ faint to distinct yellow, orange, or red, usually containing atranorin; without usnic acid and zeorin; without crystalline growth; Arizona and Chihuahua 3

3. Thallus P+ persistent, rather pale yellow (rarely P-), without phenolic substances other than atranorin .... ***L. gracilescens***
3. Thallus P+ persistent intense yellow, orange-yellow, red, with phenolic substances (e.g. psoromic or protocetraric acids) in addition to atranorin. ..... ***L. albicans***

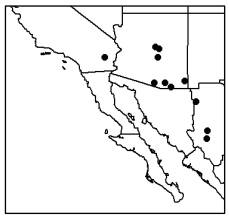
The Species

Leprocaulon albicans (Th. Fr.) Nyl. *ex* Hue, Nouv. Arch. Mus. Hist. Nat., ser. 3, 2: 248 (1890).

Basionym: *Stereocaulon albicans* Th. Fr., De *Stereocaulis* et *Pilophoris* Commentatio: 36 (1857); Synonyms: see Lamb and Ward (1974); Illustrations: Lamb and Ward (1974), Pl I, fig. 1; Hale (1979), p. 22.

Thallus: fruticose, without persistent primary thallus, extensively covering the substrate in a continuous or discontinuous pattern, sometimes low and congested-pulvinate and forming a dense crust-like growth; **pseudopodetia:** (2-) 1 (-2.5) cm long, 0.2-0.3 mm thick, crowded-caespitose, erect or interwoven, terete, not dorsiventral; sparingly branched (not dichotomously), not dendroid-plumose; without root-like basal structures; **surface:** white, whitish gray, bluish white or cream-colored, without distinct yellowish tinge, chalky, subtly whitish arachnoid-tomentose or partly glabrous, brown or brownish towards base, where often ± dying; **phyllocladial granules:** distinctly developed, subglobose, 0.10-0.25 mm diam., chalky-whitish to grayish, dull, subtly powdery but not sorediate, with central mass of algae, without medulla, surrounded by a cloudy and semi-opaque tissue of loosely interwoven and floccose hyphae forming an envelope 12-30 um thick; **central axis:** well differenttiated, cloudy and opaque, yellowish-gray, composed of longitudinally parallel hyphae 2.5-3.0 µm diam. with outer wall thinner than lumina; outer mantle 15-25 µm thick, of lax hyphae 2.5-3.0 µm diam., running chiefly longitudinally, enclosing scattered groups of algae; **Spot tests:** thallus K- to + faint to distinct yellow, C-, KC-, P+ persistent intense yellow (strains I and III), orange-yellow (strain I) or P+ intense orange-red to scarlet-red (strain II); UV- or (strain III [non-Sonoran]) + blue-white; **Secondary metabolites:** atranorin (sometimes minor), fatty acids (including rangiformic acid in strains I and II), plus (strain I) psoromic acid chemosyndrome, (strain II) protocetraric acid, or (strain III [non-Sonoran]) squamatic and baeomycesic acids.

Substrate and ecology: on detritus with mosses, or over mosses, on open rock faces or in rock crevices, sometimes on soil among grasses between rocks, in quite exposed situations or in moderately shaded places; **World distribution:** North America in the west and South America; **Sonoran distribution:** California, Arizona and Chihuahua, 1800-2250 m (all Strain 1).

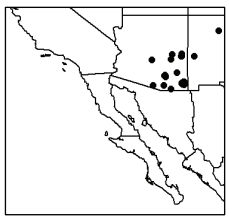


Leprocaulon gracilescens (Nyl.) Lamb & Ward, J. Hattori Bot. Lab. 38: 523 (1974).

Basionym: *Stereocaulon gracilescens* Nyl., Ann. Sci. Nat. Bot. sér. 4, 11: 210 (1859); Synonyms: see Lamb and Ward (1974); Illustrations: Lamb and Ward (1974), fig. 6; Brodo et al. (2001), p. 398.

Thallus: morphologically and anatomically indistinguishable from that of *L. albicans* (see preceeding description); **Spot tests:** thallus K+ yellow, C-, KC-, P+ persistent, rather pale yellow (rarely P-), UV-; **Secondary metabolites:** atranorin, unidentified fatty acids, rangiformic acid (accessory).

Substrate and ecology: on soil, or detritus with mosses, over volcanic or other acidic rocks, or in rock crevices, mainly Arctic-alpine; **World distribution:** western North America, South America and South Africa; **Sonoran distribution:** eastern and central parts of Arizona, 1830-3100 m.



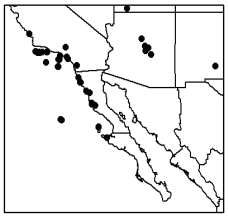
Notes: Lamb and Ward (1974) suggested that this taxon might be considered as a chemically deficient phase of *L. albicans*; they gave no rationale for their maintenance of it as a separate species in spite of lumping the other chemotypes as "chemical strains", but the distribution pattern of *L. gracilescens* is somewhat different (common in South Africa and warm temperate areas; absent from the Arctic). The occurrence of rangiformic acid is apparently rare in Sonoran specimens. One specimen from Arizona (Pima Co., 1710 m), tentatively included under this species, contains (in addition to atranorin and unidentified fatty acids), an unidentified substance (R_f 5 in solvent C, purplish and UV- after charring).

Leprocaulon microscopicum (Vill.) Gams *ex* D. Hawksw. in Hawksw. & Skinner, Trans. and Proc. Torquay Nat. Hist. Soc. 16: 128 (1974).

Basionym: *Lichen microscopicus* Vill., Histoire des Plantes de Dauphiné: 946 (1789); Synonyms: see Lamb and Ward (1974); Illustrations: Lamb and Ward (1974), fig. 7; Pl. III, fig. 1; Wirth (1995), p. 542.

Thallus: producing a weakly developed turf or a sorediate crust; primary thallus persistent, granulose-sorediate; **pseudopodetia:** usually at least partly well developed, crowded, ± erect, 2-4 (-6) mm high, 0.1-0.2 mm thick, slender, filiform, usually simple in the lower portion, in the upper portion sparingly branched; **surface:** yellowish-white to often pale greenish or occasionally slightly bluish; subtly arachnoid-tomentose, towards the base glabrous and darkened (brown-blackish or aeruginose-bluish), in herbarium usually developing very fine, azure-blue to whitish, downy mold-like covering (composed of crystals of unknown composition); **phyllocladial granules:** ± completely covering the surface, mealy-powdery, sorediate, disintegrating and turning green, 35-100 µm in diam.; hyphae: slightly over 0.3 µm in diam., loosely interwoven; **central axis:** with hyphae parallel, conglutinated, 2.5-3.0 µm diam., outer wall thinner than lumina; **outer mantle:** with hyphae slightly wider than those of axial strand, loosely interwoven; **Spot tests:** thallus K- or indistinct yellowish, C-, KC+ yellow, P- or indistinct yellowish, UV-; **Secondary metabolites:** usnic acid and zeorin; rangiformic acid, unidentified fatty acid, and three unidentified substances (all accessory).

Substrate and ecology: on thin soil, detritus, or moss, especially in shaded areas or in crevices associated with ± dry sides of cliff faces and walls, most frequent in coastal sites; **World distribution:** western North America, Europe, Asia Minor, N. Africa, Macaronesia, Australia; **Sonoran distribution:** rare in Arizona at *c.* 2000 m; common in southern California, Baja California and Baja California Sur, at 15-360 m.



Notes: The mold-like covering, similar to that found in various other lichens containing terpenoids along with usnic acid [e.g., many *Vermilacinia* spp.], is a very distinctive feature of this species, and starts becoming evident (at least under a dissecting microscope) within 5 years or less in the herbarium (much less than the "50 years or more" suggested by Lamb and Ward 1974); it should not be confused with occasional true fungal molds (which sometimes occur on specimens of other species, but can usually be distinguished by the presence of tiny globular conidiophores). The color of the thallus in *L. microscopicum* is rather variable, in our area often more greenish or bluish then yellowish, but is rarely as distinctly whitish or bluish as in *L. albicans* and *L. gracilescens*, and (in contrast to some material from other parts of the world) Sonoran specimens consistently contain usnic acid as shown by TLC. The only specimens reported from the Sonoran Region (southern California) by Lamb and Ward (1974) were of "Deficient phase IV" (containing only usnic acid and zeorin), but we have found occasional specimens from the southern California coast containing atranorin (one also with rangiformic acid and an unknown substance) or various unidentified terpenoids or fatty acids.

LEPTOCHIDIUM

by T. H. Nash III

Leptochidium M. Choisy., Bull. Mens. Soc. Lyon 21: 165 (1952).

Family: Placynthiaceae; Type: *Leptochidium albociliatum* (Desm.) M. Choisy; No. species: one world-wide; Selected lit.: Thomson (1984).

Because the genus is monospecific, a generic description would simply recapitulate the specific description given below.

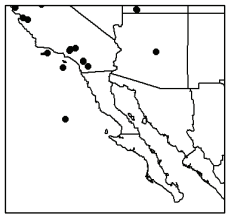
Notes: Superficially *Leptochidium* is similar to large species of *Leptogium* and *Collema*, both of which contain *Nostoc* as the photobiont. *Collema* does not have either an upper or lower cortex. *Leptochidium* is the only genus of the three to have white hairs on the upper surface, although one group of *Leptogium* species (sect. *Mallodium*) has either very short, white hairs or white tomentum on the lower surface and occasionally the margins (e.g. *L. hirsutum*).

The Species

Leptochidium albociliatum (Desm.) M. Choisy, Bull. Mens. Soc. Lyon 21: 165 (1952).

Basionym: *Leptogium albociliatum* Desm., Annal. Sci. Nat. Bot., ser. 4, 4: 132 (1855); Synonyms: *Polychidium albociliatum* (Desm.) Zahlbr.; *Collema albociliatum* (Desm.) Nyl.; Illustrations: Thomson (1984), p. 252; Brodo et al. (2001), p. 399.

Life habit: lichenized; **Thallus:** foliose, continuous with margin rounded or lobate, 3-10 cm wide, loosely adnate; **lobes:** irregular, broadly elongate, marginally entire or crenulate, often folded; lobe tips usually subrotund to rotund, often ascending, eciliate but with numerous white hairs; **upper surface:** dark greenish black, covered with scattered, white hairs, epruinose; lacking soredia or isidia; **upper cortex:** multilayered, paraplectenchymatous, 10-30 µm thick; **medulla:** white or yellow, loose hyphae, 40-260 µm thick; **photobionts:** primary one a cyanobacterium (*Scytonema*), secondary photobiont absent; **lower cortex:** multilayered, paraplectenchymatous, 20-40 µm thick; **lower surface:** dark greenish black, glabrous, rhizinate; rhizines: fasciculate; cyphellae and pseudocyphellae absent; **Ascomata:** apothecial, up to 1.2 mm wide, sessile, laminal on the upper surface, orbicular, cup-shaped; margin: paraplectenchymatous; disc: reddish brown, flat; **anatomy:** exciple: hyaline or light brown, 20-30 µm thick, epithecium: brown or brownish yellow; hymenium: colorless, 60-90 µm tall; paraphyses: ± branched, septate, apically capitate; hypothecium: hyaline; **asci:** clavate, 8-spored; **ascospores:**, oblong ellipsoid to ellipsoid, hyaline, 1-septate, 18-26 x 5-9 µm; **Conidiomata:** pycnidial, marginal, semi-immersed, punctiform, ostiole dark; **conidia:** bacilliform, 9-16 x 1 µm; **Spot tests:** all negative; **Secondary metabolites:** none detected.



Habitat and ecology: on rocks and soil among mosses in moist habitats; **World distribution:** rare in northern Europe and western North America, especially in California; **Sonoran distribution:** scattered locations in Arizona, southern California and Baja California (Guadalupe Island).

LEPTORHAPHIS

by A. Aptroot

Leptorhaphis Körb., Syst. Lich. Germ.: 371 (1855).

Family: Xanthopyreniaceae; Type: *Leptorhaphis oxyspora* (Nyl.) Körb.; No. species: 12 world-wide; Selected lit.: Aguirre-Hudson (1991).

Life habit: non-lichenized, saprobic or weakly lichenized; **Thallus:** absent or crustose, mostly immersed in substrate, not well delimited; **upper surface:** whitish gray to greenish, smooth, continuous; **photobiont:** absent or facultatively a trentepohlioid alga; **Ascomata:** perithecial, scattered singly or sometimes confluent, circular to ellipsoid, immersed or becoming superficial, ostiolate; **involucrellum:** dark brown to greenish black, hyphae K-, clypeate, radiating hyphae sometimes extending to form a basal fringe; true **exciple:** pseudoparenchymatous, colorless to pale brown, developed within the involucrellum, inconspicuous or not, continuous below the asci; **ascomatal wall:** black, not continuous below the hamathecium; **hamathecium:** mostly unbranched pseudoparaphyses, not anastomosing, periphyses and periphysoids absent, hymenial gelatin hemi-amyloid (I+ yellowish orange to bluish green, never deep blue); **asci:** bitunicate, cylindrical to clavate or pyriform, with tholus, with a quite short-pointed apex, fissitunicate, non-amyloid, 8 (-16)-spored; **ascospores:** hyaline, filiform, arcurate or sigmoid, 0-3-septate with eusepta, 1.5-3.5 x 20-45 µm; walls: not ornamented; **Conidiomata:** pycnidial, immersed to semi-superficial, hemispherical to spherical; **conidia:** colorless, producing both macroconidia (almost size and shape of the spores) that are acicular-fusciform, arcuate and smooth and microconidia that are bacilliform to fusiform; **Secondary metabolites:** absent; **Geography:** mostly temperate in the Northern Hemisphere; **Substrate:** only on bark.

Notes: It is separated from other pyrenocarpous genera by its acicular-fusiform ascospores.

The Species

Leptorhaphis atomaria (Ach.) Szatala, Magyar Bot. Lapok 26: 31 (1928).

Basionym: *Lichen atomarius* Ach., Lichenogr. suec. prodr.: 16 (1798); Illustration: Harris (1973), p. 56.

Thallus: continuous, smooth, immersed in the substrate, not well delimited; **upper surface:** whitish gray, smooth; **photobiont:** absent or associated with *Trentepohlia*; **Perithecia:** hemispherical, black, circular, scattered singly, semi-immersed in the thallus, 0.1-0.2 mm diam.; **involucrellum:** greenish brown, composed of leptodermatous cells; true **exciple:** colorless to dark brown, continuing below the hymenium; hymenium I+ bluish; **ascomatal wall:** black, absent below the hamathecium; **hamathecium:** mostly unbranched pseudoparaphyses, not anastomosing; filaments: *c.* 2 µm wide, not inspersed with oil droplets; **asci:** pyriform, *c.* 40-55 x 10-28 µm, with 8, irregularly arranged ascospores; **ascospores:** hyaline, fusiform to bacilliform, curved, sometimes sigmoid, 1-3 septate with a median euseptum, 24-28 x 2.5-3.5 µm; walls: not ornamented, without a gelatinous sheath; **Pycnidia:** black; **conidia:** (macroconidia): fusiform, 12-18 x 1.5-2.5 µm; **Spot tests:** all negative, UV negative; **Secondary metabolites:** none detected.

Substrate and ecology: on bark of *Populus*; **World distribution:** temperate in Northern Hemisphere; **Sonoran distribution:** only collected in southern Arizona.

Note: The specimen had been incorrectly identified as the related *Leptorhaphis epidermidis* (Ach.) Th. Fr., which differs by its ellipsoid ascomata and its different host preference (*Betula* instead of *Populus*).

LETHARIA

by B. D. Ryan

Letharia (Th. Fr.) Zahlbr., Hedwigia 31: 36 (1892), nom. cons.

Family: Parmeliaceae; Type: *Letharia vulpina* (L.) Hue; No. species: at least two world-wide [see Notes]; Selected lit.: Keissler (1960), Thomson (1969), Goward (1999), and Kroken and Taylor (2000 & 2001).

Life habit: lichenized; **Thallus:** fruticose, semi-erect and caespitose to subpendent or pendent, 40-80 (-100) mm long, pliant (to rather stiff and cartilaginous in very coarse specimens), solid, with a basal attachment disc, irregularly and richly branched, branching isotomic to anisotomic; **branches:** principally radial and irregularly rounded in cross-section, yet at least the main branches usually angular or flattened, 1-2 mm wide; **surface:** usually intensely green-yellow to yellow ("fluorescent" yellow-green or chartreuse when fresh), the older parts turning light yellowish brown; dull, epruinose, or occasionally slightly yellowish to whitish pruinose on ridges; weakly to often wrinkled or ridged and lacunose or foveolate, especially on the smallest branches; irregularly shaped abraded areas ± present, slightly paler and brighter yellow than the cortex; soredia and/or isidia present or absent; **cortex:** present on all sides, *c.* 50 µm thick, densely filled with yellowish crystals (soluble in K) apparently concentrated around the cell walls; hyphae in K ± anticlinal, branched, with ± thick-wall, short, roundish cells *c.* 5.-7.5 µm across; **medulla:** white, arachnoid, solid or with a loosely filled center, with solid medullary strands or filaments: variable in number (*c.* 5-12), often together, relatively thin in the upper branches, thicker near the base, fusing into a single large strand that almost fills the inside of the branch; loose hyphae: *c.* 4-7 µm wide with lumina 1-2 µm wide; hyphae in bundles: strongly conglutinated, narrower, periclinal; cell walls with *Cetraria*-type lichenan (Common, pers. comm.); **photobiont:** primary one a *Trebouxia*, secondary photobiont absent; algal layer: under the cortex on all sides, in rounded groups of up to 20 (-30) cells, each *c.* 10-20 µm diam.; **Ascomata:** apothecial, sessile to short-stipitate, lateral or terminal, roundish to rather irregular in outline, bowl-shaped when young, ± soon shallow and flattened; disc: deep or dark red-brown to grayish brown; thalline exciple: concolorous with the thallus, prominent, raised or level with the disc, lobulate or cornute on the outer edge, with elongated, attenuate projections similar in structure and appearance to the thallus; exciple: hyaline above, lower layers hyaline or pale yellowish, not strongly gelatinized but the hyphae rather strongly conglutinated and thick-walled, at least partly periclinal to the disc; epihymenium: yellow-brown; hymenium: thin, hyaline to pale yellowish; paraphyses: thick, coherent, strongly conglutinate and difficult to see clearly, septate, not branched or anastomosing; ostiolar filaments absent; **asci:** broadly clavate, thick-walled, *Lecanora*-type, amyloid reaction in the tholus moderate (compared to that in *Vulpicida*), 8-spored; **ascospores:** biseriate or triseriate, simple, hyaline, narrowly to broadly ellipsoid or subglobose, obtuse at the poles, 5-7 (-8) x (3.5-) 4-5 µm, wall smooth, without distinct endospore thickening, not amyloid; **Conidiomata:** pycnidial, mainly towards the tips or spreading downward somewhat along ridges, scattered or crowded, laminal, immersed, but usually within low, rounded elevations, *c.* 0.1-0.2 mm diam., internally almost spherical, ostioles dark brown to black, punctiform (≤ 0.05 mm diam.), conspicuous under moderate magnification of a dissecting microscope [but not appearing as raised black structures as in the illustration by Keissler (1960)]; conidiophores ± type V of Vobis (1980); **conidia** borne pleurogenously, on tips of ± elongated projections from conidiogenous cells (see Keissler 1960, fig. 27c), acicular or sublageniform, 8-9 (-10) x ≤ 1 µm, straight; **Secondary metabolites:** cortex always with pulvinic acid derivatives (vulpinic acid), ß-orcinol depside (atranorin), ß-orcinol depsidone (accessory), usnic acids, and aliphatic acids; **Geography:** cool temperate to temperate, western North America, Europe, southern Asia; **Substrate:** bark or wood, rarely , rarely on acidic rock; the species are good indicators of the height of the snowpack on tree trunks, since they do not grow under snow.

Notes: This is the most conspicuous lichen genus in the montane forests of California because of the large bushy, brightly colored thallus, which covers branches and tree trunks profusely, at least in areas away from the major cities. Today in many mainland areas of southern California (e.g., the San Gabriel Mountains) the thalli are often few and very small and poorly developed. The thalli, which are somewhat poisonous from the yellow pigment vulpinic acid, and have been known to cause allergic reactions, are often gathered in quantity for crafts or decorations.

Preliminary studies by Kroken and Taylor (2000 & 2001) suggest that, based on on-going molecular, chemical, and morphological/anatomical investigations, may support a new taxonomy of the taxa currently treated in *Letharia*". Although these authors provide a little information on distribution, morphology, and apothecial chemistry of the tentatively named variants, much further study is needed before these variants can be adequately circumscribed and distinguished from each other.

Key to species of ***Letharia*** from the Sonoran region:

1. Thallus sorediate or isidiate-sorediate (often also with isidia-like branchlets); apothecia and pycnidia rare (usually absent) ..... ***L. vulpina*** *s. lato*
1. Thallus not sorediate (but sometimes with isidia-like branchlets); apothecia, pycnidia, or both, usually present ..... ***L. columbiana*** *s. lato*

The Species

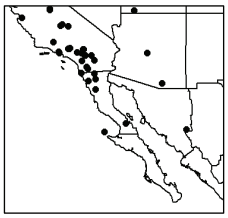
Letharia columbiana (Nutt.) J. W. Thomson, Taxon 18: 536 (1969).

Basionym: *Borrera columbiana* Nutt., Journ. Acad. Nat. Sci. Philadelphia 7: 59 (1834); Synonym: *L. californica* (Lév. *ex* Nyl.) Hue and see Thomson (1969) for further synonymy; Illustrations: McCune and Geiser (1997), p. 147; Goward (1999), p. 183; Brodo et al. (2001), p. 412.

Thallus: (2-) 3-11 (-17) cm tall, tufted to subpendulous, attached by a distinct basal disc, *c.* 0.2 mm diam. near the base; branching loose, intricately irregular or anisotomically di-(tetra-)chotomous to almost isotomic near the ultimate branches, often divaricate, axils acute to obtuse, rounded; **branches:** *c.* 0.5-3 (-4) mm wide, unevenly thickened, subterete to angular, or irregularly flattened, especially just below the axils; higher order branches: terminating in attenuated, subulate, forked divisions; short, narrow, ± isidia-like "branchlets" sometimes abundant near base; **surface:** bright greenish yellow or chartreuse yellow-green, abraded areas often slightly paler or brighter yellow, extreme tips of branches and branchlets often ± brown, trunk near the base dark grayish brown to blackish; dull to ± shiny, shallowly to rather deeply lacunose/ foveolate (smaller branches) or channelled/ grooved, with wrinkles and ridges, which are often reticulate and strongly flexuous-sinuous; **cortex:** sometimes cracked transversely, occasionally finely and shallowly rimulose in places; **medulla:** white, appearing slightly lustrous, arachnoid or fibrous, ± loose but partly conglutinated into several (*c.* 5-10) narrow, ± longitudinal hyphal bundles ± separated by gaps; **Apothecia:** usually common, up to 22 mm diam., solitary or often occurring in two's or three's, sessile, terminating the shorter restricted branches, and irregularly hollow in the center; disc: dark grayish to reddish brown, or deep brown, occasionally with patches the thin brown layer broken off or abraded, showing a distinctly yellow layer underneath), dull to lustrous or slightly shiny, epruinose, deeply concave when young (≤ *c.* 3 mm across, becoming undulate and irregularly folded, often deeply depressed towards the center; thalline margin: *c.* 0.1 (-0.2) mm wide, strongly raised and inflexed when young, soon level with the disc, with few to many ± elongated projections ("lobules" or "fibrils") formed almost from the start and having similar appearance and structure to the smaller branches of the thallus, 0.5-1 cm long and 1 mm wide at the base but soon narrowing and gradually attenuating to roundish or ± pointed tips, the longer ones often branching; surface of lobules and underside of margin often strongly foveolate or lacunose; epihymenium: *c.* 15 µm ± deep yellow-brown; hymenium: *c.* 25-40 µm, hyaline to pale yellowish; **asci:** *c.* 20-25 x 10-15 µm, 8-spored; **ascospores:** ellipsoid, *c.* 7.5-8 x 3.5-4 µm; **Pycnidia:** absent to more often frequent, in section *c.* 0.75 µm diam.; **conidia** arcuate, apparently uniform in thickness, *c.* 8-10 µm long; **Spot tests:** cortex and me-

dulla: K-, C-, KC-, P-; **Secondary products:** cortex with vulpinic acid.

Substrate and ecology: on bark or wood of conifers, in open, well-ventilated intermontane forests, usually growing high on trunks, sometimes on dead branches; **World distribution:** western North America with a distribution similar to that of *L. vulpina*; **Sonoran distribution:** frequent in southern California at 1525-2570 m; Baja California at 980-1400 m in chaparral; rare in Sonora and Arizona.



Notes: It often occurs with *L. vulpina* and differs from it mainly in lacking soredia and usually having abundant apothecia and/or pycnidia. At least in the Sonoran region, *L. columbiana* often has rather coarse and weakly divided main branches, but occasionally smaller specimens are finer and more densely branched. Most older North American descriptions of "*L. vulpina*" (e.g., those of Herre 1910, Hasse 1913, Fink 1935, and Howard 1950, include fertile material (now *L. columbiana*). The information in the present account is based on my own observations, primarily of material from the Sonoran Region, and may not entirely apply over the full geographic range of these taxa. Small, globose to elongate and branched, isidia-like structures, which can break off and establish new thalli, are often present in both species.

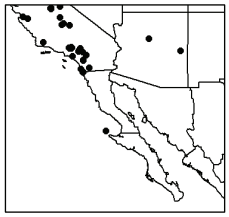
Morphologically, material of *L. columbiana* s. lato from the Sonoran region, though rather variable in color, branching, and development of isidia, appears to correspond mostly to the *L. "rugosa"* type of Kroken and Taylor (2001), characterized mainly by the wrinkled or veined surface (especially evident on the larger branches and the undersides of the apothecial margins). However, these authors also report the *L. "barbata"* morph (with a smoother thallus and more richly ciliate apothecial margins) from southern California. Material from chaparral and other rather arid low to moderate elevation sites may represent an additional taxon.

Letharia vulpina (L.) Hue, Nouv. Arch. Mus., sér. 4, 1: 57 (1899).

Basionym: *Lichen vulpinus* L., Sp. Pl.: 1155 (1753); Synonyms: *Evernia vulpina* (L.) Ach. and see Keissler (1960) for further synonymy; Illustrations: Hale and Cole (1988, cover photo); Brodo et al. (2001), p. 413; Goward (1999), p. 183; Wirth (1995), p. 71.

Thallus: usually to (1-) 3-5 (-20) cm tall, pliant, 3-8 cm wide, erect or spreading, caespitose to subpendent and beard-like, ± copiously branched and entangled; branching: irregular, often forked and divaricate especially towards the tips; **branches:** ± crowded, 0.5-1.5 (-3) mm wide, angular, rarely cylindrical, repeatedly bent, loose; long branches: with densely crowded, thin, subulate; side branches: somewhat curved terminally, often with acuminate tips; **surface:** lemon yellow, golden yellow-green to chartreuse, often distinctly greenish yellow, rarely sulfur yellow, in age or towards the base, usually pale orange-yellow to light yellowish brown; older branches: sometimes greenish gray to gray with the younger branches brighter yellow; extreme tips: often dark grayish brown; lacunate or foveolate; **soredia:** diffuse, often isidioid, generally dense, often developing from paler, brighter yellow areas or cracks on the angles and ridges, where the cortex has degenerated; isidia absent to few when soralia abundant, < 0.05 mm diam., globular and ± constricted at the base, or irregularly elongated to *c.* 0.1-0.2 mm and narrowing towards the tips, or sometimes becoming dense especially near the base, then ± cylindrical, becoming more elongated and branched (± coralloid); **Apothecia:** very rare (usually absent in material from Sonoran region), up to 20 mm wide; disc brown; **Pycnidia:** rare (usually absent); **Spot tests:** cortex and medulla K-, C-, KC-, P-; **Secondary products:** cortex with vulpinic acid.

Substrate and ecology: on bark or wood, usually the trunks or branches of living or dead conifers or man-made wooden structures, rarely on acidic rock; to the north very common and often covering large areas of tree surfaces above the snow line; **World distribution:** western North America and western Eurasia; **Sonoran distribution:** southern California and Baja California at 800-2000 m, often on north-facing slopes or in shaded



areas, but also sometimes in chaparral; rare, eastern Arizona at 2950 m.

Notes: Based on morphology and distribution, material of *L. vulpina* s. lato from the Sonoran region appears to include both *L. vulpina* s. str. (especially near the coast, and similar to European material) and the *L. "lupina"* (especially away from the coast, and yellower, more highly branched, and with larger and more diffuse soralia) morph of Kroken and Taylor (2001). However, in my opinion the differences between these two morphs, as given by these authors and by Goward (1999), are not very consistent and are difficult to apply to the often poorly developed specimens found in southern California, where the distributions of the two morphs overlap. A few specimens from the San Gabriel Wilderness are much more robust and have sparsely divided main branches 2-3 (-7) mm wide with narrow branches mostly in the upper parts; in these morphs the narrow branches are either divaricately branched in scattered dense clusters, or more parallel and sinuous and concentrated towards the tips with extensive coverage by isidioid soredia concentrated on these smaller branches. These and other populations from arid areas may represent additional species (Barreno, pers. comm.).

LOBARIELLA

by I. Yoshimura

Lobariella Yoshim., **nom. nov.**

Lobaria subg. *Durietzia* C. W. Dodge, Beih. Nova Hedwigia 12: 146 (1964) = *Durietzia* (C. W. Dodge) Yoshim., in Marcelli, M. P. and Ahti, T. (eds.) Recollecting Edvard August Vainio, p. 90 (1998), hom. Illeg.: non *Durietzia* Gyeln. (1935) = *Ionaspis* Th. Fr. (1871) (Hymeneliaceae), see Jørgensen, Graphis Scripta 2: 118 (1989).

Family: Lobariaceae; Type: *Lobariella crenulata* (Hook. in Kunth) Yoshim.; No. species: five world-wide; Selected lit.: Yoshimura (1984 & 1998a &b).

Life habit: lichenized; **Thallus:** foliose, circular in outline or irregularly spreading, 4-30 cm wide, loosely adnate to adnate, lobate; **lobes:** flat to convex, discrete, often loosely imbricate, elongate, mostly >4 mm wide, tips sometimes ascending, eciliate; **upper surface:** pale tan or gray, dull or somewhat shiny, maculate or not, pseudocyphellate or not; with or without isidia; soredia absent; **upper cortex:** scleroplectenchymatous (separate hyphae not distinguishable) with a non-pored epicortex; **medulla:** white, with or without a condroid strand, hyphae walls containing *Cetraria*-type lichenan; **photobiont:** either chlorococcoid alga (often with internal cephalodia with a cyanobacterium) or a cyanobacterium; **lower cortex:** poorly developed prosoplectenchymatous; **lower surface:** pale tan, tomentose, rhizinate; rhizines simple or sparingly branched, stout, apically with a squarrose tuft; **Ascomata:** apothecial, lecanorine, laminal, sessile to substipitate; margin: initially inrolled, strongly and irregularly crenate; disc: light brown to brown, eperforate; epithecium: pale brown; hymenium and hypothecium colorless; paraphyses: simple or forked above, apices clavate, pale brown with a dark brown cap; **asci:** cylindrical, *Lecanora*-type; 8-spored; **ascospores:** acicular, colorless, straight to slightly curved, 7-septate at maturity; **Conidiomata:** pycnidial, brown-black, immersed, punctiform; **conidia:** simple, bacilliform, colorless; **Secondary metabolites:** depsides, depsidones and aliphatic acids; **Geography:** neotropics, from Brazil to central Mexico; **Substrate:** common on rocks; less common on bark.

Notes: *Durietzia* was initially proposed as subgenus by Dodge (1964) and is a recent segregate from *Lobaria* for species that have white dots (maculae and/or pseudocyphellae) on the upper surface (Yoshimura 1998a & b) but this name was previously used (Gyelnik 1940) and consequently is emended here to *Lobariella*. In contrast to *Pseudocyphellaria*, which has pseudocyphellae on the lower surface, *Lobariella* has pseudocyphellae on the upper surface. *Lobaria* in the restricted sense lacks pseudocyphellae on either surface. Occasionally species of *Punctelia*, a parmelioid genus with pseudocyphellae on

the upper surface, may be mistaken for *Lobariella*, but the former genus does not have tomentum on the lower surface, usually is more narrow lobed and has simple spores.

Key to the species of ***Lobariella*** from the Sonoran region:

1. Thallus isidiate 2
1. Thallus not isidiate ..... ***L. crenulata***

2. Isidia cylindrical or coralloid; 4-*O* methylgyrophoric acid absent ..... ***L. exornata***
2. Isidia dorsiventral, subgranular, subcylindrical, microphyllous or peltate; 4-*O* methylgyrophoric acid present ..... ***L. subexornata***.

The Species

Lobariella crenulata (Hook. in Kunth) Yoshim., **comb. nov.**

Basionym: *Parmelia crenulata* Hook. in Kunth, Syn. Pl. Aequinoct. Otb. Nov. 1: 23 (1822); Synonyms: *Durietzia crenulata* (Hook. In Kunth) Yoshim., *Lobaria crenulata* (Hook. In Kunth) , *Sticta crenulata* (Hook. In Kunth), *Ricasolia crenulata* (Hook. In Kunth); Illustrations: Yoshimura (1984), pp. 121 & 124-6 as *Lobaria crenulata.*

Thallus: foliose, circular in outline or irregularly spreading, up to 15 cm wide, loosely adnate to adnate, lobate; **lobes:** flat to convex, discrete, loosely imbricate, short linear, 2-5 mm long, mostly 0.5-2 mm wide, tips truncate, strongly crenulate; **upper surface:** pale gray to ash colored (ochre in herbarium), dull or somewhat shiny, emaculate; pseudocyphellae punctiform to sublinear, up to 1.3 mm long and 0.12 mm wide; without soredia or isidia; **upper cortex:** paraplectenchymatous, *c.* 35 µm thick, composed of 4-5 layers, lumina 2-4 µm diam., brown; **medulla:** white, *c.* 200 µm thick, often with internal cephalodia; **lower cortex:** *c.* 20-25 µm thick**,** composed of 3-4 layers, pale brown; **lower surface:** pale brown, densely short (>10 [or 25] µm long) tomentose, moderately rhizinate; rhizines: simple, up to 0.1 mm long, concolorous with lower surface; **Apothecia:** laminal, stipitate, up to 8 mm diam., margin crenulate; disc: red brown; epithecium: brown, *c.* 10 µm thick; hymenium: hyaline below, *c.* 120 µm thick, I+ blue; subhymenium colorless, *c.* 40 µm thick; hypothecium *c.* 20 µm thick; paraphyses: simple, cylindrical, septate; **asci:** obclavate, 8-spored; **ascospores:** acicular, 7-septate at maturity, colorless, 70-90 x 5 µm; **Pycnidia:** immersed, punctiform, upper portion blackish brown; **conidia:** not seen; **Spot tests:** upper surface K+ yellow, C-, KC-, P-; medulla K-, C-, KC+ rose, P-; **Secondary metabolites:** cortex with substance "A"; medulla with gyrophoric acid (major) and 4-*O*-methyl gyrophoric acid (minor).

Habitat and ecology: on bark or rock in very humid microclimates; **World distribution:** Mexico to northern Chile, northern New Zealand and Pacific Islands from Easter Island to Hawaii; **Sonoran distribution:** Sierra Madre Occidental region of central Sinaloa.

Lobariella exornata (Zahlbr.) Yoshim., **comb. nov.**

Basionym: *Lobaria crenulata* var. *exornata* Zahlbr., Ann. Mycolog. 19: 235 (1921); Synonym: *Durietzia exornata* (Zahlbr.) Yoshim., *Lobaria exornata* Zahlbr.; Illustration: Yoshimura (1984), p. 122.

Thallus: foliose, circular in outline or irregularly spreading, up to 10 cm wide, loosely adnate to adnate, irregularly lobate; **lobes:** flat to convex, discrete, loosely imbricate, short linear, 2-5 mm long, mostly 0.5-2 mm wide, tips rounded, entire or weakly crenulate; **upper surface:** pale gray to ash colored (pale brown in herbarium), dull or somewhat shiny, emaculate; pseudocyphellae irregularly rounded to sublinear, up to 0.7 mm long and 0.13 mm wide, isidiate; **isidia:** laminal, cylindrical, simple; soredia absent; **upper cortex:** paraplectenchymatous, 20-30 µm thick, composed of 4-5 layers, lumina up to 7 µm diam., pale brown; **medulla:** white, 100-110 µm thick, often with internal cephalodia; **lower cortex:** *c.* 20-25 µm thick**,** composed of 3-4 layers, pale brown; **lower surface:** brown to brownish black centrally, densely short (>8 [or 35] µm long) tomentose, moderately rhizinate; rhizines: simple, up to 1.2 mm long, pale brown initially and darkening with age; **Apothecia:** rare, laminal, stipitate, up 3 mm diam., margin weakly lobate, often densely isidiate; disc: reddish to blackish brown; epithecium: red-

dish brown, *c.* 10 µm thick; hymenium: hyaline below, *c.* 100-120 µm thick, I+ blue; subhymenium pale brown, 20-30 µm thick; hypothecium colorless, *c.* 20 µm thick; paraphyses: simple, cylindrical, septate; **asci:** obclavate, 8-spored; **ascospores:** acicular, 7-septate at maturity, colorless, 90-105 x 8-9 µm; **Pycnidia:** not seen; **Spot tests:** upper surface K+ yellow, C-, KC-, P-; medulla K-, C-, KC+ rose, P-; **Secondary metabolites:** cortex with substance "A"; medulla with gyrophoric acid (major).

Habitat and ecology: on bark or rock in very humid microclimates; **World distribution:** Mexico to Brazil, including the West Indies; **Sonoran distribution:** Sierra Madre Occidental region of central Sinaloa.

Notes: *Lobariella exornata* is only tentatively identified for the Sonoran region, although it does occur at the northern end of the Sierra Madre Oriental in Tamaulipas.

Lobariella subexornata (Yoshim.) Yoshim., **comb. nov.**

Basionym: *Lobaria subexornata* Yoshim., Journ. Hattori Bot. Lab. 57: 112 (1984); Synonym: *Durietzia subexornata* (Yoshim.) Yoshim.; Illustrations: Yoshimura (1984), pp. 123 & 125 as *Lobaria subexornata*.

Thallus: foliose, circular in outline or irregularly spreading, up to 15 cm wide, loosely adnate, lobate; **lobes:** flat to convex, irregular, loosely imbricate, mostly 0.5-2 mm wide, tips rounded, entire or weakly crenulate; **upper surface:** ashy colored to whitish ochre (olive ochre in herbarium), dull or somewhat shiny, emaculate; pseudocyphellae irregularly punctiform to sublinear, up to 1.5 mm long and 0.05 mm wide, isidiate; **isidia:** laminal to marginal, hemispherical initially, becoming dorsiventral, simple or branched; soredia absent; **upper cortex:** paraplectenchymatous, *c.* 30 µm thick, composed of *c.* 4 layers, lumina up to 7 µm diam., pale brown to brown externally; **medulla:** white, 85–150 µm thick, often with internal cephalodia; **lower cortex:** *c.* 20 µm thick**,** composed of 2-3 layers, pale brown; **lower surface:** brown to brownish black centrally, densely (up to 200 µm long) tomentose, moderately rhizinate; rhizines: simple, up to 2 mm long, pale brown initially and darkening with age; **Apothecia:** rare, laminal, stipitate, up 3 mm diam., margin weakly lobate, often densely isidiate; disc: reddish to blackish brown; epithecium: reddish brown, *c.* 10 µm thick; hymenium: hyaline below, *c.* 100-120 µm thick, I+ blue; subhymenium pale brown, *c.* 20-30 µm thick; hypothecium colorless, *c.* 20 µm thick; paraphyses: simple, cylindrical, septate; **asci:** obclavate, 8-spored; **ascospores:** acicular, 7-septate at maturity, colorless, 90-105 x 8-9 µm; **Pycnidia:** not seen; **Spot tests:** upper surface K+ yellow, C-, KC-, P-; medulla K-, C-, KC+ rose, P-; **Secondary metabolites:** cortex with pseudocyphellarin A; medulla with gyrophoric acid (major), 4-*O*-methyl gyrophoric acid (minor) and unknowns.

Habitat and ecology: on bark or rock in very humid microclimates; **World distribution:** central Mexico to Brazil, including the West Indies and Hawaii; **Sonoran distribution:** Sierra Madre Occidental region of Sinaloa.

MASSALONGIA

by T. H. Nash III

Massalongia Körber, Syst. Lich. Germ.: 109 (1855).

Family: Peltigeraceae; Type: *Massalongia carnosa* (Dickson) Körber; No. species: two world-wide; Selected lit.: Henssen (1963c).

Habit: lichenized; **Thallus:** squamulose at least initially, becoming small foliose in one species, 1-3 cm diam., rosette-forming on smooth substrates, lobate; **lobes:** roundish and scattered initially, becoming aggregated and in one species elongate; **upper surface:** red brown to brown when dry, pale brown to deep green when wet, smooth, nodulose or sometimes with globose to cylindri-

cal isidia; soredia lacking; **upper cortex:** paraplectenchymatous, composed of 3-8 rows of cells; **medulla:** white with loosely interwoven hyphae; **photobiont:** primary one a cyanobacterium (*Nostoc* occurring in colonies throughout the medulla), secondary photobiont absent; **lower cortex:** absent, but longitudinally oriented, ± densely interwoven hyphae delimit the lower side; **lower surface:** brownish white, rhizinate; rhizines brown, sparse to densely tufted, at base of the lobes; **Ascomata:** apothecial, rather rare, laminal or marginal, up to 2 mm diam., sessile to substipitate; margin: proper, paraplectenchymatous, sometimes tomentose, with or without supporting tissue (pseudoexciple); disc: flat, red-brown, smooth, paler marginally; hymenium: brown above, K-, colorless below, I+ blue; paraphyses: septate, simple or branched, 3-5 µm wide, apically ± swollen and pigmented; **ontogeny:** hemiangiocarpic development; **asci:** cylindrical, *Peltigera*-type (with apically thickened walls, I+ blue), 8-spored; **ascospores:** polymorphous (broadly ellipsoid initially, becoming narrowly ellipsoid to fusiform), hyaline, 1-(-3) septate; **Conidomata:** pycnidial, brown above, pale below, immersed; **conidia:** bacilliform to weakly bifusiform, colorless, simple, 2.5-6 x 1 µm; **Spot tests:** all negative; **Secondary metabolites:** none detected; **Geography:** temperate to arctic regions of the Northern Hemisphere, Australasia and South America; **Substrate:** mosses or sandstone.

Notes: The genera *Massalongia*, *Koerberia*, *Placynthium* and *Vestergrenopsis* are all small, rosette-shaped, cyanobacterial-containing lichens that may may appear superficially similar. *Vestergrenopsis* has 12-16 spores per ascus and the other genera 8 spores or less per ascus. *Koerberia* has acicular, 0-1 septate spores whereas *Massalongia* and *Placynthium* have broader spores that are 1-3 septate. The photobiont in *Massalongia* is *Nostoc* whereas *Placynthium* has a photobiont belonging to the Rivulariaceae or Scytonemataceae.

Key to the species of ***Massalongia*** in the Sonoran region:

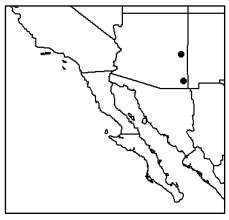
1. Lobes soon elongate (up to 10 mm long); spores mostly 1-septate; paraphyses simple; on mosses ... ***M. carnosa***
1. Lobes remaining roundish; spores mostly 3-septate; paraphyses branched; on sandstone .. ***M. microphylliza***

The Species

Massalongia carnosa (Dickson) Körber, Syst. Lich. Germ.: 113 (1855).

Basionym: *Lichen carnosus* Dickson, Fasc. Plan. Crypt. Brit.: 21 (1790); Illustrations: Henssen (1963c), pp. 1343-8; Wirth (1995), p. 569; Brodo et al. (2001), p. 428.

Thallus: squamulose to small foliose, 1-3 cm diam., often broken up due to growing among mosses, rosette-forming, lobate; **lobes:** initially rounded, becoming ± flattened and elongate (0.5-1.5 mm wide and up to 5 [-10] mm long), irregularly branched, becoming imbricate; apices: sometimes ascending; **upper surface:** red-brown when dry, pale brown to deep green when wet, smooth, nodulose or sometimes with globose to cylindrical isidia marginally; **upper cortex:** paraplectenchymatous, 25-30 µm thick; **medulla:** whitish, loosely interwoven hyphae around *Nostoc* colonies; **lower surface:** brownish white, rhizinate; rhizines: brown, sparse, at base of the lobes; **Apothecia:** not known in Sonoran material, elsewhere rather rare, laminal or marginal, up to 2 mm diam., sessile to substipitate; margin: paler, with short hairs; disc: flat, brown to red-brown, smooth; exciple: 100-145 µm wide, true portion paraplectenchymatous, supported by a pseudoexciple; hymenium: brown above, K-, colorless below, I+ blue, 70-130 µm; paraphyses: septate simple, 2-6 µm wide, ± swollen at the apices and pigmented; subhymenium: hyaline, 45-80 µm thick; **asci:** cylindrical, 55-80 x 11.5-14.5 µm, 8-spored; **ascospores:** fusiform to narrowly ellipsoid, hyaline, 1 (-2)-septate, 11-27 x 4.5-8.5 µm; **Pycnidia:** brown or black above, pale below, immersed, up to 0.6 mm diam.; **conidia:** bacilliform or slightly bifusiform, colorless, simple, 4-6 x 1 µm; **Spot tests:** all negative; **Secondary metabolites:** none detected.



Substrate and ecology: among mosses on a range of different acidic rocks in moist habitats at intermediate elevations; **World distribution:** temperate regions of North and South America, Europe, eastern Asia and Australasia; **So-**

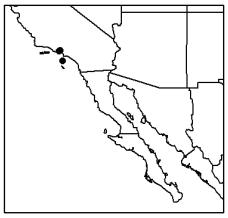
noran distribution: rare, widely scattered in eastern Arizona.

Massalongia microphylliza (Nyl. *ex* Hasse) Henssen, Canad. J. Bot. 41: 1340 (1963).

Basionym: *Pannularia microphylliza* Nyl. *ex* Hasse, Lich. South. Calif.: 9 (1898); Synonyms: *Placynthium microphyllizum* (Nyl. *ex* Hasse) Hasse, *Placynthium dubium* Herre; Illustrations: Henssen (1963c), pp. 1343-4 & 1347-8.

Thallus: squamulose, 1-2 cm diam., rosette-forming, lobate; **lobes:** initially rounded and scattered, becoming densely aggregated and imbricate, 0.1-0.5 mm wide (rarely elongating to 2 mm); **upper surface:** brown when dry, pale brown to deep green when wet, smooth; **isidia:** marginal to submarginal, globose to cylindrical; **upper cortex:** paraplectenchymatous, 30-65 µm thick; **medulla:** whitish, loosely interwoven hyphae around *Nostoc* colonies; **lower surface:** brownish, rhizinate; rhizines: blackish, densely tufted, at base of the lobes; **Apothecia:** rather rare, brown or black, laminal or marginal, up to 1.5 mm diam., sessile to substipitate; margin: pale brown; disc: flat, brown to black, smooth; true exciple: paraplectenchymatous, 85-170 µm wide, outer part brown pigmented, not supported by pseudoexciple; hymenium: brown above, K-, colorless below, I+ blue, 100-175 µm high; paraphyses: septate, branched, *c.* 2 µm wide, ± swollen at the apices and pigmented; subhymenium: colorless to brown, 115-190 µm thick; **asci:** cylindrical, 58-90 x 8-20 µm, 8-spored; **ascospores:** fusiform to narrowly ellipsoid, hyaline, (1-) 3-septate, 17-28 x 6.5-9 µm; **Pycnidia:** brown to black above, pale below, immersed, up to 0.2 mm diam.; **conidia:** bacilliform or slightly bifusiform, colorless, simple, 2.5-4 x 1 µm; **Spot tests:** all negative; **Secondary metabolites:** none detected.

Substrate and ecology: on sandstone in moist habitats from near sea level to 800 m; **World distribution:** western North America from southern California to British Columbia; **Sonoran distribution:** rare in southern California in the Santa Monica Mountains and on Catalina Island.



MELANELIA

by T. L. Esslinger

Melanelia Essl., Mycotaxon 7: 46 (1977).

Family: Parmeliaceae; Type: *Melanelia stygia* (L.) Essl.; No. species: 38 world-wide; Selected lit.: Ahti (1966), Esslinger (1977 & 1978a).

Life habit: lichenized; **Thallus:** foliose, continuous, lobate; **lobes:** narrow, sublinear to more rounded, moderately to loosely attached, eciliate; **upper surface:** pale to dark brown (lacking atranorin, the pigment HNO_3-), plane to foveolate, shiny or dull, pruinose or not, with or without isidia, soralia, and lobules; pseudocyphellae: common (but not universal), obscure to very conspicuous; **upper cortex:** with non-pored epicortex, paraplectenchymatous; **medulla:** white or rarely pigmented in the lower part, cell wall containing isolichenan; **photobiont:** primary one a *Trebouxia*, secondary photobiont absent; **lower surface:** tan to dark brown or black, shiny to dull, usually moderately to somewhat more densely rhizinate, the rhizines usually concolorous with the lower surface, not or little branched; **Ascomata:** absent or present, apothecial, laminal, with thalline exciple; **asci:** clavate and usually 8-spored (in two species, up to 32 spores/ascus); **ascospores:** simple and hyaline, ellipsoid to ovoid or almost globose, 8-18.5 x 4-11.5 µm; **Conidiomata:** laminal, blackened and immersed; **conidia:** acerose to cylindrical or more often bifusiform, 5.5-8 x *c.* 1 µm; **Secondary metabolites:** upper cortex with unidentified brown pigment(s) and lacking atranorin; medulla lacking secondary substances, or, commonly with various orcinol

para-depsides or β-orcinol depsidones, less often with aliphatic acids or anthraquinones; **Geography:** primarily in temperate, boreal or arctic/alpine areas of the Northern Hemisphere, or temperate areas of the Southern Hemisphere; **Substrate:** bark, wood, or rocks (especially non-calciferous ones), sometimes with or on mosses.

Key to the species of ***Melanelia*** from the Sonoran region:

1. Thallus without soredia or isidia, sometimes becoming lobulate or panniform; apothecia frequent in some species, rare in others 2
1. Thallus with either isidia or soredia (or isidioid soredia) or both; apothecia usually absent or rare 7

2. Medulla C+ rose or red (gyrophoric or lecanoric acid) 3
2. Medulla C- 5

3. Thallus with obscure to very distinct laminal pseudocyphellae, medulla C+ rose (gyrophoric and ovoic acid); growing on rock ..... ***M. tominii***
3. Thallus without laminal pseudocyphellae, although sometimes irregular warts on the upper surface may have pseudocyphellae; medulla C+ red (lecanoric acid). 4

4. Thallus usually growing on bark, ± rosette-forming; lobes smooth to irregularly pitted or becoming rugose; usually fertile, tiny hyaline cortical hairs nearly always present, at least on lobe edges and/or apothecial margins ..... ***M. glabra***
4. Thallus usually growing on rock or mosses over rock, becoming divided and lobulate to irregularly pulvinate; lobes often rather strongly reticulately ridged and pitted; seldom fertile; hyaline cortical hairs very few or none ..... ***M. glabroides***

5. Thallus saxicolous, becoming distinctly panniform, containing perlatolic and stenosporic acids .... ***M. panniformis***
5. Thallus corticolous or rarely lignicolous, sometimes papillate or lobulate but not at all panniform, without secondary products 6

6. Spores 8 per ascus ..... ***M. subolivacea***
6. Spores 12-32 per ascus ..... ***M. multispora***

7. Medulla C+ rose or red (gyrophoric or lecanoric acid) 8
7. Medulla C- 14

8. Thallus with true isidia which have a cortex like that of the rest of the upper surface 9
8. Thallus with soredia or with both soredia and isidia 11

9. Thallus with very fine isidia, mostly less than 0.3 mm long and 0.02-0.06 mm in diam., usually simple (unbranched); fine granular soredia also usually present ..... ***M. subaurifera***
9. Thallus with larger isidia, up to 1 mm long and 0.05-0.2 mm in diam., often branched; soredia never present (cortex at times eroded around the isidia, but no true soredia) 10

10. Isidia coarse, up to 0.2 mm in diam.; lobes usually somewhat ascending at the periphery, dull to somewhat shiny, not distinctly maculate, weakly or not at all pitted; rare ..... ***M. villosella***
10. Isidia finer, usually less than 0.1 mm in diam.; lobes usually ± appressed at the periphery, oily-shiny over most of the upper surface, often distinctly maculate, sometimes distinctly reticulately pitted ..... ***M. fuliginosa***

11. Soralia marginal and distinctly labriform ***M. albertana***
11. Soralia laminal or both laminal and marginal, not distinctly labriform 12

12. Upper surface with usually conspicuous, ± pitted pseudocyphellae which may be pale or concolorous with the surrounding cortex; gyrophoric and ovoic acids; on rock ..... ***M. tominii***
12. Upper surface without conspicuous, pitted pseudocyphellae; on bark or rock 13

13. Soralia laminal and marginal, the laminal ones arising from small pustules, the soredia granular or becoming isidioid (the surface dull and not a true cortex like that of the thallus surface); tiny hyaline cortical hairs usually present at least on some lobe-ends .... ***M. subargentifera***
13. Soralia laminal, arising from very obscure pseudocyphellae or other flat areas on the cortex, the soredia farinose to granular or isidioid, often with very fine true isidia developing within and between the soralia; cortical hairs absent ..... ***M. subaurifera***

14. Thallus sorediate, the soralia laminal and submarginal, punctiform to capitate, dark gray to black; on rocks ..... ***M. disjuncta***
14. Thallus isidiate or sometimes becoming covered with numerous small imbricate lobules (panniform) 15

15. Isidia arising near the thallus periphery as small spherical papillae which sometimes elongate slightly as isidia, but soon grow into small, loosely to tightly imbricate lobules covering the thallus center; with stenosporic and perlatolic acids; on rock ..... ***M. panniformis***
15. Isidia cylindrical to spherical or clavate, not growing into imbricate lobules; without secondary products 16

16. Isidia arising as small conical to hemispherical papillae with obscure to distinctive pseudocyphellae at the tip, growing into ± cylindrical, branched isidia; most common on bark or wood, but also on rock ..... ***M. elegantula***
16. Isidia arising as small spherical to hemispherical papillae without pseudocyphellae at the tip, growing into spherical to compressed-clavate or spatulate, inflated isidia; primarily on bark or wood ..... ***M. exasperatula***

The Species

Melanelia albertana (Ahti) Essl., Mycotaxon 7: 47 (1978).

Basionym: *Parmelia albertana* Ahti, Bryologist 72: 236 (1969); Illustrations: Ahti (1969), p. 237; Brodo et al. (2001), p. 432; Esslinger (1977), p. 186.

Thallus: moderately to loosely adnate, appressed throughout or somewhat reflexed at the periphery, foliose, up to 9 cm diam., lobate; **lobes:** short and rounded to somewhat elongate, discrete to subimbricate, 2-4 mm broad, ± flat; **upper surface:** olive-brown to darker reddish brown, smooth to weakly pitted at the periphery, inward often more coarsely rugose; dull throughout or often somewhat shiny near the lobe-ends, sometimes with a few scattered cortical hairs, especially on or near the lobe margins, without typical pseudocyphellae, but lobe edges at times with linear, sometimes pale, pseudocyphelloid abrasions (like those of *M. glabra)*; **soredia:** granular, whitish or darkening to brown and becoming isidioid, in marginal and distinctly labriform soralia; **lower surface:** dark brown to black, generally with a paler zone at the periphery, 5-6 x 1µm, ± smooth to weakly rugulose, mostly dull; moderately rhizinate, the rhizines ± concolorous with the lower surface; **Apothecia:** not seen; **Pycnidia:** not seen; **Spot tests:** upper cortex K-, C-, KC-, P-, HNO_3-; medulla K-, C+ rose-red or red, KC+ red, P-; **Secondary metabolite:** lecanoric acid.

Substrate: bark, or occasionally on rocks among mosses; **World distribution:** western and northern North America, Mongolia, Siberia; **Sonoran distribution:** known only from a single rather sparse collection on rock at 3,000 m in the Mt. Baldy Wilderness Area (Apache Co., Arizona).

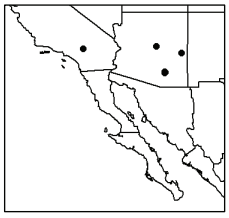
Notes: When poorly developed, this species can be confused with the related *M. subargentifera*, which differs by having both laminal and marginal soralia. The marginal soralia of *M. subargentifera* occasionally become reflexed, but are never distinctly labriform like those of *M. albertana*. *Melanelia albertana* also seems to consistently lack the pruina that are so common (but not universal) in *M. subargentifera*.

Melanelia disjuncta (Erichsen) Essl., Mycotaxon 7: 46. (1978).

Basionym: *Parmelia disjuncta* Erichsen, Ann. Mycol. 37: 78. (1939) (*nom. nov.* for *Parmelia sorediata* var. *coralloidea* Lynge); Synonym: *Melanelia granulosa* (Lynge) Essl.; Illustrations: Wirth (1995), p. 650; Brodo et al. (2001), p. 433; Esslinger (1977), p. 182.

Thallus: adnate to rather loosely adnate, appressed to occasionally subpulvinate, foliose, up to 6 (-9) cm diam., lobate; **lobes:** short and rounded to somewhat elongate, often distinctly flabellate at the end, contiguous or becoming imbricate, (0.4-) 0.8-1.5 (-3) mm broad, flat to slightly convex or concave; **upper surface:** dark olive-brown to blackish, infrequently paler olive to olive-brown, smooth or occasionally somewhat pitted near the

lobe-ends, inward smooth to variously rugulose and/or warted, especially on larger thalli; frequently shiny, especially near the periphery, only occasionally dull throughout, rarely lightly pruinose; pseudocyphellate, the pseudocyphellae small and obscure to frequently quite distinct, submarginal on the lobes; **soredia:** granular to isidioid, dark gray to black (appearing white sometimes when abraded or eroded), in laminal and submarginal soralia arising in part from the pseudocyphellae; soralia: punctiform to capitate and frequently short stipitate but sometimes eroded and crateriform, remaining discrete or becoming confluent in older parts, **lower surface:** very dark brown to black, flat to weakly channeled, smooth to rugulose, dull or slightly shiny in part; moderately rhizinate, the rhizines concolorous with the lower surface; **Apothecia**: infrequent, up to 3 (-5.5) mm diam., sessile or very short stipitate, somewhat concave or flattening, the margin usually partly to completely sorediate, occasionally remaining entire but then usually rugose, pseudocyphellate; **asci:** clavate, 8-spored; **ascospores:** ellipsoid, 9-12.5 x 5-7 µm; **Pycnidia:** rare, immersed; **conidia:** acerose to almost fusiform, 6-7.5 x 1 µm; **Spot tests:** cortex K-, C-, KC-, P-, HNO_3-; medulla K- or rarely dingy, C -, KC- or rarely KC+ very faint rose, P-; **Secondary metabolites:** perlatolic and stenosporic acids (both major).



Substrate: rocks, extremely rare on bark or old wood; **World distribution:** circumboreal, central and northern Europe, Siberia, Central Africa, and North America; **Sonoran distribution:** infrequent in montane areas from 2,000 to 3,000 m.

Notes: The only other sorediate, and obligately saxicolous species in this genus occurring in the study area is *M. tominii*, which usually has much more conspicuous pseudocyphellae, and has a distinctly C+ reddish medullary reaction. Closely related *M. sorediata* is not yet known from the Sonoran region, although it does occur in western North America south to Colorado and Oregon, and might still be found here. It can easily be distinguished by the lack of pseudocyphellae, and presence of discrete soralia, primarily on the ends of short, erect, lateral lobes (Esslinger 1977).

Melanelia elegantula (Zahlbr.) Essl., Mycotaxon 7: 47 (1978).

Basionym: *Parmelia olivacea* * *Parmelia aspidota* var. *elegantula* Zahlbr., Verh. Vereins Natur-und Heilk. Pressburg 8: 39 (1894); Synonyms: *Parmelia elegantula* (Zahlbr.) Szatala and *Melanelia incolorata* (Parrique) Essl.; Illustrations: Esslinger (1977), p. 186, fig. 83; McCune and Geiser (1997), p. 159; Brodo et al. (2001), p. 433; and Fig. 58 below.

Thallus: adnate to loosely adnate, appressed throughout or somewhat raised near the periphery, foliose, up to 6 (10) cm diam., lobate; **lobes:** short and rounded to slightly elongate, ± contiguous to imbricate, 1-4 (-7) mm broad, ± flat; **upper surface:** pale olive-green to dark olive-brown, red-brown or darkening, ± smooth to irregularly and slightly pitted or wrinkled; usually dull, occasionally weakly shiny, especially

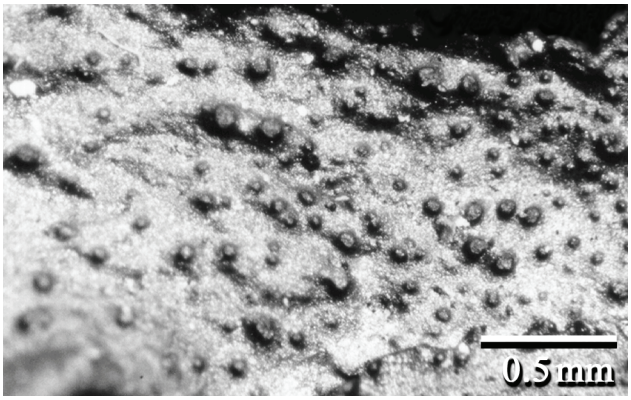
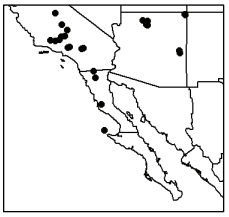


Fig. 58. *Melanelia elegantula*, young isidia with pseudocyphellae at top, photo by T.L Esslinger.

near the lobe ends, frequently lightly to quite heavily pruinose; **isidia:** arising near the lobe ends as small rather evenly scattered, conical to hemispherical papillae (not constricted at the base) with obscure to distinct pseudocyphellae at the tips, growing into usually ± cylindrical isidia up to 1 or occasionally 1.5 mm long and (0.03-) 0.05-0.2 (-0.4) mm diam., often developing unequal side branches; **lower surface:** pale tan to dark brown or black, generally paler near the periphery, or often mottled pale and dark throughout, smooth to irregularly wrinkled or trabeculate in spots, dull to slightly shiny; moderately to

somewhat sparsely rhizinate, the rhizines mostly concolorous with the lower surface; **Apothecia:** infrequent, up to 3.5 mm diam., sessile to very short- stipitate, concave or flattening, the margin entire to crenulate at first, becoming papillate to strongly isidiate; **asci:** clavate, 8-spored; **ascospores:** ellipsoid to broadly ovoid or occasionally almost subglobose, 8-11.5 x 4.5-7 µm; **Pycnidia:** rare, immersed; **conidia:** acerose to fusiform, *c.* 7 x 1 µm; **Spot tests:** upper cortex K-, C-, KC-, P-, HNO_3-; medulla K-, C-, KC-, P-; **Secondary metabolites:** none detected.

Substrate: most common on bark or wood, also on rocks; **World distribution:** northern and western North America, Europe, North and Central Africa, Asia, southern South America; **Sonoran distribution:** widely distributed, from boojum forest in Baja California to montane conifer forests.



Notes: Very few species within the Sonoran region can be confused with *M. elegantula*. *Melanelia fuliginosa*, *M. villosella*, and sometimes *M. subaurifera* and *M. subargentifera* have isidia or isidioid structures, but all are easily distinguished by the C+ red medulla (lecanoric acid), among many other differences. Within the region, only *M. exasperatula* has true isidia and a C- medulla, but clearly differs by its lack of pseudocyphellate papillae, isidia which are spherical to clavate or spatulate and usually hollow, and a much shinier thallus. The extremely variable and usually fertile species *M. subolivacea* sometimes has irregular isidia-like warts or knobs, and occasionally also has pseudocyphellate papillae on the lobes, and such specimens have sometimes been misidentified as *M. elegantula*. However, the warts of *M. subolivacea* are usually very irregular and seldom become elongate or branched as do the true isidia of *M. elegantula*, and so the distinction should usually be easy to make.

Melanelia exasperatula (Nyl.) Essl., Mycotaxon 7: 47 (1978).

Basionym: *Parmelia exasperatula* Nyl., Flora 56: 299 (1873); Illustrations: McCune and Geiser (1997), p. 160; Wirth (1995), p. 643; St. Clair (1999), p. 117; Brodo et al. (2001), p. 434; and Fig. 59 below.

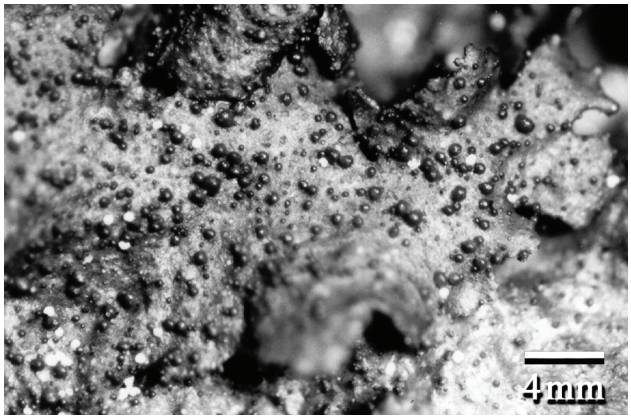


Fig. 59. *Melanelia exasperatula* young isidia, photo by T.L Esslinger.

Thallus: loosely adnate to adnate, appressed throughout or more often somewhat raised at the periphery, foliose, up to 5 cm diam., lobate; **lobes:** broadly rounded, contiguous to ± imbricate, (l-) 2-5 mm broad, ± flat but often with reflexed margins; **upper surface:** pale olive-green to dark olive-brown or red-brown, smooth to slightly and irregularly wrinkled or occasionally ± shallowly and reticulately pitted; often very oily-shiny, especially near the periphery, central areas (and rarely the lobes as well) becoming ± dull, occasionally with a scattered, light pruina; without pseudocyphellae; **isidia:** arising as small hemispherical to spherical papillae, enlarging to form distinctly inflated, clavate to spatulate (rarely spherical), 0.3-1 (-2) mm long, remaining simple or sometimes becoming notched or bifurcate at the tip; **lower surface:** pale tan to dark brown or rarely blackening, uniformly colored or often mottled, ± flat and smooth to irregularly or reticulately wrinkled, somewhat shiny to dull, especially inward; moderately rhizinate, the rhizines ± concolorous with the lower surface or paler; **Apothecia:** uncommon, up to 3 mm diam., ± sessile, weakly concave or flattening, margin at first entire, becoming crenate or crenate-papillate; **asci:** clavate, 8-spored; **ascospores:** broadly ellipsoid to almost subglobose, 8-10.5 x 5.5-8 µm; **Pycnidia:** not seen; **Spot tests:** cortex K-, C-, KC-, P-, HNO_3-; medulla K-, C-, KC-, P-; **Secondary metabolites:** none detected.

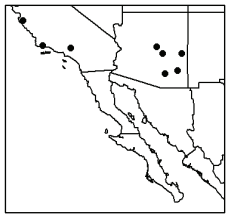
Substrate: bark or wood, rarely on rocks; **World distribution:** western and northern North America, Europe, Asia; **Sonoran distribution:** known from only three Arizonan collections on fir or spruce in mixed conifer forest above 2800 m.

Notes: This species is still most frequently confused with *M. elegantula*, the only other isidiate species with a C- medulla that occurs in the study area. The two are sometimes found growing together, although *M. elegantula* is the much more common of the two. *Melanelia elegantula* is easily distinguished by the less shiny thallus with pseudocyphellate papillae near the margin, and the more cylindrical, usually branched isidia.

Melanelia fuliginosa (Fr. *ex* Duby) Essl. in Egan, Bryologist 90: 163 (1987).

Basionym: *Parmelia olivacea γ. fuliginosa* Fr. *ex* Duby, Bot. Gallicum: 2. 602 (1830); Synonyms: *Parmelia fuliginosa* (Fr. *ex* Duby) Nyl. and *Melanelia glabratula* (Lamy) Essl.; Illustrations: McCune and Geiser (1997), p. 161; Wirth (1995), p. 653; Brodo et al. (2001), p. 435.

Thallus: loosely adnate to adnate; appressed throughout or somewhat reflexed at the periphery, foliose, up to 7 (10) cm diam., lobate; **lobes:** short and rounded to somewhat elongate, contiguous to imbricate, l-3 (-5) mm broad, ± flat; **upper surface:** pale olive-green to olive-brown, reddish brown, dark brown or blackening, smooth to weakly and irregularly pitted and/or wrinkled, rarely becoming lobulate in the center; dull to more often strongly shiny, especially near the periphery; without pseudocyphellae; **isidia:** sparse to dense, ± cylindrical, often branched, attenuate or distinctly knobbed at the end, up to 0.8 (-1.5) mm long and 0.05-0.1 (-0.5) mm diam., easily and frequently broken off near the base and leaving conspicuous white spots; **lower surface:** dark brown to black, somewhat paler near the periphery, occasionally almost smooth but more often rather evenly rugulose, usually distinctly shiny, occasionally dull; moderately rhizinate, the rhizines ± concolorous with the lower surface; **Apothecia:** occasional, up to 6 mm diam., sessile, concave to flattening or somewhat irregular, margin entire when small, soon papillate and/or isidiate, easily and commonly eroded; **asci:** clavate, 8-spored; **ascospores:** ellipsoid to rarely almost subglobose, 10-14 x 5.5-9.5 µm; **Pycnidia:** rare, immersed; **conidia:** weakly bifusiform, 6-7.5 x 1 um; **Spot tests:** cortex K-, C-, KC-, P-, HNO_3-; medulla K- (or K+ violet in occasional pigmented parts), C+ red, P-; **Secondary metabolites:** lecanoric acid, unknown TE-12 (minor) (Esslinger 1977), skyrin (minor, in the lower part of the medulla).



Substrate: rocks or bark, occasionally wood; **World distribution:** western and eastern North America, south in the mountains, Europe; **Sonoran distribution:** on bark in oak forests in California and on rock in montane conifer forests in Arizona.

Notes: This species, with its true isidia and C+ red medulla, is most commonly confused with *M. subaurifera*, a similar species distinguished by much finer, usually unbranched isidia which are accompanied by soredia, and having a much less shiny upper cortex. Poorly developed or otherwise questionable specimens can be distinguished chemically, because *M. subaurifera* lacks unknown TE-12 (Esslinger 1977), which is uniformly present in *M. fuliginosa*. The skyrin often found in the lower part of the medulla in this species is also missing from *M. subaurifera*. An even rarer species that might be confused with *M. fuliginosa* is *M. villosella*.

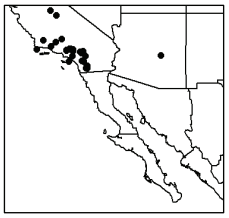
Melanelia glabra (Schaer.) Essl. in Egan, Bryologist 90: 163 (1987).

Basionym: *Parmelia olivacea α. corticola a. glabra* Schaer., Lich. Helvet. Spicileg.: 466 (1840); Synonym: *Parmelia glabra* (Schaer.) Nyl.; Illustrations: Hale and Cole (1988), pl. 5d; Brodo et al. (2001), p. 435.

Thallus: adnate to rather loosely adnate, ± appressed throughout or ascending somewhat at the periphery, foliose, up to 11 (-15) cm diam., lobate; **lobes:** short and rounded to slightly elongate, contiguous to imbricate, 2-5 (-7) mm broad, ± flat; **upper surface:** olive-green to dark olive-brown, sometimes tinged yellowish or reddish,

smooth to somewhat wrinkled or pitted on the lobes, inward soon becoming ± strongly rugose or irregularly papillate, occasionally foliolate; ± dull throughout or occasionally rather shiny on the lobe-ends or over larger areas, occasionally lightly pruinose, bearing tiny, hyaline, cortical hairs, these dense to sparse (rarely totally absent) but usually present at least on some lobe ends and apothecial margins; pseudocyphellae limited to the warts of the upper surface, but, on many thalli, there are pale, pseudocyphelloid lines on the extreme outer edge of the lobes; **lower surface:** dark brown or black, often paler at the margin, smooth to uneven or locally wrinkled, dull to slightly shiny; moderately rhizinate, the rhizines concolorous with the lower surface; **Apothecia:** common, up to 8 (-11) mm diam., sessile to short stipitate, at first concave, becoming irregularly flattened with age, the margin entire when young, soon becoming crenate, crenate-papillate, or even reticulately ridged, the papillae or ridges bearing ± obscure pseudocyphellae, nearly always bearing cortical hairs; **asci:** clavate, 8-spored; **ascospores:** ellipsoid to broadly ovoid, 11-15 x 5.5-8 (-10) µm; **Pycnidia:** common, immersed; **conidia:** ± acerose or cylindrical, (6.5-) 8-9 x 1 µm; **Spot tests:** cortex K-, C-, KC-, P-, HNO_3-; medulla K-, C+ rose or red, KC+ red, P-; **Secondary metabolite:** lecanoric acid.

Substrate: bark, occasionally on rocks; **World distribution:** SW North America, southern Europe, northern Africa, Asia; **Sonoran distribution:** common in California oak forests, known from a single locality in Arizona.



Notes: The other fertile, corticolous species occurring in the Sonoran Region, *M. subolivacea* and *M. multispora*, are easily distinguished by their thinner thalli and C- medulla. Rare saxicolous specimens of *M. glabra* are most likely to be confused with *M. glabroides*, which can be identified by its more lobulate/subpanniform habit, with lobes that are commonly somewhat to strongly reticulately pitted and have few or no cortical hairs, and its sparse or absent apothecia.

Melanelia glabroides (Essl.) Essl., Mycotaxon 7: 48 (1978).

Basionym: *Parmelia glabroides* Essl., Journ. Hattori Bot. Lab. 42: 72 (1977); Illustration: Fig. 60 below.

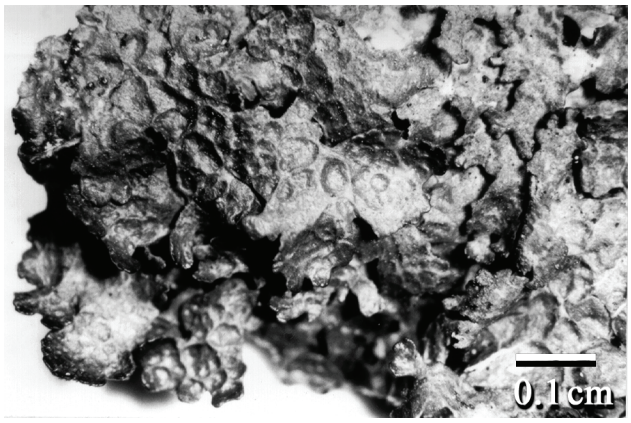
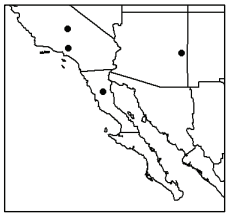


Fig. 60. *Melanelia glabroides*, photo by T.L Esslinger.

Thallus: adnate to loosely adnate, appressed to pulvinate, foliose, up to 8 (-11) cm diam., lobate; **lobes:** short and rounded to somewhat elongate and irregular, contiguous to more often imbricate, 2-3 (-5) mm broad, ± flat; **upper surface:** olive-green to brown or reddish-brown, smooth to more often reticulately ridged and pitted, especially near the periphery, inward often becoming warted and/or lobulate; somewhat shiny on the lobe ends, the central parts or occasionally the entire thallus rather dull, only rarely bearing tiny, hyaline, cortical hairs (like those of *M. glabra*); without pseudocyphellae, but some lobes with linear, pale, pseudocyphelloid lines on the margins (as in *M. glabra*); **lower surface:** usually uniformly black, sometimes brown or even tan on the lobe ends; rather smooth to minutely and irregularly wrinkled or occasionally weakly reticulately ridged, usually dull; moderately rhizinate, the rhizines concolorous with the lower surface; **Apothecia:** rare, up to 6 mm diam., sessile, concave to flattened or irregularly convex; the margin entire when small, becoming minutely to grossly crenate, sometimes with sparse cortical hairs; **asci:** clavate, 8-spored; **ascospores:** ellipsoid, 11-13 x 7-8 µm; **Pycnidia** frequent, immersed; **conidia:** ± acerose to weakly fusiform, 6.5-7.5 x 1 µm; **Spot tests:** cortex K-, C-, KC-, P-,

HNO_3-; medulla K-, C+ rose or red, KC+ red, P-; **Secondary metabolite:** lecanoric acid.

Substrate: rocks, sometimes with mosses; **World distribution:** western North America, from Washington to Colorado, California, Arizona, and Baja California, Mexico; **Sonoran distribution:** infrequent throughout its range; in the study area, this species is known from only four localities.



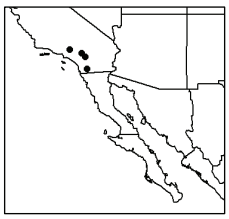
Notes: This species is most closely related to the primarily corticolous species *M. glabra*. Although otherwise completely typical for *M. glabroides*, the single Arizona specimen seen (*Esslinger 15826)*, has a few tiny hyaline cortical hairs on some lobes and on the rim of a single old apothecium. These hairs have not so far been observed in any other specimens of this species. Among herbarium specimens, the species most commonly confused with *M. glabroides* is unrelated *M. tominii*, which sometimes lacks soredia, and also has a C+ rose or reddish medulla (but due to gyrophoric, not lecanoric acid). It can be distinguished from *M. glabroides* by the presence on the lobes of laminal pseudocyphellae, which vary from conspicuous to somewhat obscure, but are not easy to overlook.

Melanelia multispora (A. Schneid.) Essl., Mycotaxon 7: 48 (1978).

Basionym: *Parmelia multispora* A. Schneid., Guide Study Lich.: 154 (1898); Illustrations: McCune and Geiser (1997), p. 162; Brodo et al. (2001), p. 436.

Thallus: adnate to loosely adnate appressed or somewhat raised at the periphery, foliose, up to 7 cm diam., lobate; **lobes:** short and rounded to somewhat elongate and angular, discrete to contiguous or subimbricate, 1-3 (-4) mm broad, flat; **upper surface:** olive-brown to dark reddish-brown, smooth to weakly rugose or pitted at the periphery, inward usually even more so, occasionally developing scattered papillae or tubercles; dull throughout or slightly shiny at the periphery; occasionally pruinose in scattered areas; usually with pseudocyphellae only on the occasional tubercles; **lower surface:** dark brown to black, sometimes pale tan at the periphery or (rarely) throughout; smooth to distinctly rugulose or weakly traberculate; usually somewhat shiny; moderately to densely rhizinate, the rhizines ± concolorous with the lower surface; **Apothecia:** common, up to 4 mm diam., sessile, concave to flat or somewhat convex with age, the margin entire to tuberculate, the tubercles usually pseudocyphellate; **asci:** clavate, 12-32 (usually *c.* 26)-spored; **ascospores:** subglobose to broadly ovoid or ellipsoid, 5.5-10 (-11.5) x 5-8 µm; **Pycnidia:** common, immersed; **conidia:** acerose to slightly fusiform, 5-8 x 1 µm; **Spot tests:** cortex K-, C-, KC-, P-, HNO_3-; medulla K-, C-, KC-, P-; **Secondary metabolites:** none detected.

Substrate: bark of shrubs or trees; **World distribution:** west coast of North America, south-central Alaska to southern California; **Sonoran distribution:** southern California.



Notes: Based on external morphology alone, this species is not consistently distinguishable from closely related *M. subolivacea*. However, fertile specimens are easily identified by their 12-32 ascospores occurring in each ascus. *Melanelia multispora* also has a narrower distribution in western North America, and is not found in the main part of the study area.

Melanelia panniformis (Nyl.) Essl., Mycotaxon 7: 46 (1978).

Basionym: *Parmelia prolixa* f. *panniformis* Nyl., Synop. Method. Lich.: 397 (1860); Synonym*: Parmelia panniformis* (Nyl.) Vain.; Illustrations: Esslinger (1977), p.183; Wirth (1995), p. 655; Brodo et al. (2001), p. 437.

Thallus: adnate to loosely adnate, appressed to pulvinate, usually ± panniform, foliose, up to 7 (-10) cm diam., but at times coalescing into larger patches, lobate; **lobes:** short and rounded to more often somewhat elongate, discrete to ± imbricate, (0.3-) 0.5-1 (-1.5) mm broad, mostly flat; **upper surface:** olive-brown to reddish-brown or dark brown, smooth to weakly pitted at the periphery,

inward essentially the same but usually hidden by numerous small and imbricate lobules; dull or somewhat shiny, occasionally lightly pruinose; without pseudocyphellae on the primary lobes, but occasionally present (but obscure) near the ends of the lobules; without true isidia, the marginal primary lobes with small ± spherical to clavate isidioid lobules, inward these soon developing into dorsiventral lobules; **lower surface:** black, paler at the periphery; smooth to irregularly wrinkled or plicate, dull or slightly shiny; moderately to somewhat sparsely rhizinate, the rhizines concolorous with the lower surface; **Apothecia:** uncommon, up to 3 mm diam., sessile, flat to somewhat concave, the margin at first entire, very soon papillate to tuberculate or becoming lobulate; **asci:** clavate, 8-spored; **ascospores**: ellipsoid, 9-11.5 x 4.5-7 µm; **Pycnidia:** common, immersed; **conidia:** ± cylindrical to weakly fusiform or acerose, (4-) 5-7 x *c.* 1 µm,; **Spot tests:** cortex K-, C-, KC-, P-, HNO_3-; medulla K-, C-, KC- or rarely KC+ faint dingy rose, P-; **Secondary metabolites:** perlatolic and stenosporic acids (both major), occasionally with trace unknowns.

Substrate: rocks; **World distribution:** ± circumpolar in the Northern Hemisphere, south in North America to Arizona and Baja California in the West and to New York in the East, northern and central Europe and possibly throughout Siberia, South America; **Sonoran distribution:** known from only two localities, one in the Chiricahua Moutains of Arizona, and the other in Baja California.

Notes: Within the area of study, the only related species is *M. disjuncta*, which is easily distinguished by the presence of soralia and of obscure submarginal pseudocyphellae on the lobes. The collection of *M. panniformis* from Arizona is typical, although not a very large specimen. The specimen from Baja California is very sparse and poorly developed, and has only a few small lobules beginning to develop. Nevertheless, the morphology is otherwise characteristic, and its identity was confirmed by TLC.

Melanelia subargentifera (Nyl.) Essl., Mycotaxon 7: 48 (1978).

Basionym: *Parmelia subargentifera* Nyl., Flora 58: 359 (1875); Illustrations: Wirth (1995), p. 656; St. Clair (1999), p. 119; Brodo et al. (2001), p. 440; and Fig. 61 below.

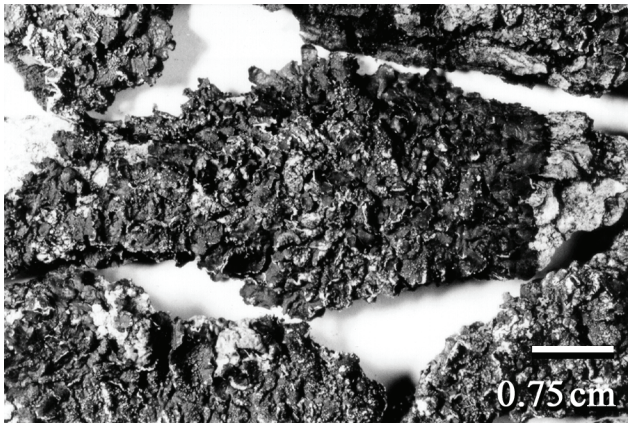
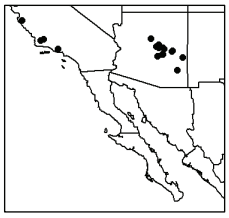


Fig. 61. *Melanelia subargentifera*, photo by T.L. Esslinger.

Thallus: adnate to loosely adnate, appressed but often somewhat raised on the margins and ends of the lobes, foliose, up to 8 (-11) cm diam., lobate; **lobes:** short and rounded to somewhat elongate, discrete to more often contiguous or imbricate, (1-) 2-4 (-7) mm broad, ± flat; **upper surface:** pale olive-brown to dark brown, often with a distinctly reddish or yellowish cast, smooth to distinctly rugose or pitted at the periphery, inward usually somewhat more strongly rugose; dull throughout or occasionally somewhat shiny, very often lightly to rather heavily pruinose, especially near the lobe margins; usually bearing tiny, hyaline, cortical hairs especially near lobe edges, these dense to sparse, but rarely missing altogether; without typical pseudocyphellae, but the lobes in places with linear, sometimes pale, pseudocyphelloid lines on the margins (like those of *M. glabra)*; **soredia:** granular to occasionally rather strongly isidioid, brown to dark brown (whitish when abraded), in laminal and marginal (rarely weakly labriform) soralia; laminal soralia: mostly developing from small pustules by gradual dissolution of the cortex; soralia: punctiform to weakly capitate, often becoming numerous and ± confluent in older parts of the thallus; **lower surface:** dark brown to black, paler at the periphery, smooth to weakly rugose or weakly trabeculate, dull to somewhat shiny; moderately rhizinate, the rhizines ± concolorous with the lower surface;

Apothecia: rare, up to 3 mm diam., sessile, concave to ± flat, the margin very soon becoming sorediate; **asci:** clavate, 8-spored; **ascospores:** ellipsoid to broadly ellipsoid, 11-13 x 7-8.5 µm; **Pycnidia:** rare, immersed; **conidia:** acerose to weakly fusiform or weakly bifusiform, 5-7.5 x 1 µm; **Spot tests:** cortex K-, C-, KC-, P-, HNO_3-; medulla K-, C+ rose-red or red, KC+ red, P-; **Secondary metabolite:** lecanoric acid.



Substrate: bark, wood, and rocks; **World distribution:** western and northern North America, Europe, Central Africa, Asia; **Sonoran distribution:** forested regions, usually between 1500 and 2500 m in Arizona, lower in California.

Notes: This is the most common sorediate species of *Melanelia* in the study area, especially on bark. The usually somewhat uplifted lobes (i.e., not appressed out to the ends), presence of at least sparse hyaline cortical hairs, possession of both laminal and marginal soralia, and the C+ medulla should adequately distinguish it from all others. Much rarer (in the study area) *M. subaurifera* is sometimes confused, but has primarily laminal soredia, usually with very slender true isidia interspersed, and is usually appressed. The most closely related species is *M. albertana*, known from only a single collection in the Sonoran region, and differing by the very distinctly labriform soralia.

Melanelia subaurifera (Nyl.) Essl., Mycotaxon 7: 48 (1978).

Basionym: *Parmelia subaurifera* Nyl., Flora 56: 22 (1873); Illustrations: McCune and Geiser (1997), p. 163; Wirth (1995), p. 657; Hale and Cole (1988), pl. 6a; Brodo et al. (2001), p. 440; and Fig. 62 to right.

Thallus: adnate to loosely adnate appressed throughout or occasionally slightly reflexed at the periphery, foliose, up to 8 (-10) cm diam., lobate; **lobes:** short and rounded to somewhat elongate, discrete to more often contiguous or subimbricate, 1-4 (-6) mm broad, ± flat; **upper surface:** olive-green or olive-brown to rather dark reddish brown, smooth to weakly pitted or rugulose near the periphery, inward usually somewhat more strongly rugose; dull throughout or occasionally shiny, especially near the periphery; sometimes with small and very obscure, concolorous pseudocyphellae on the lobes; sorediate or isidiate or (usually) both; **soredia:** granular, frequently becoming brownish and isidioid or isidiate; in laminal soralia that often arise from the obscure pseudocyphellae and are punctiform and discrete, or become ± confluent in central parts; **isidia:** arising within but also between the soralia, cylindrical, not or infrequently branched, to 0.2 (-0.4) mm long and 0.02-0.06 mm diam.; **lower surface:** pale brown to dark brown or black, often paler at the periphery; ± smooth to rugose, dull to rather shiny; moderately rhizinate, the rhizines concolorous with the lower surface; **Apothecia:** rare, up to 2.5 mm diam., sessile, ± flat, the margin entire when young, soon sorediate and isidiate; **asci:** clavate, 8-spored; **ascospores:** ellipsoid, 10-13 x 5.5-7 µm; **Pycnidia:** rare, immersed; **conidia:** weakly fusiform to weakly bifusiform, 5.5-7 x 1µm; **Spot tests:** cortex K-, C-, KC-, P-, HNO_3-; medulla K-, C+ rose-red or red, KC+ red, P-; **Secondary metabolite:** lecanoric acid.

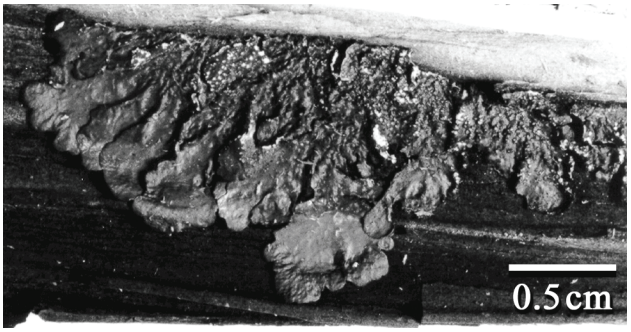


Fig. 62. *Melanelia subaurifera*, photo by T.L Esslinger.

Substrate: bark or wood, rarer on rocks; **World distribution:** much of temperate and boreal North America and Europe, North and Central Africa, Asia; **Sonoran distribution:** infrequent, only in the California part of the Sonoran region.

Notes: The presence of both soredia and true, very slender isidia on the lamina, a C+ medulla, and a mostly appressed thallus will distinguish this species from most others in the genus. *Melanelia subargentifera* has soredia

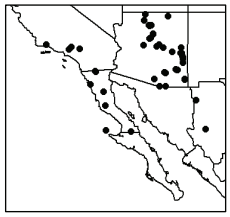
which sometimes become isidioid, but they are much coarser than the isidia of *M. subaurifera*, which also lacks the hyaline cortical hairs characteristic of that species. *Melanelia fuliginosa* sometimes has the thallus surface eroded around its isidia, and this situation has been mistaken for the presence of soredia.

Melanelia subolivacea (Nyl.) Essl., Mycotaxon 7: 49 (1978).

Basionym: *Parmelia subolivacea* Nyl. in Hasse, Bull. Torrey Bot. Club 24: 445 (1897); Illustrations: McCune and Geiser (1997), p. 165; Hale and Cole (1988), pl. 6b; St. Clair (1999), p. 120; Brodo et al. (2001), p. 441.

Thallus: adnate to loosely adnate appressed throughout or somewhat raised at the periphery, foliose, up to 8 (-11) cm diam., lobate; **lobes:** short and rounded, ± contiguous to imbricate, (1-) 2-6 (-l 0) mm broad, ± flat; **upper surface:** olive-brown to dark brown, smooth to weakly rugose or pitted near the periphery, inward becoming more strongly rugose and often grossly so, sometimes with isidioid papillae or tubercles, these verging on true isidia in extreme cases; dull throughout or somewhat shiny on the lobe-ends; pseudocyphellae usually sparse or absent, occasionally rather numerous but even then small and rather obscure, the laminal tubercles developed by some specimens often bearing distinctive pseudocyphellae; **lower surface:** dark brown or black, pale brown to tan at the periphery or occasionally throughout; smooth to rugulose, dull to rather shiny; moderately to rather densely rhizinate, the rhizines concolorous with the lower surface or paler; **Apothecia:** common, up to 5 mm diam., sessile to short stipitate, concave to flattening or sometimes convex, the margin entire to more often crenate or tuberculate, often with rather numerous pseudocyphellae, especially on the tubercles; **asci:** clavate, 8-spored; **ascospores:** ellipsoid to subglobose, (7-) 8-10.5 x 5-8 (-9) µm; **Pycnidia:** common, immersed; **conidia:** acerose to weakly fusiform or weakly bifusiform, 6.5-8.5 (-10) x 1 µm; **Spot tests:** cortex K-, C-, KC-, P-, HNO_3-; medulla K-, C-, KC-, P-; **Secondary metabolites:** none detected.

Substrate: bark or rarely wood; **World distribution:** western North America, Michigan, Canary Islands;



Sonoran distribution: frequent, from coastal islands to mountains of Arizona.

Notes: Typical specimens of *M. subolivacea* are only likely to be confused with *M. multispora*, which is essentially indistinguishable in outward morphology, but has more than eight spores per ascus (usually 12-32), and a more restricted distribution. However, *M. subolivacea* is extremely variable in size, general appearance, and in the amount and size of papillae or tubercles it produces. Specimens with distinctive papillae, especially if they are rather uniformly distributed, are still sometimes misidentified as *M. exasperata*, a species occurring in eastern North America. At times the papillae and tubercles of *M. subolivacea* become so elongate that they appear like very irregular isidia, and these specimens have been often misdetermined as e.g. *M. elegantula*.

Melanelia tominii (Oksner) Essl., Lichenologist 24: 17 (1992).

Basionym: *Parmelia tominii* Oksner, Zh. Bio.-Bot. Tsŷklu, Kŷev 1933 (7-8): 171 (1933); Synonyms: *Melanelia substygia* (Räsänen) Essl., *Parmelia substygia* Räsänen and *Parmelia saximontana* R. A. Anderson & W. A. Weber; Illustrations: Esslinger (1992), pp. 16-18, figs. 1, 2 & 3; Brodo et al. (2001), p. 441 and Fig. 63 on next page.

Thallus: adnate to loosely adnate, appressed to pulvinate or subpanniform, foliose, up to 10 (-14) cm diam., lobate; **lobes:** short and rounded or flabellate to somewhat elongate or occasionally linear-elongate, ± discrete to imbricate, (0.5-) 1-3 (-4) mm broad, flat to weakly convex; **upper surface:** pale olive-brown to yellowish-brown or reddish-brown, dark brown or blackening, sometimes paler at the periphery, smooth to weakly pitted on the lobe-ends, inward smooth to rather strongly fissured and/or rugose; dull throughout or rather shiny, especially near the periphery; pseudocyphellate, the pseudocyphellae laminal, whitish to dark or ± concolorous with the upper surface, very distinct to occasionally rather obscure or

rarely almost lacking; **soredia:** granular to weakly isidioid, but highly variable in number of soralia produced (totally esorediate material is not rare), pale to rather dark brown, in laminal and marginal, punctiform to capitate soralia that arise in part from the pseudocyphellae; **lower surface:** dark brown to black, paler on the lobe ends; smooth to somewhat plicate or rugose, dull to slightly shiny; moderately rhizinate, the rhizines ± concolorous with the lower surface; **Apothecia:** frequent, up to 6 mm diam., sessile to short stipitate, concave to flattening or irregular, the margin entire to weakly crenate, pseudocyphellate and often becoming sorediate; **asci:** clavate, 8-spored; **ascospores:** ellipsoid, 8.5-11 x 4.5-7 µm; **Pycnidia:** common, immersed; **conidia:** cylindrical to weakly fusiform or subbifusiform, 5-7 x *c.* 1 µm; **Spot tests:** cortex K-, C-, KC-, P-, HNO_3-; medulla K-, C+ rose or rose-red, KC+ rose-red, P-; **Secondary metabolites:** gyrophoric acid (major), ovoic acid (minor), unknown WG-2 (minor) (Esslinger 1992).

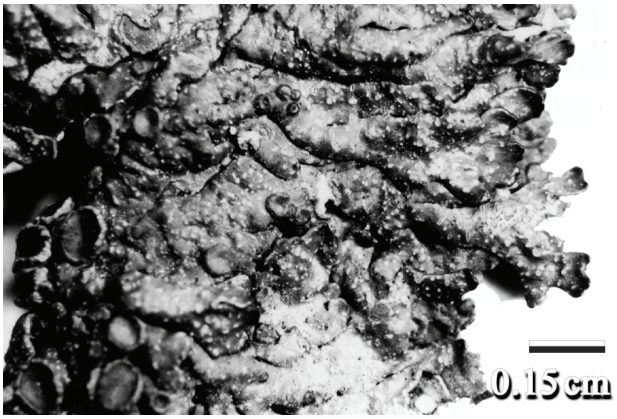
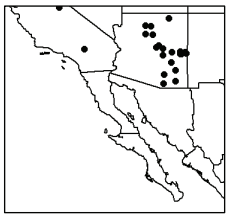


Fig. 63. *Melanelia tominii*, photo by T. Esslinger.



Substrate: rocks; **World distribution:** North America, Europe, North Africa, Asia; **Sonoran distribution:** in forested regions, above 1800 m.

Notes: Unless the sometimes rather obscure pseudocyphellae are overlooked, this species should not be easily confused with any other. The C+ rose or rose-red medulla and laminal pseudocyphellae, usually on relatively narrow lobes, will distinguish it from all others, especially in the study area. When the pseudocyphellae were not recognized, the sparsely sorediate or esorediate specimens have been misidentified as unrelated *M. glabroides*. A more closely related species, *M. disjuncta*, also occurs in the study area and has a somewhat similar appearance, with obscure submarginal pseudocyphellae and darkened soralia, but is easily distinguished by the C- medulla.

Melanelia villosella (Essl.) Essl., Mycotaxon 7: 49 (1978).

Basionym: *Parmelia villosella* Essl., Journ. Hattori Bot. Lab. 42: 96 (1977); Illustration: Fig. 64 below.

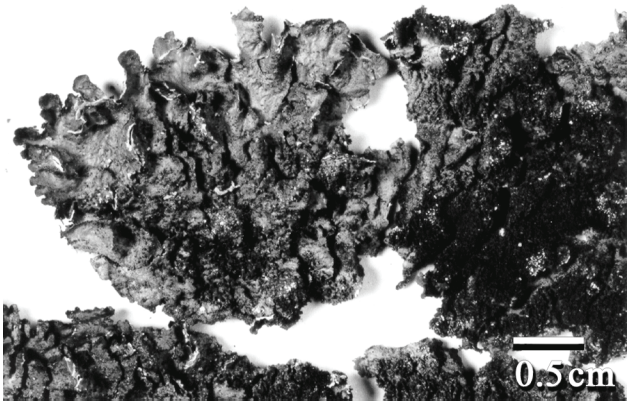


Fig. 64. *Melanelia villosella*, photo by T.L Esslinger.

Thallus: adnate to loosely adnate ± appressed throughout or somewhat ascending at the periphery, foliose, up to 6 cm diam., lobate; **lobes:** short and rounded to somewhat elongate, ± contiguous to imbricate, 2-4 (-5) mm broad, ± flat; **upper surface:** olive-brown to reddish brown, smooth to weakly wrinkled or pitted on the lobe-ends, inward smooth to rugose, dull throughout or slightlv shiny on some lobe ends, with usually rather numerous small, hyaline cortical hairs; without typical pseudocyphellae, but lobe edges in places with linear, sometimes pale abrasions (like those of *M. glabra)*; **isidia:** sparse or more abundant, largely marginal to more often evenly scattered over the thallus, cylindrical, simple or much branched, up to 0.8 mm long and 0.05-0.2 mm diam., usually with many cortical hairs (but see discussion); **lower surface:**

pale tan to black or mottled; smooth to rather strongly wrinkled, especially on the lobe-ends, ± dull; moderately to somewhat sparsely rhizinate, the rhizines concolorous with the lower surface or darkening; **Apothecia:** frequent, up to 3.5 mm diam., sessile to very short stipitate, concave when small, becoming irregularly flattened with age, the margin at first entire, becoming ± crenulate or lacerate, densely hairy, sometimes becoming sparsely isidiate; **asci:** clavate, 8-spored; **ascospores:** ellipsoid, 11.5-14 x 5.5-8 µm; **Pycnidia:** infrequent, immersed; **conidia:** ± acerose to filiform, 6.5-8 (-10) x *c.* 1 µm; **Spot tests:** cortex K-, C-, KC-, P-, HNO_3-; medulla K-, C+ red, KC+ red, P-; **Secondary metabolite:** lecanoric acid.

Substrate: bark or rocks; **World distribution:** Arizona, Utah, northern India, Pakistan, Nepal; **Sonoran distribution:** known from a single locality in Gila County, Arizona.

Notes: This species has not previously been reported for North America, and the identification of the single specimen from Arizona has to be considered tentative. It is a well developed specimen, and although it matches most characters observed in the original Asian material, it lacks the usually numerous cortical hairs of those specimens. However, the pattern of occurrence of these hyaline cortical hairs is variable enough in other species of this group (*M. glabra*, *M. glabroides*, *M. subargentifera*), that their absence from one specimen is inconclusive. There is also one scrappy specimen from Utah (San Juan Co., Devil's Canyon, *Nash 14956* [ASU]) that appears to be this same taxon. If more material is found, and the lack of hairs is constant, a more careful comparison may require recognition of a new taxon. Because of the isidia, this species, especially when lacking cortical hairs, is most likely to be confused with *M. fuliginosa*, but the isidia are coarser, more branched, and rounded at the end (instead of tapered), and the form of the lobes (e.g. ± up-turned lobe margins with pseudocyphelloid lines on the edges) clearly indicate a closer relationship with *M. subargentifera*. That species does sometimes have rather strongly isidioid soredia (when the pustules don't break open in the usual way) and such specimens could be confused with *M. villosella*, but the cortex of these "pseudoisidia" in *M. subargentifera* is dull and unlike that of the rest of the cortex on the upper surface.

MOELLEROPSIS

by P. M. Jørgensen

Moelleropsis Gyeln., in Rabenh., Krypt. Flora 9,2: 257 (1940).

Family: Pannariaceae; Type: *Moelleropsis nebulosa* (Hoffm.) Gyeln.; No. species: one world-wide; Selected lit.: Jørgensen (1978 & 2000a) and Purvis et al. (1992).

Notes: Because the genus is monospecific, it would be repetitious to have a separate generic description. Another species, *Biatora humida* Kullh. has been proposed for transfer into this genus, but that is not supported by molecular data (unpublished).

The Species

Moelleropsis nebulosa (Hoffm.) Gyeln., in Rabenh., Krypt. Flora 9,2: 257 (1940).

Basionym: *Psora nebulosa* Hoffm., Plantae lichenosae: 55 (1794) ; Illustration: Jørgensen (2000a), p. 690.

Life habit: lichenized; **Thallus:** crustose, leprarioid, thin to thick, granular to effuse, becoming irregularly cracked with age; **granules:** crowded, ellipsoid, corticate, 0.03-0.1 mm diam.; **upper surface:** blue-gray to gray-blue-black, smooth to roughened; **upper cortex:** poorly differentiated; **photobiont:** primary one a species of *Nostoc*, secondary photobiont absent; **Apothecia:** sessile or often sunken between thallus

granules that may form a thalline exciple, up to 1 mm diam.; disc: becoming convex, pinkish brown to brown, with an irregular, granular thalline margin; proper exciple: paraplectenchymatous, composed of radiating hyphae, up to 100 µm thick; hymenium: I+ blue-green turning brown, up to 100 µm high; paraphyses: simple, straight, septate, conglutinate, externally brown; hypothecium: pale brown, of intricately interwoven hyphae; **asci:** apically thickened, narrowly cylindrical, thin-walled; apex with an I+ blue apical dome, 8-spored; **ascospores:** simple, colorless, ellipsoid, smooth, sometimes attenuated at one end with a single large oil droplet, 10-15 (-20) x 5-8 µm; **Pycnidia:** unknown; **Spot tests:** all negative; **Secondary metabolites:** none detected.

Substrate and ecology: on sandy, well-drained soil, frequently as a short-lived pioneer species on disturbed soil; **World distribution:** temperate regions of the Northern Hemisphere, rare; **Sonoran distribution:** thus far only known in the Channel Islands on Santa Cruz in southern California.

Notes: Potentially *M. nebulosa* may be confused with *Fuscopannaria cyanolepra*, a species that also occurs on soil. The latter species has a more striking plumbeous color and has corticated, olive-brown squamules centrally. A second subspecies, *M. nebulosa* ssp. *frullaniae* Maass is known from eastern Canada and southwestern Europe, but has not been found in the Sonoran region.

MYCOPORUM

by A. Aptroot

Mycoporum Flot. *ex* Nyl., Mém. Soc. Sci. Nat. Cherbourg 3: 186 (1855).

Family: Xanthopyreniaceae; Type: *Mycoporum elabens* Flot. *ex* Nyl.; No. species: five world-wide; Selected lit.: Harris (1995), and Purvis et al. (1992).

Life habit: non-lichenized, saprobic or rarely lichenized; **Thallus:** crustose, mostly immersed within the substrate, inconspicuous, causing a slight bleaching effect of the substrate; **photobiont:** absent or a trentepohlioid alga; **Ascomata:** perithecial, circular or irregular in outline, often aggregated in pseudostromata; **involucrellum:** dark brown, overlying the locules, K-, clypeate, composed of compacted hyphae mixed with bark cells; outer and lower edges of locules without a distinct true exciple; **ascomatal wall:** black, not continuous below the hamathecium; **hamathecium:** branched, short-celled, ± moniliform pseudoparaphyses, not anastomosing, or only pseudoparenchymatous tissue, often disintegrating at maturity, non-amyloid; **asci:** bitunicate, globose to pyriform, with tholus, non-amyloid, 8-spored; **ascospores:** hyaline, ellipsoid to clavate, transversely 3-5-septate to submuriform with eusepta, 10-18 x 4.5-7µm; walls: not ornamented; **Conidiomata:** unknown; **Secondary metabolites:** none detected; **Geography:** mostly temperate; **Substrate:** on bark, but also on non-calcareous rock.

Notes: The genus is characterized by the globose to pyriform asci and the absence of filamentous hamathecium. Most taxa have multilocular ascomata.

The Species

Mycoporum hippocastani (DC.) Coppins, in Coppins and P. James, Lichenologist 11: 34 (1979).

Basionym: *Verrucaria hippocastani* DC., Fl. Fr., ed. 3, 6: 172 (1815).

Thallus: absent or immersed in the substrate, **upper surface:** grayish; **photobiont:** absent; **Perithecia:** hemispherical, ± circular in outline, unilocular, black, semi-immersed in the bark, 0.1-0.2 mm diam.; **ascomatal wall:** black, absent below the hamathecium; **hamathecium:** pseudoparenchymatic tissue, lacking filaments, not inspersed with oil droplets; **asci:** globose, *c.* 17-25 µm diam., 40-45 µm tall, with 8, irregularly arranged ascospores; **ascospores:** hyaline, clavate, 3-septate (starting

with a median euseptum), becoming submuriform, 14-15 x 5-6 µm; walls: not ornamented, without a gelatinous sheath; **Spot tests:** all negative, UV negative; **Secondary metabolites:** none detected.

Substrate and ecology: on bark of *Quercus* (in Europe often on *Aesculus*); **World distribution:** temperate in the Northern Hemisphere; **Sonoran distribution:** only collected in southern Arizona, on *Quercus*.

Notes: The distantly related *Mycoporum compositum* (A. Massal.) R. C. Harris has been erroneously reported from the area; it has a filamentous hamathecium and is lichenized. It may be confused with *Arthopyrenia* species that have 1 (-3)-septate spores.

MYELOCHROA

by T. H. Nash III and J.A. Elix

Myelochroa (Asahina) Elix and Hale, Mycotaxon 29: 240 (1987).

Family: Parmeliaceae**;** Type: *Myelochroa. aurulenta* (Tuck.) Elix and Hale; No. species: 19 world-wide; Selected lit.: Hale (1976b); Elix (1994g).

Life habit: lichenized; **Thallus:** foliose, ± circular, 5-10 cm diam., loosely adnate to adnate, subdichotomously to irregularly lobate; **lobes:** usually subirregular, sometimes sublinear, 1-4 mm wide, lobe tips subrotund to rotund, ciliate; cilia: simple, in axils of lobes; **upper surface:** gray, sometimes with a yellowish tinge or pale greenish white, emaculate or with simple maculae; with or without soredia or isidia; pseudocyphellae: absent; **upper cortex:** fragile, pored epicortex, palisade plectenchymatous; **medulla:** at least partially pale yellow, yellow-orange or orange-red; cell walls: containing isolichenan; **photobionts**: primary one a *Trebouxia*, secondary photobiont absent; **lower surface:** black, moderately to densely rhizinate; rhizines: black, simple, sparsely furcated or squarrose; **Ascomata:** apothecial, laminal, sessile to subpedicellate; disc: imperforate, brown to dark brown; exciple: gray or hyaline; epihymenium: light brown; hypothecium: hyaline; **asci:** lecanoral, with thickened wall layers apically, with divergent axial body towards apex; apex: amyloid; **ascospores:** *c.* 8 per ascus, spores simple, broadly ellipsoid, 8-15 x 5-8 µm; **Conidiomata:** pycnidial, laminal, immersed; **conidia:** bacilliform or weakly bifusiform, 4-7 x 1 µm; **Secondary metabolites:** upper cortex with atranorin, chloroatranorin and secalonic acides; medulla with ß-orcinol depsidones, hopane triterpenes and secalonic acids; **Geography:** temperate and tropical regions with a distribution center in Japan; **Substrate:** on bark, rarely rock.

Notes: This genus is segregated from *Parmelina*, from which it differs in having a yellow or orange medulla, slightly larger ascospores, and at least partly squarrose rhizines. Also it contains secalonic acids and lacks lecanoric acid. Another segregatge, *Parmelinopsis,* has simple and dichotomously branched rhizines, a white medulla, and lacks secalonic acid derivatives and hopane triterpenes.

The Species

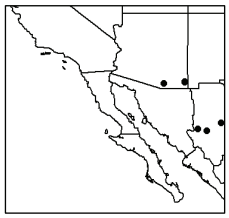
Myelochroa aurulenta (Tuck.) Elix and Hale, Mycotaxon 29: 240 (1987).

Basionym: *Parmelia aurulenta* Tuck.; Synonym: *Parmelina aurulenta* (Tuck.) Hale and see Hale (1976d); Illustration: Hale (1976d), p. 21; Hale (1979), p. 80, both as *Parmelina aurulenta*.

Thallus: foliose, moderately to loosely adnate, ± circular, 4-10 cm broad, subdichotomously to irregularly lobate; **lobes:** sublinear to subirregular, 2-4 mm wide, sinuous in the axils, contiguous to somewhat imbricate; apices: subrotund; margin: entire or crenulate, ciliate; cilia: short, up to 0.8 mm, mostly in lobe axils; **upper surface:** pale green to bluish gray (whitish gray in herbarium), shiny, smooth to rugulose centrally, sorediate; **soredia:** farinose

to granular, arising from coarse pustules or soralia that become broad and diffuse; isidia: absent; **medulla:** white to pale yellow, yellow-orange under the soralia; algal layer continuous; **lower surface:** black with a brown zone (1-5 mm wide) peripherally, smooth to rugulose, densely rhizinate; rhizines: simple to furcate, or squarrosely branched; **Apothecia:** rare, sessile to subpedicellate, 2-5 mm diam.; **ascospores:** poorly developed, 10-12 x 5-7 µm; **Pycnidia:** rare, immersed; **conidia:** bifusiform, 5-6 x 1 µm; **Spot tests:** cortex: K+ yellow, C-, KC-, P-; medulla: K-, C-, KC-, P- or pigmented area turning darker yellow in K; **Secondary metabolites:** upper cortex with atranorin and chloroatranorin and secalonic acid A; medulla with zeorin, leucotylic acid, and, where pigmented, secalonic acid A.

Substrate and ecology: on trees and rocks, in woodlots and along roads in open habitats; **World distribution:** pantropical, eastern North America and Japan; **Sonoran distribution:** rare in the mountains of SE Arizona and extending southwards along the Sierra Madre Occidental in Chihuahua.



NEOFUSCELIA

by T. L. Esslinger

Neofuscelia Essl., Mycotaxon 7: 49 (1977).

Family: Parmeliaceae; Type: *Neofuscelia pulla* (Ach.) Essl..; No. species: 100+ world-wide; Selected lit.: Esslinger (1977 & 1978a).

Life habit: lichenized; **Thallus:** foliose to subcrustose, lobate, tightly to loosely attached or sometimes totally unattached; **lobes:** narrow and linear to broader and rounded, eciliate, with or without isidia, soralia unknown (although pustular isidia are not uncommon), without true pseudocyphellae; **upper surface:** usually some shade of brown, less often greenish black, lacking atranorin, the pigment usually HNO_3+ blue-green or (rarely) HNO_3+ violet, occasionally HNO_3-; plane to rugose, dull to shiny, lightly or not pruinose; **upper cortex:** with pored epicortex, paraplectenchymatous to palisade plectenchymatous; **medulla:** white or rarely pigmented, cell wall containing *Xanthoparmelia*-type lichenan; **lower surface:** tan to dark brown or black, usually moderately rhizinate, but rhizines sparse or missing in some species, the rhizines usually concolorous with the lower surface, not or very little branched; **Ascomata:** apothecial, laminal, with thalline exciple, the **asci:** clavate, 8-spored; **ascospores:** simple and hyaline, ellipsoid to almost globose, 7-12.5 x 3.5-6.5 µm; **Conidiomata:** pycnidial, laminal, blackened and immersed; **conidia:** bifusiform to acerose, 4-7.5 (-9) x *c.* 1 µm; **Secondary metabolites:** upper cortex with unidentified brown pigments (glomellifera brown), medulla with various orcinol depsides or depsidones, β-orcinol depsides or depsidones, aliphatic acids, or scabrosin derivatives; **Geography:** temperate regions of both the Northern and Southern Hemispheres, with centers of diversity in the south, particularly South Africa; **Substrate:** rocks (usually acidic ones) or soil, very rare on wood or bark.

Key to the species of ***Neofuscelia*** from the Sonoran region:

1. Thallus isidiate, the isidia ± cylindrical and with a firm cortex, or becoming pustular and with a soft cortex, often fragmenting into soredioid masses 2
1. Thallus without isidia, usually fertile 5

2. Medulla K+ and/or P+ 3
2. Medulla K- and P- 4

3. Thallus olive-green to greenish-black, upper cortex K+ and HNO_3+ violet; isidia ± cylindrical and with a firm cortex, not pustular ..... ***N. chiricahuensis***
3. Thallus brown, upper cortex K- and HNO_3+ blue-green; isidia pustular, sometimes fragmenting into soredioid masses ..... ***N. subhosseana***

4. Pustular isidia relatively small, 0.1-0.2 mm diam., often darker than the upper cortex (unless abraded/ fragmented); major constituent divaricatic acid, medulla usually C- and KC- but gyrophoric acid or other accessory traces sometimes causing a slight C+ and/or KC+ rose reaction ..... ***N. verruculifera***
4. Pustular isidia often somewhat larger, 0.1-0.5 mm diam., usually not noticeably darkened; major constituents glomelliferic, glomellic, and perlatolic acids, medulla C- to C+ rose or pale yellow, KC+ red turning dingy orange-red ..... ***N. loxodes***

5. Medulla (sometimes only the upper part) K+ and/or P+, β-orcinol depsidones present 6
5. Medulla K- and P-, fatty acids present 7

6. Medulla K+ yellow or turning red-orange, P+ yellow or orange-yellow; major constituents stictic and norstictic acids ..... ***N. atticoides***
6. Medulla K- or faintly yellow, P+ yellow to red-orange (usually darkest near the upper cortex, which is often also P+ red-orange); major constituent fumarprotocetraric acid ..... ***N. occidentalis***

7. Lobes mostly less than 1.5 mm broad; major constituents a pair of unidentified fatty acids (TE-10 and TE-11) ..... ***N. brunella***
7. Lobes 1-3.5 mm broad; major constituents different unidentified fatty acids 8

8. Major constituent unidentified fatty acid TE-8 .... ***N. ahtii***
8. Major constituent unidentified fatty acid TE-13 .... ***N. infrapallida***

The Species

Neofuscelia ahtii (Essl.) Essl., Mycotaxon 7: 49 (1977).

Basionym: *Parmelia ahtii* Essl., Journ. Hattori Bot. Lab. 42: 99 (1978); Illustrations: Esslinger (1977), p. 192 and Fig. 65 to upper right.

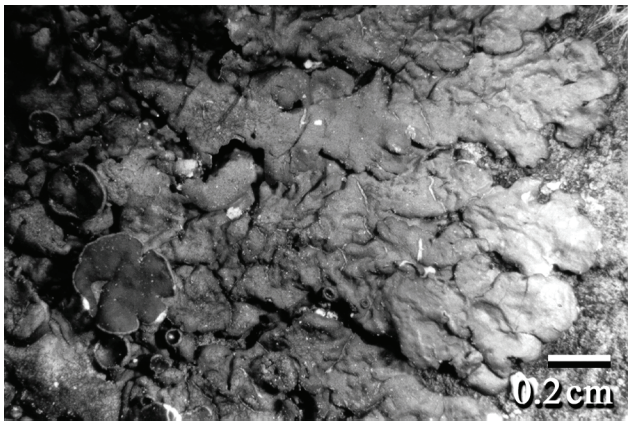
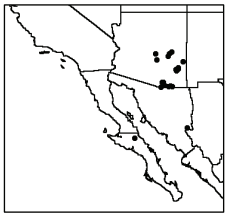


Fig. 65. *Neofuscelia ahtii*, photo by T. L Esslinger.

Thallus: tightly adnate to adnate, appressed throughout or the margins and ends of the lobes somewhat reflexed, foliose, up to 8 cm diam., lobate; **lobes:** somewhat paler near the periphery, short and rounded to somewhat elongate, discrete (but often crowded) to subimbricate, (0.5-) 1-2.5 (-3.5) mm broad, flat to weakly convex; **upper surface:** olive-brown to yellowish or reddish brown, smooth to weakly wrinkled or pitted on the lobes, inward becoming rugose and fissured; dull throughout or slightly shiny on the lobe-ends; **lower surface:** pale tan to pale brown, sometimes with a slightly pinkish tinge, smooth to weakly and irregularly wrinkled, dull; moderately to somewhat more densely rhizinate, the rhizines concolorous with the lower surface or blackening; **Apothecia:** common, up to 3 mm diam., often crowded in the thallus center, sessile to short stipitate, almost flat when young, becoming concave or infolded; margin entire to irregularly incised and ± wavy; **asci:** clavate, 8-spored; **ascospores:** ellipsoid, 8.5-11 x 4.5-6 µm; **Pycnidia:** common, immersed; **conidia:** bifusiform, sometimes very indistinctly so, 5.5-6.5 x 1 µm; **Spot tests:** cortex K-, C-, KC-, P-, HNO_3+ dark green-blue; medulla K-, C-, KC-, P-; **Secondary metabolite:** unknown fatty acid (TE-8).



Substrate: rock; **World distribution:** SW North America; **Sonoran distribution:** Arizona, Baja California Sur in forested regions from 1,000 to 2,000 m.

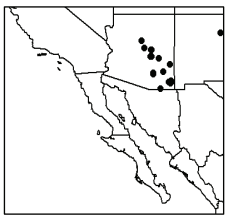
Notes: This is one of three fatty-

acid producing species of *Neofuscelia* occurring in the study area. All three share a usually fertile thallus and a lack of positive spot tests in the medulla, and although some minor tendencies in morphological variation can be observed, positive determinations nevertheless require analysis by thin-layer chromatography, as discussed in the protologue (Esslinger 1977).

Neofuscelia atticoides (Essl.) Essl., Mycotaxon 7: 49 (1978).

Basionym: *Parmelia atticoides* Essl., Journ. Hattori Bot. Lab. 42: 101 (1977); Illustrations: Esslinger (1977), p. 193; Hale (1979), p. 146; Brodo et al. (2001), p. 450.

Thallus: tightly adnate to adnate, appressed, foliose, up to 6 cm diam., lobate; **lobes:** and rounded to slightly elongate and sublinear, contiguous to subimbricate, 0.5-3 mm broad, flat to weakly convex; **upper surface:** olive-brown to reddish brown or dark brown, short rather smooth throughout or becoming fissured and/or rugose inward, the central parts sometimes developing scattered upward-arching lobules; dull to somewhat shiny, especially near the lobe-ends; **lower surface:** pale tan to pale brown, occasionally darkening on some lobe ends; ± smooth, dull; moderately to rather sparsely rhizinate, the rhizines concolorous with the lower surface; **Apothecia:** common, up to 5 (-7) mm diam., sessile, concave or flattening to slightly convex, the margin entire to slightly crenate or lacerate; **asci:** clavate, 8-spored; **ascospores:** ellipsoid, 9-10.5 x 4.5-5 µm; **Pycnidia:** common, immersed; **conidia:** bifusiform, 4.5-7 x 1 µm; **Spot tests:** cortex K -, C-, KC-, P-, HNO_3 + dark blue-green; medulla K+ yellow or yellow turning red-orange, C-, P+ yellow-orange or orange; **Secondary metabolites:** stictic acid (major), norstictic acid (minor), constictic acid (trace).



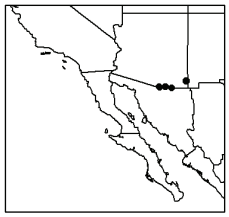
Substrate: rock; **World distribution:** SW North America; **Sonoran distribution:** Arizona, forested regions from 1000 to 2800 m.

Notes: In the American Southwest, five fertile and non-isidiate species of *Neofuscelia* occur, but this one is easily distinguished from the others by its distinctive medullary chemistry (stictic and norstictic acids) and corresponding medullary spot test reactions. Only *N. occidentalis* has similar spot tests, although usually either the medulla or the cortex (or both) are distinctly P+ red-orange, a more pronounced reaction than that observed in *N. atticoides*.

Neofuscelia brunella (Essl.) Essl., Mycotaxon 7: 50 (1978).

Basionym: *Parmelia brunella* Essl., Journ. Hattori Bot. Lab. 42: 103 (1977); Illustration: Esslinger (1977), p. 193.

Thallus: tightly adnate to adnate, appressed, foliose, up to 7 cm diam., lobate; **lobes:** short and rounded to somewhat elongate and sublinear, discrete to ± contiguous, 0.3-1.5 mm broad, flat to slightly convex; **upper surface:** olive-brown or yellowish brown to rather dark brown, smooth throughout or weakly fissured or rugose in the older parts; dull throughout or slightly shiny near the lobe ends; **lower surface:** pale tan (some specimens have scattered areas of lower cortex with a purplish-red pigment which reacts K+ purple), ± smooth, dull; moderately to rather sparsely rhizinate, the rhizines concolorous with the lower surface; **Apothecia:** common, sometimes occurring even close to the thallus periphery, up to 1.5 mm diam., sessile, flat to slightly concave when young, usually becoming convex, the margin entire to weakly lacerate; **asci:** clavate, 8-spored; **ascospores:** ellipsoid, 8.5-10 x 4-5 µm; **Pycnidia:** common; **conidia:** bifusiform, 4-5 (-6) x 1 µm; **Spot tests:** cortex K-, C-, KC-, P-, HNO_3+ dark blue-green; medulla K-, C-, KC-, P-; **Secondary metabolites:** unknown fatty acids TE-10 and TE-11 (both major) (Esslinger 1977).



Substrate: rocks; **World distribution:** SW North America; **Sonoran distribution:** Arizona, forested regions from 1200 to 2000 m.

Notes: Three fertile species of *Neofuscelia* in SW North America produce only fatty acids in the medulla and therefore lack any positive spot tests. Although *N. brunella* is usually smaller and narrower lobed than the other two of these (*N. ahtii, N.*

infrapallida), certain differentiation of these three species requires analysis by thin-layer chromatography and comparison of Rf values according to those published in the protologue (Esslinger 1977).

Neofuscelia chiricahuensis (R. A. Anderson & W. A. Weber) Essl., Mycotaxon 7: 53 (1978).

Basionym: *Parmelia chiricahuensis* R. A. Anderson & W. A. Weber, Bryologist 65: 234 (1962); Illustrations: Esslinger (1977), p. 211; and Fig. 66 below.

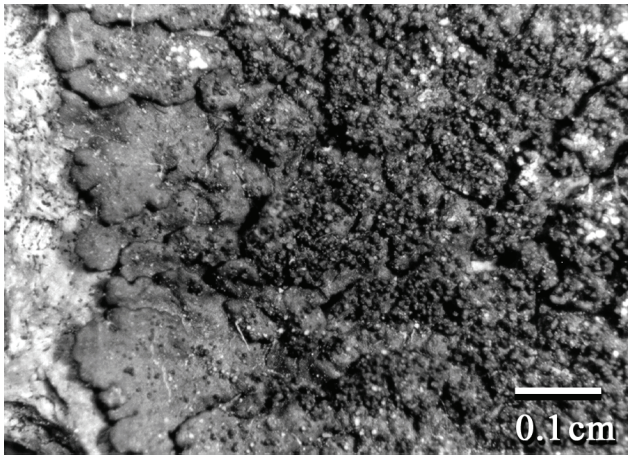
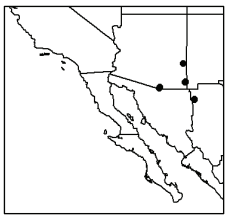


Fig. 66. *Neofuscelia chiricahuensis*, photo by T.L Esslinger.

Thallus: tightly adnate to adnate, appressed, foliose, up to 4 cm diam. but sometimes coalescing into larger patches, lobate; **lobes:** short and rounded to more elongate or irregularly sublinear, subdiscrete to contiguous or slightly imbricate, 0.5-2.5 mm broad, flat to somewhat convex; **upper surface:** dark olive-green to greenish black, mostly smooth at the periphery, inward becoming fissured or rugose-areolate; dull throughout or slightly shiny on the lobe ends; **isidia:** becoming numerous, cylindrical or sometimes knobbed at the end, simple or branched, up to *c.* 0.6 (-1) mm long and 0.1-0.15 mm in diam.; **lower surface:** black, ± smooth and flat, dull to slightly shiny; moderately to somewhat sparsely rhizinate, the rhizines simple and concolorous with the lower surface; **Apothecia:** frequent, up to 4 mm diam., sessile, concave when young, flattening to weakly convex, the margin at first entire, becoming papillate-crenate and sometimes isidiate; **asci:** clavate, 8-spored; **ascospores:** ellipsoid to subglobose, 7-8 x 4.5-6.5 µm; **Pycnidia:** infrequent, immersed; **conidia:** bifusiform, 4.5-6 x *c.* 1 µm; **Spot tests:** cortex K+ and HNO_3+ violet, C-, KC-, P-; medulla K+ yellow turning orange-red, C-, KC-, P+ orange; **Secondary metabolites:** stictic acid, (major), norstictic acid (minor), constictic acid (accessory).



Substrate: rocks; **World distribution:** SW North America, including west Texas; **Sonoran distribution:** mountains of Arizona and Chihuahua, from *c.* 1,000 to 2,000 m.

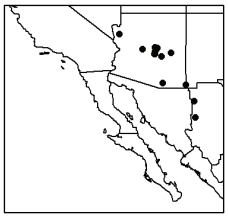
Notes: This is the most distinctive species of *Neofuscelia* in the study area. The closely appressed, isidiate thallus, and unusual greenish-black upper surface with a K+ violet spot test, make this species difficult to confuse with any other. Other isidiate species in the genus have the more typical HNO_3+ blue-green reaction on the cortex, and those occurring in the Sonoran region all have pustular rather than the distinctly cylindrical isidia of *N. chiricahuensis*. The only closely related species is *N. atroviridis*, a species from southern Africa with similar cortical and medullary spot tests, which lacks isidia. A few saxicolous and isidiate species in the related genus *Melanelia* might be initially confusable, but they lack positive cortical spot tests and medullary spot tests are either negative or only C+.

Neofuscelia infrapallida (Essl.) Essl., Mycotaxon 7: 50 (1978).

Basionym: *Parmelia infrapallida* Essl., Journ. Hattori Bot. Lab 42: 116 (1977); Illustration: Esslinger (1977), p. 197.

Thallus: rather tightly adnate to adnate, ± appressed throughout, foliose, up to 6 cm diam., lobate; **lobes:** short and rounded or slightly elongate, contiguous or becoming imbricate, 1-3 mm broad, ± flat; **upper surface:** olive-brown to yellowish or copper-brown, paler at the periphery, smooth to weakly wrinkled or pitted at the periphery, inward becoming rather strongly rugose-warted or fissured; dull throughout or slightly shiny on the lobe

ends; **lower surface:** pale tan (some specimens have scattered areas of lower cortex with a purplish-red pigment which reacts K+ purple), smooth and dull to slightly shiny; moderately to somewhat more densely rhizinate, the rhizines concolorous with the lower surface or darkening; **Apothecia:** common, up to 6.5 mm diam., sessile or short stipitate, concave to irregularly folded inward, the margin entire at first, but soon grossly crenate or lacerate; **asci:** clavate, 8-spored; **ascospores:** ellipsoid, 8-10.5 x 4.5-6 µm; **Pycnidia:** common, immersed; **conidia:** bifusiform, 5.5-8.5 x l-1.5 µm; **Spot tests:** cortex K-, C-, KC-, P-, HNO_3+ dark blue-green; medulla K-, C-, KC-, P-; **Secondary metabolite:** unknown fatty acid TE-13.



Substrate: rocks; **World distribution:** SW North America; **Sonoran distribution:** Arizona and Chihuahua, in mountainous regions, from 1200 to 2100 m.

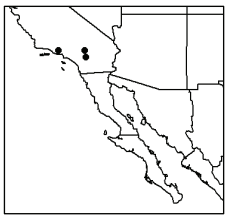
Notes: This species can only be distinguished from *N. ahtii* and *N. brunella* with certainty on the basis of chemistry. All three produce unidentified fatty acids in the medulla, and must therefore be distinguished by TLC analysis and comparison of Rf values as published in the protologue (Esslinger 1977).

Neofuscelia loxodes (Nyl.) Essl., Mycotaxon 7: 51 (1978).

Basionym: *Parmelia loxodes* Nyl., Flora 55: 426 (1872); Synonym: *Parmelia isidiotyla* Nyl., Flora 58: 8 (1875); Illustrations: Esslinger (1977), p. 199; Hale (1979), p. 128; McCune and Geiser (1997), p. 168; Brodo et al. (2001), p. 450; and Fig. 67 to right.

Thallus: adnate to rather loosely adnate, appressed to pulvinate, foliose, up to 11 (-14) cm diam., lobate; **lobes:** short and rounded to somewhat elongate and angular, ± contiguous to imbricate or somewhat entangled, (0.5-) 1-3 (-5) mm broad, ± flat; **upper surface:** pale yellow (rarely) to yellowish or reddish brown, occasionally dark brown, usually paler at the periphery, smooth to weakly wrinkled or pitted at the periphery, inward becoming rugose and/or fissured; dull throughout or slightly shiny on the lobe ends, occasionally pruinose, especially on the lobe ends; **isidia:** laminal, sparse to dense, ± spherical and distinctly pustular, 0.1-0.5 mm in diam., sometimes proliferating to form rather deep cushions, easily abraded and then mistaken for soredia; **lower surface** dark brown to black, sometimes paler on the lobe ends; smooth to somewhat rugulose, ± dull; moderately rhizinate, the rhizines concolorous with the lower surface; **Apothecia:** uncommon, up to 6 mm diam., sessile to short stipitate, concave or flattening, the margin entire to slightly crenate, when older often bearing pustular isidia; **asci:** clavate, 8-spored; **ascospores:** ellipsoid, 8-10 x 4-5 µm; **Pycnidia:** rare, immersed; **conidia:** bifusiform, 5-6 x 1 µm; **Spot tests:** cortex K-, C-, KC-, P-, HNO_3+ pale to dark blue-green; medulla K- or dingy, C- or C+ slow yellow or (rarely) C+ rose, KC+ red turning dingy orange-red, P-; **Secondary metabolites:** glomelliferic and glomellic acids (both major), perlatolic acid (minor), rarely with gyrophoric acid (minor).

Fig. 67. *Neofuscelia loxodes*, photo by T.L Esslinger.



Substrate: rock, very rare on wood or bark; **World distribution:** western North America, Europe, North Africa, Asia; **Sonoran distribution:** infrequent, in southern California.

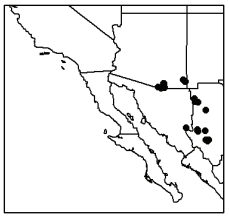
Notes: *Neofuscelia loxodes* is morphologically most like *N. subhosseana*, which however can be easily distinguished by the K+ yellow turning red medullary spot test (hypostictic acid, et al.). A mor-

phologically similar species which also has spot tests similar to those of *N. loxodes*, is *N. verruculifera*, which differs by the somewhat darker, smaller thalli, with narrower and thinner, mostly emaculate lobes, and production of divaricatic acid as the major constituent. That species is usually KC- or very faint in the medulla, unless accessory gyrophoric acid is present. Occasional specimens of these two species will require TLC analysis to be certain of their identity, especially poorly developed ones.

Neofuscelia occidentalis (Essl.) Essl., Mycotaxon 7: 51 (1978).

Basionym: *Parmelia occidentalis* Essl., Journ. Hattori Bot. Lab. 42: 128 (1977).

Thallus: moderately to somewhat loosely adnate, appressed, foliose, up to 8.5 cm diam., lobate; **lobes:** short and rounded or somewhat elongate and sublinear, ± contiguous or imbricate, (0.5-) 1-2 mm broad, ± flat; **upper surface:** olive- to yellowish brown or dark brown, smooth near the periphery, inward becoming moderately fissured or fissured-rugose, occasionally somewhat warted; dull throughout or slightly shiny on the lobe ends; **lower surface:** pale tan to pale brown; ± smooth and dull; moderately rhizinate, the rhizines concolorous with the lower surface or darkening; **Apothecia:** common, up to 3 mm diam., sometimes rather crowded inward, sessile, flat to concave or sometimes irregularly convex; the margin entire to somewhat crenulate; **asci:** clavate, 8-spored; **ascospores:** ellipsoid to broadly ovoid, 7-9.5 x 4.5-5.5 µm; **Pycnidia:** common, immersed; **conidia:** bifusiform to unequally bifusiform or weakly clavate, 4.5-5.5 x 1 µm; **Spot tests:** cortex K-, C-, KC-, P-, HNO_3- blue-green; medulla K-, C-, KC-, P+ yellow to orange-red, especially near the upper cortex, occasionally P- in some parts; **Secondary metabolites:** fumarprotocetraric and often caperatic acids (both major), protocetraric acid (minor or trace), virensic acid (accessory).



Substrate: rocks; **World distribution:** SW North America in Mexico and U.S.A.; **Sonoran distribution:** from 1350 to 2750 in the mountains of Arizona, Chihuahua and Sonora.

Notes: This species has been found to be more chemically variable than originally reported. Fumarprotocetraric acid is constant, but caperatic acid, in somewhat variable amounts, was detected in only 60-70% of the specimens. Protocetraric acid and virensic acid also occur in relatively low frequency and low concentration. The medullary spot test with P is variable, and specimens with caperatic acid often have only a slight P reaction in the medulla, but a stronger reaction near and in the upper cortex. The cortical P reaction is also visible on the surface, at least in some of the paler lobe ends. Specimens with a weak P reaction in the medulla might be mistaken for *N. atticoides*, but that species usually has a fairly distinctive K+ yellow turning red-orange reaction.

Neofuscelia subhosseana (Essl.) Essl., Mycotaxon 7: 52 (1978).

Basionym: *Parmelia subhosseana* Essl., Journ. Hattori Bot. Lab. 42: 148 (1977); Illustration: Brodo et al. (2001), p. 451.

Thallus: adnate to somewhat more loosely adnate; ± appressed, foliose, up to 7 cm diam., lobate; **lobes:** short and rounded, contiguous to somewhat imbricate, (0.5-) 1-2 (-3) mm broad, ± flat; **upper surface:** reddish brown to dark olive-brown, often paler and more yellowish at the periphery, smooth on the lobe ends, inward often becoming rather strongly rugose; dull throughout or slightly shiny on the lobe ends, sometimes lightly pruinose on some lobe ends; **isidia:** sparse to dense, pustular, 0.05-0.3 mm in diam., sometimes clustered; **lower surface:** dark brown to black, sometimes much paler on the lobe ends, ± smooth and dull; moderately rhizinate, the rhizines concolorous with the lower surface; **Apothecia** and **pycnidia:** not seen; **Spot tests:** cortex K-, C-, KC-, P-, HNO_3+ dark blue-green; medulla: K+ yellow tuming red, C-, P+ very pale orange or P-; **Secondary metabolites:** hypostictic acid (major), hyposalazinic and hypoconstictic acids (both minor), usually with a trace of unknown TE-2 (Esslinger1977).

Substrate: rock; **World distribution:** western North America, South America, New Zealand, South Africa; **Sonoran distribution:** see note below.

Notes: This species is most like *N. loxodes*, with similar thallus coloration and pustular isidia, but clearly distinguished by the production of hypostictic acid and other related β-orcinol depsidones in the medulla. The K+ spot test will easily distinguish *N. subhosseana* from *N. loxodes*. *Neofuscelia subhosseana* has not yet been found from the Sonoran Region as defined for this study. However, it occurs just outside the study area, in central California (San Mateo and Mono Counties) and in Utah (Zion National Park), and seems a likely candidate to eventually be found here as well.

Neofuscelia verruculifera (Nyl.) Essl., Mycotaxon 7: 53 (1978).

Basionym: *Parmelia verruculifera* Nyl., Flora 61: 247. (1878); Illustrations: Esslinger (1977), p. 210; Wirth (1995), p. 658; and Fig. 68 below.

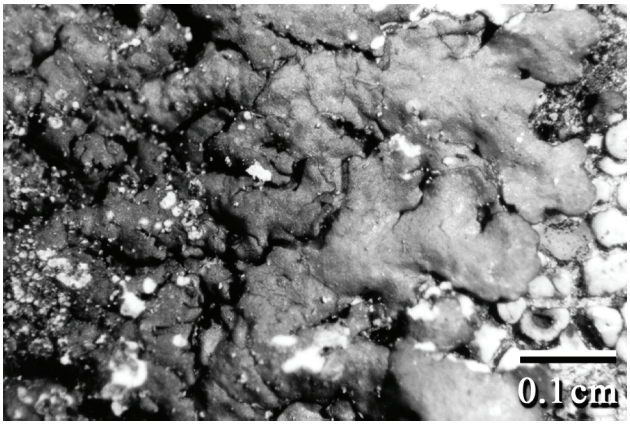
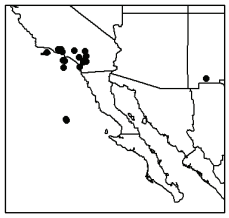


Fig. 68. *Neofuscelia verruculifera*, photo by T.L Esslinger.

Thallus: adnate to rather loosely adnate, ± appressed throughout, foliose, up to 11 cm diam., lobate; **lobes:** short and rounded to somewhat elongate, contiguous to imbricate, only rarely discrete, (0.3-) 1-2 (-3) mm broad, ± flat; **upper surface:** olive-brown to reddish brown or dark brown, at times distinctly paler and more yellowish at the periphery, smooth to weakly wrinkled or pitted on the lobe ends, inward usually somewhat rugose or fissured, sometimes strongly so; dull throughout or slightly shiny on the lobe ends, occasionally lightly pruinose; **isidia:** sparse to dense, pustular, 0.06-0.2 (-0.3) mm diam., sometimes proliferating to form rather deep patches, these at times resembling soralia, especially when abraded; **lower surface:** very dark brown to black sometimes paler on the lobe ends; ± smooth and dull; moderately rhizinate, the rhizines concolorous with the lower surface; **Apothecia:** rare, up to 3.5 mm diam., sessile to short stipitate, concave or flattening, the margin entire to weakly crenulate, becoming isidiate; **asci:** clavate, 8-spored; **ascospores:** ellipsoid, 8-10 x 4.5-6 µm; **Pycnidia:** rare, immersed; **conidia:** bifusiform to almost fusiform, 5-6.5 x 1 µm; **Spot tests:** cortex K-, C-, KC-, P-, HNO_3+ dark blue-green; medulla K-, C- or C+ rose, KC- or KC+ rose or red, P-; **Secondary metabolites:** divaricatic acid (major), oxostenosporic and gyrophoric acid (both minor or trace), and unknown TE-3 (accessory).



Substrate: rocks, very rarely on wood or bark; **World distribution:** western North America, Europe, North Africa; **Sonoran distribution:** central and southern California and Guadalupe Island (Baja California).

Notes: In North America, the only species that might be easily confused with this one is *N. loxodes*, which can have similar spot test reactions, and also has pustular isidia. Although considerable overlap occurs, normally, that species has slightly paler thalli with lobes that are wider, thicker and more distinctly maculate, and the pustular isidia are also usually somewhat larger. Chemically, the two are very distinct, since *N. loxodes* produces glomelliferic, glomellic and perlatolic acid, which give a distinctive KC+ red turning dingy orange-red spot test in the medulla. *Neofuscelia verruculifera* often has a KC- spot test, although the presence of accessory gyrophoric acid can result in spot test reactions confusingly similar to those of *N. loxodes*. Among collections examined, this species was occasionally confused with various sorediate species of *Melanelia* such as *M. disjuncta* (all HNO_3-).

NEPHROMA

by C. M. Wetmore and T. H. Nash III

Nephroma Ach., Lich. Univ. 521 (1810).

Family: Peltigeraceae; Type: *Nephroma arcticum* (L.) Torss.; No. species: *c.* 36 world-wide; Selected lit.: Wetmore (1960) and James and White (1987).

Life habit: lichenized; **Thallus:** foliose, continuous and rosette-forming or rarely fragmentary, 3-10 cm wide, loosely adnate, lobate; **lobes:** irregular, broadly elongate, marginally entire or indented, with or without lobules; apices: usually subrotund to rotund, often ascending, ecilliate; **upper surface:** gray brown to brown or yellow-green (non-Sonoran species), pruinose or not, with or without soredia or isidia; **upper cortex:** pseudoparenchymatous, 10-30 µm thick; **medulla:** white or yellow, with loose hyphae, 40-260 µm thick; **photobionts:** primary one either a chlorococcoid alga (*Coccomyxa*) or cyanobacterium (*Nostoc*); secondary photobiont of *Nostoc* present in internal cephalodia in chlorococcoid species; **lower cortex:** pseudoparenchymatous, 20-40 µm thick; **lower surface:** pale brownish to brown or yellow-green, glabrous, pubescent or tomentose; rhizinae, cyphellae and pseudocyphellae absent; **Ascomata:** apothecial, sessile or immersed on the lower surface at tips of lobes, orbicular or reniform, cup-shaped, sessile, margin: prominent with thalloid rim; disc: pale brown or red-brown to dark brown; exciple: hyaline or light brown, 20-30 µm thick, epithecium: brown or brownish yellow; hymenium: colorless, 60-90 µm tall; paraphyses: unbranched; hypothecium: hyaline; **asci:** simplified "*Peltigera*"-type, *c.* 8-spored; **ascospores:** subfusiform to fusiform, pale brown, 3-septate, thin walled, 10-18 x 6-10 µm; **Conidiomata:** pycnidial, marginal, semi-immersed, punctiform, ostiole dark; **conidia:** bacilliform, 9-16 x 1 µm; **Secondary metabolites:** hopane triterpenoids, depsides and pigments; **Geography:** cosmopolitan, polar, boreal-montane and coastal, temperate forests; both Northern and Southern Hemispheres; **Substrate:** commonly on bark, acidic rock or soil.

Notes: It is similar chemically and morphologically to *Peltigera* but lacks the veins found on the lower surface of the latter genus. The presence of a lower cortex in *Nephroma* also distinguishes it from *Peltigera*. Among all foliose genera in this region, the presence of apothecia on the lower surface of the lobes in *Nephroma* is unique.

Key to the species of ***Nephroma*** from the Sonoran region:

1. Lower surface papillate, usually tomentose ..... ***N. resupinatum***
1. Lower surface not papillate, tomentose or not 2

2. Thallus sorediate ..... ***N. parile***
2. Thallus not sorediate 3

3. Thallus isidiate; isidia thick; margin often lobulate ..... ***N. helveticum***
3. Thallus not isidiate; margin not lobulate ..... ***N. bellum***

The Species

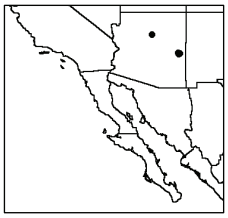
Nephroma bellum (Spreng.) Tuck., Boston J. Nat. Hist. 3: 293 (1840).

Basionym: *Peltigera bella* Spreng., Syst. Veg. ed. 16. 4: 306 (1827); Synonyms: see Wetmore (1960); Illustrations: McCune and Geiser (1997), p. 170; Brodo et al. (2001), p. 453.

Thallus: foliose, 3-8 cm wide, loosely adnate, lobate; **lobes:** irregular, 2-6 mm wide, elongate; apices: usually subrotund, entire or with small lobules; **upper surface:** medium to dark brown, shiny or very slightly pubescent; without soredia or isidia but very rarely with regeneration squamules; **medulla:** white; **photobiont:** the cyanobacterium *Nostoc*; **lower surface:** pale brown to yellow-brown, usually rugulose, glabrous to weakly pubescent; **Apothecia:** immersed on lower surface at tips of lobes, orbicular, cup-shaped, sessile; margin: prominent with

thalloid rim; disc: medium brown to dark brown; exciple: hyaline or light brown, 20-30 µm thick; epithecium: brown or brownish yellow; hypothecium: hyaline; **asci:** *c.* 8-spored; **ascospores:** subfusiform, 3-septate, 17-21 x 5-6 µm; wall thick, light brown; **Pycnidia:** laminal, immersed, punctiform, 0.09-0.15 mm diam.; **conidia:** rod-shaped, 4-5 x 1-2 µm; **Spot tests:** upper surface: K-, C-, KC-, P-; medulla K+ pale yellow or K-, C-, KC-, P-; **Secondary metabolites:** upper cortex with an unknown brown pigment; medulla with triterpenes with: hopane-6α, 22-diol [zeorin] (major) and 15α-acetoxyhopane-22-ol [nephrin?].

Habitat and ecology: on rocks and tree trunks in moist canyons at mid- to high elevations, most common in spruce-fir regions; **World distribution:** Africa and Northern Hemisphere, where it occurs in subarctic, boreal and north temperate regions and extends south along the mountain chains; **Sonoran distrbution:** central and eastern Arizona.

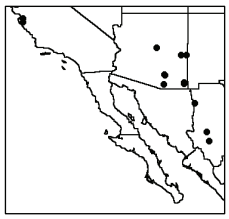


Nephroma helveticum Ach., Lich. Univ. 523 (1810).

Synonyms: see Wetmore (1960); Illustrations: McCune and Geiser (1997), p. 171; Brodo et al. (2001), p. 454.

Thallus: foliose, continuously or irregularly forming rosettes, 3-8 cm wide, loosely adnate, lobate; **lobes:** irregular, 2-4 mm wide, elongate; lobe tips: usually subrotund, frequently dissected marginally in teeth-like pattern; **upper surface:** usually medium to dark brown or red-brown, rarely gray-brown, shiny or somewhat pubescent, isidiate; **isidia:** initially cylindrical but becoming flattened, 0.1-0.2 mm diam.; without soredia but frequently with regeneration squamules that may cover the whole thallus; **medulla:** white; **photobiont:** the cyanobacterium *Nostoc*; **lower surface:** dark brown to black but paler at the margins, pubescent or tomentose but not papillate; **Apothecia:** common, immersed on lower surface at tips of lobes, orbicular, up to 8 mm diam., cup-shaped, sessile; dorsal surface: scabrid and often markedly honey-combed; margin: prominent with thalloid, pectinate rim; disc: dark brown; exciple: hyaline or light brown, 20-30 µm thick; epithecium: brown or brownish yellow; hypothecium: hyaline; **asci:** 8-spored; **ascospores:** subfusiform; 3-septate, 20-27 x 6-8 µm; wall: thick, light brown; **Pycnidia:** marginal, immersed, punctiform, 0.09-0.15 mm diam.; **conidia:** rod-shaped, 3-4 x 1-2 µm; **Spot tests:** upper surface: K-, C-, KC-, P-; medulla K+ pale yellow or K-, C-, KC-, P-; **Secondary metabolites:** upper cortex with unknown brown pigment; medulla with triterprenes 7β acetoxyhopan-22-ol, hopane-7β, 22-diol and an accessory unknown.

Habitat and ecology: on acidic rocks among mosses in moderate shade and tree trunks in moist canyons at mid- to high elevations, most common in spruce-fir regions; **World distribution:** Africa, Australasia and throughout the Northern Hemisphere, where it occurs in boreal and north temperate regions and extends south along the west coasts in maritime influenced regions; **Sonoran distribution:** central and SE Arizona and the Sierra Madre Occidental region of Chihuahua.



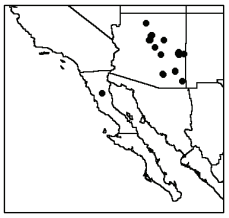
Nephroma parile (Ach.) Ach., Lich. Univ. 522 (1810).

Basionym: *Lichen parilis* Ach., Lich. Suec. Prod. 164 (1798); Synonyms: see Wetmore (1960); Illustrations: Wirth (1995), p. 607; McCune and Geiser (1997), p. 174; Brodo et al. (2001), p. 456.

Thallus: foliose, continuously forming rosettes or fragmentary, 3-8 (-15) cm wide, loosely adnate, lobate; **lobes:** irregular, broad (3-8 mm wide), elongate, often thin; apices: usually subrotund, entire or frequently dissected marginally in teeth-like pattern, rarely ascending; **upper surface:** usually medium to dark red-brown, occasionally with a bluish gray cast, shiny or somewhat pubescent, epruinose; isidia absent; **soredia**: granular, marginal or laminal, in bluish gray, maculiform soralia; occasionally regeneration squamules present; **medulla:** white; **photobiont:** the cyanobacterium *Nostoc*; **lower surface:** pale

brown, naked or weakly pubescent or rarely tomentose, smooth to rugulose; **Apothecia:** rare, immersed on lower surface at tips of lobes, orbicular, up to 8 mm diam., cup-shaped, sessile; margin: prominent with thalloid rim; disc: light brown; exciple: hyaline or light brown, 20-30 µm thick; epithecium: brown or brownish yellow; hypothecium: hyaline; **asci:** 8-spored; **ascospores:** subfusiform, 3-septate, 17-20 x 5-7 µm; wall: thick, light brown; **Pycnidia:** rare, marginal, immersed, punctiform, 0.18-0.32 mm diam.; **conidia:** rod-shaped, 4-5 x 1-2 µm; **Spot tests:** upper surface: K-, C-, KC-, P-; medulla K+ pale yellow or K-, C-, KC-, P-; **Secondary metabolites:** upper cortex with unknown brown pigment; medulla with hopane-6α, 22-diol [zeorin] (major), 15α-acetoxyhopane-22-ol [nephrin?] and hopane-15α, 22-diol (trace or accessory) and an unknown.

Habitat and ecology: on acidic rocks among mosses and tree trunks in moist canyons at mid- to high elevations, most common in spruce-fir regions; **World distribution:** Northern Hemisphere where it occurs in boreal and north temperate regions and extends south along the inland mountain ranges; **Sonoran distribution:** relatively common in central and SE Arizona and rarely in the northern part of Baja California.



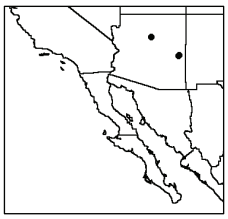
Note: The soredia separate it from any other Sonoran *Nephroma* species. If the cyanobacterial photobiont of *N. parile* is not recognized, then this species might be mistaken for *Melanelia subargenitifera*.

Nephroma resupinatum (L.) Ach., Lich. Univ. 522 (1810).

Basionym: *Lichen resupinatus* L., Sp. Pl. 1148 (1753); Synonyms: see Wetmore (1960); Illustrations: McCune and Geiser (1997), p. 175; Wirth (1995), p. 608; Brodo et al. (2001), p. 457.

Thallus: foliose, continuously forming rosettes, 3-10 cm wide, loosely adnate, lobate; **lobes:** irregular, broad (5-17 mm wide), elongate; apices: usually subrotund, entire or crenulate, sometimes ascending; **upper surface:** gray to grayish brown, dull, usually strongly pubescent; isidia and soredia absent.but frequently with regeneration squamules marginally or along cracks; **medulla:** white; **photobiont:** the cyanobacterium *Nostoc*; **lower surface:** pale brown to yellow-brown or whitish, densely tomentose, white papillate (scarcely to densely); **Apothecia:** common, on lower surface at tips of lobes, orbicular, up to 15 mm diam., cup-shaped, sessile; dorsal surface: tomentose, coarsely scabrid and foveolate-reticulate; margin: prominent with thalloid rim; disc: dark brown; exciple: hyaline or light brown, 20-30 µm thick; epithecium: brown or brownish yellow; hypothecium: hyaline; **asci:** 8-spored; **ascospores:** fusiform, 3-septate, 21-24 x 4-6 µm; wall: thin, light brown; **Pycnidia:** marginal, immersed, punctiform, 0.15-0.20 mm diam.; **conidia:** rod-shaped, 4-5 x 1-2 µm; **Spot tests:** upper surface: K-, C-, KC-, P-; medulla K-, C-, KC-, P-; **Secondary metabolites:** none detected.

Habitat and ecology: on acidic rocks among mosses and tree trunks in moist canyons at mid- to high elevations, most common in spruce-fir regions; **World distribution:** South Pacific and Northern Hemisphere, where it occurs in boreal and north temperate regions and extends south along the west coasts in maritime influenced regions; **Sonoran distribution:** central and eastern Arizona.



NODOBRYORIA

by B. D. Ryan

Nodobryoria Common & Brodo, Bryologist 98: 198 (1995).

Family: Parmeliaceae; Type: *Nodobryoria abbreviata* (Müll. Arg.) Common & Brodo; No. species: three worldwide; Selected lit.: Brodo and Hawksworth (1977); Brodo and Alstrup (1981); Common and Brodo (1995); Thell and Goward (1996).

Life habit: lichenized; **Thallus:** fruticose, erect and tufted to decumbent or pendent; typically attached to substrate by basal holdfasts; branching: frequently anisotomic; **branches:** generally angular or flattened in cross-section, slender, up to 2.5-10 (-17) cm long and 0.3-1.0 mm wide at base, 0.1-0.4 mm diam. on main branches, uneven in diam., foveolate and channelled, brittle; lateral branches: rarely abundant, spinulose, not constricted at the base; **surface:** dull, rarely somewhat shiny, ± dark reddish brown (to greenish when wet), not becoming blackened; soredia and isidia absent; **cortex:** 2-layered, outer layer distinctly paraplectenchymatous, thin (20-25 µm thick), of periclinal hyphae with short, irregularly shaped (knobby) cells with outer wall thinner than the lumina, interdigitating and forming a jig-saw pattern as seen in surface view, inner layer prosoplectenchymatous; **medulla:** white; cell walls with isolichenan; **photobiont:** primary one chlorococcoid alga, secondary one absent; **Ascomata:** apothecial, common in most species, borne laterally (or subterminally), roundish, sessile, lecanorine; thalline exciple: prominent, ciliate; disc: reddish brown, concave to sometimes markedly convex, outer-ascomatal filaments absent; true exciple: distinct, well-developed, strongly gelatinized, hyaline, with upper layer 30-40 µm thick, lower layer 30-45 µm thick; hymenium: hyaline below and yellow-brown (K-) above, 44-52 µm high; paraphyses: branched, not anastomosing, tips distinctly capitate in K, dark brown; hypothecium: hyaline; **asci:** *Lecanora*-type s.l. (*Parmelia*-type), *c.* 25-30 x 10-12 (-15) µm, axial body 2.5-3.0 µm wide, 8-spored; **ascospores:** non-septate, ellipsoid to subspherical, obtuse at the poles, colorless, 8-9 x 5-6 µm; wall: smooth, without distinct endospore thickening, I-; **Conidiomata:** pycnidial, rather frequent, laminal, immersed to prominent and black, up to 120 µm in diam.; **conidia:** straight, bifusiform to almost bacilliform, 5-8 x 0.5-0.7 (-1.0) µm; **Secondary metabolites:** none detected; **Geography:** cool temperate areas of western North America and Greenland; **Substrate:** on bark or wood, or soil, detritus, or siliceous rock.

Notes: This genus is distinguished from *Bryoria* by the color of the thallus, the thin, 2-layered cortex with jig-saw puzzle appearance in surface view, its brown and capitate paraphyses tips, frequent pycnidia, absence of secondary substances, and absence of lichenan. The distinctive cortical structure of *Nodobryoria* is somewhat difficult to see because of the underlying layers, and seems to be most easily observed at 40x. *Kaernefeltia californica*, which has often been confused with *Nodobryoria* (*abbreviata*), is strictly coastal, and differs in its pale olive-brown to greenish black thallus, mostly 1-layered cortex, grayish olive epihymenium (K+ grayish reddish purple) and pale, clavate paraphyses tips, and in containing fatty acids and lichenan. Likewise, while the thallus surface of *Nodobryoria* is usually quite dull rather than shiny, but it is slightly lustrous in the Sonoran specimens relative to the very dull appearance given by the pruina that frequently occur on *Kaernefeltia californica*. Further comparisons of the three species now placed in *Nodobryoria* are given in Brodo and Alstrup (1981).

Key to species of ***Nodobryoria*** in the Sonoran region:

1. Thallus caespitose to erect, up to 2.5 cm long; apothecia almost always abundant, distinctly ciliate, subterminal; at lower elevations ..... ***N. abbreviata***
1. Thallus subpendent to pendent, usually larger, up to 17 cm long; apothecia usually absent or very few, almost eciliate, always clearly lateral; mostly at higher elevations ..... ***N. oregana***

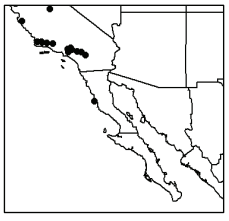
The Species

Nodobryoria abbreviata (Müll. Arg.) Common & Brodo, Bryologist 98: 198 (1995).

Basionym: *Alectoria divergens* f. *abbreviata* Müll. Arg., Flora, Jena 72: 362 (1889); Synonyms: *Alectoria abbreviata* (Müll. Arg.) R. Howe, *Bryoria abbreviata* (Müll. Arg.) Brodo & D. Hawksw.; *Bryopogon abbreviatus* (Müll. Arg.) Gyeln.; Illustrations: Brodo and Hawksworth (1977), p. 133 as *Bryoria abbreviata*; Common and Brodo (1995), fig. 5 [cortical anatomy]; Goward (1999), p. 195; McCune and Geiser (1997), p. 178; Brodo et al. (2001), p. 461.

Thallus: caespitose to erect, very small, to *c.* 0.5-1 cm tall [but 2-3 (-6) cm tall in non-Sonoran region material], brittle; branching: irregular, anisotomic dichotomous, broadly divergent at the base, occasionally anastomosing; often appearing spinulose from frequent short, pointed lateral branches; axils: usually obtuse; **branches:** roundish or ± angular or uneven to somewhat flattened in cross section, foveolate and longitudinally furrowed, terete only for the finest terminal branches and spinulose; **surface:** rather dark to somewhat pale red-brown, usually dull, occasionally partly lustrous or slightly shiny; soredia and isidia: absent; **Apothecia:** rare and immature (up to *c.* 0.5 mm diam.) in Sonoran material, but in specimens from more northern areas almost always present and often abundant, subterminal or rarely lateral, 0.5-3.0 (-3.5) mm diam.; thalline margin: concolorous with thallus, persistent and ciliate to disappearing, flat to recurved; disc: red-brown; **asci:** clavate, 8-spored; **ascospores:** subglobose [in non-Sonoran material] *c.* 5-6.5 x 4.5-5 µm; **Pycnidia:** common, on terminal branches, often in groups; **conidia:** 5-8 µm long; **Spot tests:** K-, C-, KC-, P-, UV-; **Secondary metabolites:** none detected.

Substrate and ecology: in chaparral, on conifers or wood, from near sea level to 2000 m; **World distribution:** western North America, absent from immediately coastal areas; **Sonoran distribution:** northern Baja California and southern California., mostly at 1000-2000 m.



Notes: In well-developed material it is usually easily recognized by the combination of the short, tufted, reddish brown thallus, and the very frequent, subterminal apothecia with ciliate margins, growing on bark or wood. It is probable that the species (and genus) is now close to extinction from southern California (and from Baja California). One specimen (Bratt 6454, SBBG) has a subpendent thallus with narrow, smooth and terete main (and basal) branches with primarily acute axils and very few short lateral branches, as in *N. oregana*, but is included here on the basis of the very short (1-2 cm) thallus and its occurrence a very low elevation (even for *N. abbreviata*). Hale's (1979) report of fatty acids may be based on misidentification of *Kaernefeltia californica*, which does contain fatty acids.

Nodobryoria oregana (Tuck.) Common & Brodo, Bryologist 98: 198 (1995).

Basionym: *Alectoria oregana* Tuck. *ex* Nyl., Lich. Jap.: 104 (1890); Synonyms: *Bryoria oregana* (Tuck. *ex* Nyl.) Brodo & D. Hawksw.; *Bryopogon oreganus* (Tuck. *ex* Nyl.) A. Schneid.; *Coelocaulon oreganum* (Tuck. *ex* Nyl.) M. Choisy; Illustrations: McCune and Geiser (1997), p. 179; Goward (1999), p. 195; Brodo et al. (2001), p. 461.

Thallus: usually pendent and 6-10 (-17) cm long; branching: irregularly anisotomic dichotomous, with occasional short spinulose side branches; angles between the main branches: most often acute; **branches:** 0.25-0.40 mm diam. at the base, 0.07-0.35 mm on main pendent branches, very uneven in thickness, usually terete, but in robust specimens becoming very angular or somewhat flattened in cross section at the base or axils (rare specimens that are longitudinally foveolate to ridged or channeled, or twisted may not belong in this species); **surface:** distinctly red-brown, very dull, lacking true lateral spinules, pseudocyphellae, soredia and isidia absent; **Apothecia:** usually absent or very few, always lateral, 0.5-2.0 mm diam.; disc: red-brown; thalline margin: smooth or occasionally ciliate but disappearing in age; **asci:** clavate, 8-spored; **ascospores:** broadly ellipsoid, *c.* 6.5 x 4.5 µm; **Pycnidia:** very rare, scattered on main branches (Brodo and Alstrup

1981); **conidia:** 5-8 µm long; **Spot tests:** K-, C-, KC-, P-, UV-; **Secondary metabolites:** none detected.

Substrate and ecology: usually on conifers, rarely on hardwoods or shrubs, in open to sheltered maritime and humid intermontane localities at all forested elevations; **World distribution:** mountainous areas of western North America, apparently tolerant of cooler, more humid habitats than *N. abbreviata*; **Sonoran distribution:** Although Brodo and Hawksworth (1977) cited two specimens (as *Bryoria oregana)* from southern California, the occurrence of the species in the Sonoran region today is doubtful.

Notes: In addition to its cortical structure, the typical sprinkling of a few short spinulose side branches and the relatively frequent apothecia with brown discs help distinguish this species from *Bryoria* spp., with which (in non-Sonoran areas) it is sometimes intricately entangled. Some older records of the species from southern California are probably based on misidentifications of *N. abbreviata* or *Bryoria fremontii*. The latter species tends to be reddish brown, is distinctly foveolate towards the base, usually has a distinctly shiny surface, and has basal branches that are considerably thicker than those of *N. oregana*.

OMPHALORA

by T. H. Nash III and B. D. Ryan

Omphalora T. H. Nash & Hafellner, Lichenol. 22: 358 (1990).

Family: Parmeliaceae Type: *Omphalora arizonica* (Tuck. *ex* Willey) T. H. Nash & Hafellner; No. species: one world-wide; Selected lit.: Egan (1972), Nash et al. (1990), and Henssen (1992).

Note: Because the genus is monotypic, a generic description would simply recapitulate the specific description given below.

The Species

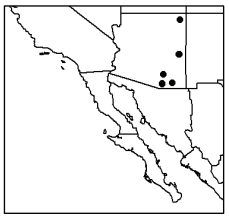
Omphalora arizonica (Tuck. *ex* Willey) T. H. Nash & Hafellner, Lichenol. 22: 358 (1990).

Basionym: *Omphalodium hottentottum* var. *arizonica* Tuck. *ex* Willey, *Bull. Torrey Bot. Club* 8: 140 (1881); Synonyms: *Parmelia arizonica* (Tuck. *ex* Willey) Nyl.; *Omphalodium arizonicum* (Tuck. *ex* Willey) Tuck.; *Lecanora arizonica* (Tuck. *ex* Willey) W. A. Weber; Illustrations: Hale (1979), p. 159; Nash et al. (1990); pp. 357 & 363; Henssen (1992), pp. 31, 34 & 36-8.

Thallus: umbilicate (foliose), (3-) 5-10 (-20) cm diam., attached only by the umbilicus, otherwise free and raised from substrate, often becoming markedly folded, leathery; **upper surface:** yellow to yellowish green or dull greenish yellow, dull to somewhat shiny, usually with a network of ridges that are rounded and not very prominent (generally less than 1 mm thick), with conspicuous papillae (verruculae) developing in circular rows; papillae less than 0.5 mm wide or tall, emaculate; pseudocyphellae: punctiform, occurring in the center of the papillae around distinct (10 x magnification) linear cracks through the upper cortex, rare in specimens with large numbers of pycnidia; **upper cortex:** densely paraplectenchymatous (sensu Hale, but perhaps better characterized as prosoplechtenchymatous sensu Henssen), with a narrow, frequently pigmented outer layer composed of densely aggregated hyphae; **medulla:** white, with strongly developed radial support tissue, cell walls with isolichenan; **lower cortex:** thin, prosoplectenchymatous; **lower surface:** dark blue-green to black (lighter around the umbilicus), pigment HNO_3+ red, dull, smooth to slightly rugose around the umbilicus, developing centrifugally-formed, irregular, sharp-edged ridges towards the margin; papillae: numerous, frequently with discolored areas (pseudocyphellae), and developing into complex, knobby, finger-like tubercles, erhizinate; **Apothecia**: very common and conspicuous, up to 10mm

diam.; thalline margin: concolorous with thallus, predominantly smooth with occasional pseudocyphellae; disc: red-brown, plane to slightly convex; exciple: 50-60 µm thick, prosoplectenchymatous; inner part 50-70 µm thick; epihymenium: reddish brown, not granular or inspersed, with brownish pigment in the paraphyses tips; hymenium: hyaline, *c.* 70-90 µm high; **asci:** clavate, 8-spored; **Ascospores:** simple, ellipsoid, 9-11 x 5-6 µm; **Pycnidia:** sometimes very abundant, at least partially immersed, surrounded by blue pigments; **conidia:** fusiform to weakly bifusiform, *c.* 8 x 1 µm; **Spot tests:** upper cortex K-, C-, KC+ yellow, P-; medulla K+ yellow then orange-red, C-, KC-, P+ orange; **Secondary metabolites:** cortex with usnic acid; medulla with a β-orcinol depsidone (norstictic acid).

Substrate and ecology: on exposed acidic rocks and cliff faces, locally abundant, at higher elevations, in the upper montane zone (mixed conifer forest); **World distribution:** southwestern USA (Arizona, Colorado & New Mexico); **Sonoran distribution:** eastern and southern Arizona, rather rare, 2680-3360 m.



Notes: As the only large yellow to yellow-green, umbilicate lichen with lecanorine apothecia, *Omphalora* is unique in the Sonoran region. Only junveniles would have the same size as the crustose genus *Rhizoplaca*. The species of the basionym refers to a South African species, that together with two other South African species was separated into the genus *Xanthomaculina* by Hale (1985) based on the presence of a vaulted cortex (not found in *Omphalora*), a feature that appears as prominent maculae from the upper surface. In addition, *Xanthomaculina* has lichenan in its fungal cell walls, has a brownish lower surface, and a different ascal structure. With the erection of *Xanthomaculina*, our species was left in the genus *Omphalodium*, the type species of which occurs in southern South America. Nash et al. (1990) separated these two *Omphalodium* species into monotypic genera *Omphalora* and *Omphalodium* based on differences of anatomy, morphology, cell wall chemistry and ascal dehiscence. Subsequently the generic separation was supported by Henssen (1992), who demonstrated that major differences in ascal ontogeny occur between the two. In contrast to *Omphalora arizonica*, *Omphalodium pisacomense* is a brown species with a very different surface topology (upper and lower).

OROPOGON

by T. L. Esslinger

Oropogon Th. Fr., Gen. Heterolich. Eur. 49 (1861).

Family: Alectoriaceae; Type: *Oropogon loxensis* (Fée) Th. Fr.; No. species: 36 known world-wide; Selected lit.: Esslinger (1989).

Life Habit: lichenized; **Thallus:** fruticose, caespitose to pendent or rarely somewhat prostrate; **branches:** terete, occasionally compressed (particularly at nodes along the segments), primarily isotomically dichotomous but sometimes anisotomically dichotomous, lateral branchlets rare; **surface:** white to gray, gray-black, tan, brown or black, sometimes mottled, generally smooth, pseudocyphellae plane and closed or more often perforate and opening into a hollow thallus center; soredia: present or absent; isidia absent; **cortex:** prosoplectenchymatous; **medulla:** composed of rather compact to loose arachnoid to distinctly granular hyphae; often with gaps associated with the pseudocyphellae , and commonly hollow centrally with a thick or thin medullary layer adjacent to the cortex; **photobiont:** primary one a trebouxioid alga, secondary photobiont absent; **Ascomata:** apothecial, usually frequent, formed laterally but sometimes appearing terminal due to recurved branch ends, up to 5 mm diam., circular; margin: thalline, persistent, smooth to crenulate or weakly spinulose, concolorous with thallus; disc: concave initially, becoming flat or convex with age, usually black or dark brown; epihymenium: red-brown to dark brown; hy-

menium: hyaline, 120-240 µm thick; hypothecium: hyaline or pale, over an algal layer; paraphyses: sparsely branched and anastomosing; **asci:** clavate, thick walled, *Lecanora*-type, I+ blue; tholus I+ blue; usually one-spored; **ascospores:** brown, muriform, ellipsoid, with or without an epispore (2-4 µm thick), 70-160 x 23-52 µm; **Pycnidia:** infrequent, immersed or partially emergent, often dark above; **conidia:** weakly or unequally bifusiform, mostly 4-7 x 0.5-1 µm; **Secondary metabolites:** medulla often with some combination of orcinol and ß-orcinol depsides, ß-orcinol depsidones, benzyl esters, aliphatic acids, anthraquinones and /or unknowns; **Geography:** neotropics and southern and eastern Asia; **Substrate:** on bark, wood, soil, or detritus.

Notes: When sterile, members of this genus are most likely to be confused with *Bryoria*, which is much more common in mountainous areas of the Sonoran region. Most species of *Oropogon*, including the two known to occur in our region, can be distinguished from *Bryoria* by the distinctly perforate pseudocyphellae. These are occasionally sparse, however, especially in poorly developed or scrappy material.

Key to species of ***Oropogon*** in the Sonoran region:

1. Thallus C-, KC-, P-, ± caespitose, tan to brown and usually distinctly mottled with black areas, at least in the oldest parts; medulla hollow and thin, granular and often patchy ..... ***O. bicolor***
1. Thallus pendent, gray-white to gray-brown or occasionally almost pure brown; medulla mostly filled and becoming granular, voids occurring only near the pseudocyphellae ..... ***O. lopezii***

The Species

Oropogon bicolor Essl., Syst. Bot. Monog. 28: 50 (1989).

Illustration: Esslinger (1989), p. 51.

Thallus: caespitose, up to 12 cm long; **branching:** isotomically dichotomous, internodes mostly 3-6 (-9) mm long; **branches:** terete, main ones up to 1 mm diam., rarely with scattered lateral and terminal spinules; **surface:** tan to brown or dark brown, with black areas that are usually more frequent and merging together in old parts, occasionally mostly black, smooth; **soredia:** very rare, granular, associated with the pseudocyphellae; pseudocyphellae: usually frequent and conspicuous, open to the hollow thallus center; **medulla:** white to dingy off-white, very rarely with yellow pigmented areas, granular, hollow and thin, often patchy in older parts; **Apothecia:** not seen in Sonoran material, elsewhere infrequent, lateral, up to 4 mm diam.; margin: entire to weakly crenulate, sometimes eroded; disc: concave to plane or slightly convex; hymenium: 145-205 µm thick; **asci:** clavate, 1-spored; **ascospores:** ellipsoid, muriform, brown, 105-135 (150) x 30-42 µm; **Pycnidia:** not seen; **Spot tests:** cortex K-, C-, KC-, P-; medulla K- or K+ dingy orange, C-, KC- or KC+ faintly rose, P- or P+ orange; **Secondary metabolites:** medulla with fumarprotocetraric acid (major to trace) and protocetraric acid (trace) and unknowns (trace or absent).

Substrate and ecology: on pine bark in montane oak-pine forests; **World distribution:** northern South America along the Andes to Bolivia, the Carribean and Central America to Mexico; **Sonoran distribution:** only known from one locality in the Sierra Madre Occidental in southern Sinaloa.

Notes: This species was initially published as *Alectoria fusconitida*, but that name is rejected as a *nomen nudum*. The mottled thallus surface, and the thin, hollow medulla distinguishes this species from all others, especially when fumarprotocetraric acid is present, giving the medulla a P+ orange reaction. This species sometimes lacks medullary substances, however, and is one of only two species known to do so (the other being the Venezuelan species *O. byssaceus* Essl., which has a loose, cottony, well-filled medulla, and can be readily distinguished from P- specimens of *O. bicolor*). Only one, rather sparse collection of this species was seen, very near the limit for inclusion in this work.

Oropogon lopezii Essl., Bryologist 83: 531 (1980).

Illustration: Esslinger (1989), p. 80.

Thallus: pendent, up to 30 (-34) cm long; **branching:** mainly isotomically dichotomous with occasional anisotomic dichotomies, internodes 6-18 (-25) mm long; **branches:** terete, main ones up to 0.7 mm in diam.; **surface:** gray-white to gray-brown or pure brown, smooth; pseudocyphellae: usually frequent, open to delimited hollow areas or voids in the medulla; **medulla:** white, hyphal to rather granular, with interspersed areas of solid-filled medulla and hollow medulla or voids; **Apothecia:** not seen in Sonoran material, elsewhere common, lateral, up to 4 mm diam.; margin: entire to strongly crenate, in larger apothecia usually with white pseudocyphellae; disc: ± flat to convex or reflexed; hymenium 125-160 µm thick; **asci:** clavate, 1-spored; **ascospores:** ellipsoid, brown, muriform, 74-97 x 23-32 µm; **Pycnidia:** not seen; **Spot tests:** cortex K- or K+ faint dingy yellow, C-, KC- or KC+ very faint rose, P- or P+ yellow-orange to red-orange (see discussion below); medulla K- or K+ dingy yellow, C-, KC+ rose, P+ orange to red-orange; **Secondary metabolites:** medulla (and sometimes the cortex) with protocetraric acid (major) and sometimes trace unknowns.

Substrate and ecology: on conifers in montane oak-pine forests; **World distribution:** northern South America, the Carribean and Central America to Mexico; **Sonoran distribution:** only known from one locality in the Sierra Madre Occidental in southern Sinaloa.

Notes: If the perforate pseudocyphellae are overlooked, this species might be mistaken for a large, pendent *Bryoria*, a genus that occurs more commonly to the north. The dark, mostly brown forms of *O. lopezii* (like the single Sonoran specimen seen) may lack cortical spot tests, although usually the palest terminal branches will react with P. These brown specimens are likely to be confused with *O. halei* Essl., which is always brown, but differs by having a distinctly hollow medulla and unusual discs of medullary tissue which delimit the area behind the pseudocyphellae.

PANNARIA

by P. M. Jørgensen

Pannaria Del. in Bory in Dictionnaire classique d'histoire naturelle 13: 20 (1828).

Family: Pannariaceae; Type: *Pannaria rubiginosa* (Ach.) Del.; No. species: *c.* 30 world-wide; Selected lit.: Jørgensen (1978 & 2000a).

Life habit: lichenized; **Thallus:** subfoliose to foliose, orbicular, growing loosely attached, frequently with a fibrous, well-developed hypothallus that sometimes extends as a blue-black zone around the thallus; **lobes:** flat to concave, sometimes producing isidia or soredia marginally; **upper surface:** mostly bluish gray, often smooth, scabrid or pruinose; **lower surface:** naked and whitish, with bluish black rhizohyphae; **upper cortex:** paraplectenchymatous; **photobiont:** primary one a *Nostoc*, secondary photobiont absent; **Ascomata:** apothecial, sessile, mainly laminal, usually with a crenulate thalline margin obscuring the proper one; disc: flat, often becoming convex, orange- or reddish brown to black; hymenium: I+ blue in vicinity of asci; **asci:** apically thickened , but without internal amyloid structures, 8-spored; ascospores: simple, colorless, ellipsoid, often apiculate at one or both end and with conspicuous epispore or epispore; **Conidiomata:** pycnidial; **conidia:** straight, bacilliform; **Secondary metabolites:** pannarin and related substances; **Geography:** widespread in warm temperate to subtropical, forested habitats; **Substrate:** on rocks and bark, particularly ones with bryophytes.

Notes: In contrast to the squamulose *Parmeliella* and *Fuscopannaria* genera, *Pannaria* now includes most of the foliose or subfoliose species. The thalline margin of the apothecial discs in *Pannaria* contrasts with the athalline, proper margin of *Parmeliella*. Most species of *Pannaria* contain pannarin and hence are P+ red.

Key to the species of ***Pannaria*** from the Sonoran region:

1. Thallus sorediate or isidiate 5
1. Thallus without isidia or soredia, usually fertile 2

2. Thallus gelatinous when wet, distinctly wrinkled when dry, containing small-celled *Nostoc* in chains ..... ***P. lurida*** ssp. ***quercicola***
2. Thallus not gelatinous when wet, never wrinkled, containing large-celled *Nostoc* in clusters 3

3. Thallus flat, uniformly brownish, small and thin-lobed (to 100 µm), P-, spores ovate ..... ***P. subfusca***
3. Thallus with raised margins, bluish gray (to partly buff), often pruinose, thicker (to 250 µm), P+ orange, spores ellipsoid 4

4. Thallus small, to 3 cm diam., resting on a distinct hypothallus, cortex only P+, richly fertile, spores 12-14 x 6-7 µm ..... ***P. malmei***
4. Thallus larger, to 5 cm diam., totally P+ orange, hypothallus poorly developed; apothecia scattered; spores 15-20 x 8-10 µm ..... ***P. rubiginosa***

5. Thallus with mostly simple, coralloid isidia ***P. tavaresii***
5. Thallus with "woolly", soredia-like, decorticated lobules ..... ***P. conoplea***

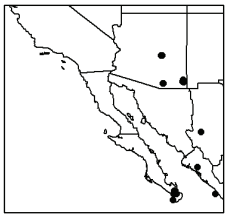
The Species

Pannaria conoplea (Ach.) Bory, Dict. Class. Hist. Nat. 13: 20 (1828).

Basionym: *Parmelia conoplea* Ach., Lich. Univ.: 467 (1810); Synonyms: *Pannaria coeruleobadia* (Lam.) A. Massal., nom. illeg., *Pannaria pityrea* sensu Degel., non sensu orig., *Pannaria rubiginosa* var. *lanuginosa* sensu Zahlbruckner, non sensu orig.; Illustrations: Hale (1979), p. 123; Jørgensen (2000a), p. 691; Thor and Arvidsson (1999), p. 296; Wirth (1995), p. 633; Brodo et al. (2001), p. 477.

Thallus: squamose to foliose, often in irregular to entire rosettes, 2-3 mm diam. (rarely larger), on a well developed hypothallus; **lobes:** contiguous to partially overlapping, fan-shapped, 4-5 mm wide, up to 9 mm long, deeply incised, ± ascending, paler margin; **upper surface:** blue-gray, ash-gray to pale brown (when in exposed habitats), shiny centrally, scabrid towards the margins; **lobules:** soredia-like (gymnidium), decorticated, marginal, sometimes totally covering the thallus, particularly in central parts; **upper cortex:** paraplectenchymatous, 40-50 µm thick; **Apothecia:** unknown in American material, elsewhere rare, up to 1.5 mm diam. in European material; disc: brown with thalline margin that is usually dissolved in "soredia"; exciple: subparaplectenchymatous, 30-40 µm thick; hymenium: mostly hyaline but brown above, partially I+ persistently blue (in vicinity of the asci), 110-150 µm high; **asci:** clavate to subcylindrical, without an amyloid apical apparatus, 8-spored; **ascospores:** simple, colorless, ellipsoid, 20-24 x 10-12 µm (with an epispore; otherwise 15-19 x 9-10 µm); **Spot tests:** thallus K-, C-, KC-, P+ orange; **Secondary metabolite:** pannarin.

Substrate and ecology: on bark or mossy rocks in the cool-temperate regions; **World distribution:** widely distributed in temperate parts of the Northern and Southern Hemispheres; **Sonoran distribution:** cool-temperate parts of Arizona and adjacent Mexico (rather high altitude, about 2.000 m).



Notes: It is the ”sorediate” counterpart of *P. rubiginosa*. Morphologically it may be confused with *Fuscopannaria mediterranea*, which is P- and lack pannarin, or in its young stages with *Pannaria tavaresii* when the latter species cylindrical isidia are not fully developed.

Pannaria lurida (Mont.) Nyl. ssp. **quercicola** P. M. Jørg., Bryol. 103: 694 (2000).

Illustrations: Hale (1979), p. 142 as *P. lurida*; Jørgensen (2000a), p. 693; Brodo et al. (2001), p. 457.

Thallus: foliose, flat, orbicular, up to 5-7 cm diam., with poorly developed hypothallus; **lobes:** confluent, apically enlarged, wrinkled; **upper surface:** olive-gray; **photobiont:** a *Nostoc* in chains; **lower surface:** whitish, naked, loosely attached by blue-black rhizohyphae; **Apothecia:** mainly

central, up to 2 mm wide; disc: brown, with squamulose thalline margin; exciple: paraplectenchymatous, 80-100 µm thick; hymenium: primarily hyaline but brown above, partially I+ blue (in vicinity of the asci); **asci:** clavate without inner amyloid apical structures, 8-spored; **ascospores:** simple, colorless, ellipsoid 10-18 x 7-9 µm with a distinct, rugulose, apiculate epispore; **Spot test:** thallus K-, C-, KC-, P+ orange; **Secondary metabolites:** pannarin.

Substrate and ecology: on hardwood trees, usually on oak, in warm-temperate, moist forests at middle altitudes; **World distribution:** main species widespread in tropical regions, but subspecies *quercicola* appears to be endemic to the hardwood forests of eastern North America, extending southwards to Mexico; **Sonoran distribution:** rare, only collected once in the montane region of Sinaloa, at the base of an oak.

Notes: It is easily recognized on the heavily wrinkled thallus and is often found on oaks. It is similar but larger morphologically than *P. lurida* ssp. *russellii*, which occurs farther north and is usually P-.

Pannaria malmei Dodge, Ann. Mo. Bot. Gard. 20: 441 (1933).

Illustartion: Jørgensen (2000a), p. 693.

Thallus: subfoliose, forming rosettes to 2-3 cm wide, resting on a distinct bluish black hypothallus; **upper surface:** blue-gray, distinctly pruinose; **Apothecia:** common, particularly centrally, flat brownish with distinct crenulate thalline margin; exciple: subparaplectenchymatous, 30-40 µm thick; hymenium: primarily hyaline but brown above, partially I+ blue (in vicinity of the asci); **asci:** clavate, without inner apical, amyloid structures, 8-spored; **ascospores:** simple, colorless, ellipsoid 12-14 x 8-9 µm; **Spot-tests:** thallus K-, C-, KC-, P+ orange; **Secondary metabolites:** pannarin.

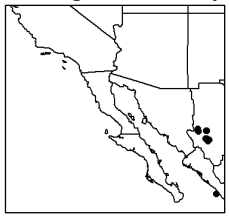
Substrate and ecology: on rocks in the Sonoran region, often corticolous elsewhere, in misty cool temperate forests; **World distribution:** The mountains of South and Central America and the Pacific coast of North America to Queen Charlotte Islands; **Sonoran distribution:** rare, only collected once, in Tomochic valley in the Sierra Madre Occidental (Chihuahua), on a rock outcrop in a pine-oak forrest, about 2000 m., but possibly more common.

Notes: It is a long misunderstood species, often confused with the larger, more leafy *P. rubiginosa,* which has a different chemistry and larger spores (see below).

Pannaria rubiginosa (Ach.) Bory, Dict. Class. Hist. Nat. 13: 20 (1828).

Basionym: *Lichen rubiginosus* Ach., Lich. suec. prodr.:99 (1799); Illustrations: Hale (1979), p. 143; Jørgensen (1978), p. 62; Jørgensen (1994), p. 200; Jørgensen (2000a), p. 693; McCune and Geiser (1997), p. 184; Swinscow and Krog (1988), p. 155; Thor and Arvidsson (1999), p. 297; Brodo et al. (2001), p. 478.

Thallus: foliose, forming orbicular rosettes, up to 5 mm diam., on fibrous, well-developed hypothallus that sometimes extends as a blue-black zone around the thallus; **lobes:** mostly concave, 3-4 mm wide, up to 8 mm long, with raised, whitish margins that are deeply incised; **upper surface:** bluish gray to fawn-colored (olive-brown), smooth to pruinose or sometimes scabrous at the apices; **upper cortex:** paraplectenchymatous, 40-50 µm thick; **Apothecia:** common, frequently centrally, up to 1.5 mm; disc: red-brown, with a persistent, crenulate thalline margin; exciple: subparaplectenchymatous, 30-40 µm thick; hymenium: primarily hyaline but brown above, partially I+ blue (in vicinity of the asci), 110-150 µm high; **asci:** clavate to subcylindrical, without internal amyloid apical structures, 8-spored; **ascospores:** simple, colorless, broadly ellipsoid, with an epispore, 20-24 x 10-12 µm (with epispore); **Pycnidia:** not seen; **Spot tests:** thallus K-, C-, KC-, P+ orange; **Secondary metabolite:** pannarin.



Substrate and ecology: on bark in cool-temperate forests; **World-distribution:** widespead in both Northern and Southern Hemispheres;

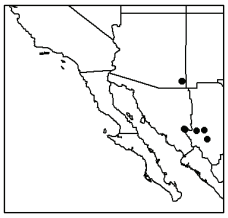
Sonoran distribution: at the upper limit of the oak forests in Sinaloa and Chihuahua, sometimes extending into the conifer forests.

Notes: It is mostly confused with *P. lurida* and *P. subfusca*. The former species is usually broader and has duller lobes, that are heavily wrinkled when dry. In contrast, *P. subfusca* is a smaller, thinner, brownish, P- species. The separation from the smaller, often abundantly fertile *P. malmei* Dodge, which is best recognized by its smaller spores (12-15 x 8-9 µm), is more difficult.

Pannaria subfusca P. M. Jørg., Bryol. 103: 695 (2000).

Illustration: Jørgensen (2000a), p. 693.

Thallus: squamulose to subfoliose, orbicular, up to 5 cm broad, flat and thin (to 100 µm); **lobes:** often delicately incised, with marginal lobules; **upper surface:** uniformily brownish gray; **Apothecia:** common, up to 2 mm diam.; disc: brownish and distinct, with a conspicuous, crenulate thalline margin; exciple: subparaplectenchymatous, 30-40 µm thick; hymenium: up to 100 µm, I+ blue only in the vicinity of the asci; **asci:** clavate, without any internal amyloid apical structures, 8-spored; **ascospores:** simple, colorless, subglobose, 9-12 x 8-11 µm; **Spot tests:** all negative; **Secondary metabolites:** none detected.



Substrate and ecology: on trees in warm, temperate deciduous forests; **World distribution:** only known from eastern North America to Central America; **Sonoran distribution:** rather common in the oak forests of SE Arizona, Sonora and Chihuahua.

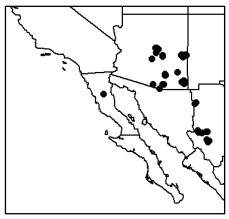
Notes: Previously it was confused with *P. rubiginosa* which is a larger, grayer species with a P+ orange thallus and much larger, more ellipsoid spores.

Pannaria tavaresii P. M. Jørg., Opera Bot. 45: 68 (1978).

Illustrations: Hale (1979), p. 127; Jørgensen (1978), p. 69; Jørgensen (2000a), p. 691; Brodo et al. (2001), p. 479.

Thallus: foliose, forming orbicular rosettes, up to 3 cm diam., growing on a well developed, black hypothallus that may extend beyond the margin; **lobes:** contiguous, with raised margins, 3-4 mm wide and up 8 mm long; **upper surface:** whitish or gray-blue to partly fawn-colored, scabrid or slightly pruinose; **isidia:** granular to coralloid, predominantly marginal, sometimes black-tipped; **upper cortex:** paraplectenchymatous, 40-50 µm thick; **Apothecia:** fairly common, mostly central, up to 1 mm diam.; disc: red-brown to brown, conspicuous isidiate, with a thalline margin; exciple: subparaplectenchymatous, 30-40 µm thick; hymenium: primarily hyaline but brown above, partially I+ persistently deep blue (vicinity of the asci), 110-150 µm high; **asci:** clavate to subcylindrical, with no internal amyloid, apical structures, 8-spored; **ascospores:** simple, colorless, ellipsoid, 20-24 x 10-12 µm (with an epispore; otherwise 15-19 x 9-10 µm); **Conidia:** not seen; **Spot tests:** thallus K-, C-, KC-, P+ orange, **Secondary metabolite:** pannarin.

Substrate and ecology: mainly on trees, but also on mossy rocks, in moist habitats, mainly in forests, rarely above the forest limit; **World distribution:** widespread in temperate regions of both Northern and Southern Hemispheres; **Sonoran distribution:** fairly common in moist forests, and at the forest limit (to 3000 m) in the SE mountains of Arizona and along the Sierra Madre Occidental in Chihuahua, and in Baja California.



Notes : It was previously confused with *P. conoplea*, from which *P. tavaresii* differs in having corticate coralloid isidia rather than decorticated, dorsiventral lobules of *P. conoplea*. Because of this *P tavaresii* is a less "fuzzy"-appearing species.

PARMELIA

by T. H. Nash III and J.A. Elix

Parmelia Ach., Methodus 153 (1803).

Family: Parmeliaceae; Type: *Parmelia saxatilis* (L.) Ach.; No. species: 38 world-wide; Selected lit.: Elix (1993a & 1994h) and Hale (1987).

Life habit: lichenized; **Thallus:** foliose, ± circular, lobate; **lobes:** narrow, sublinear, contiguous, rarely imbricate; apices: truncate, eciliate; **upper cortex:** non-pored epicortex, prosoplechtenchymatous; **upper surface:** gray, plane to foveolate, shiny or dull, strongly white, simple or reticulate maculae, pruinose or not; with or without isidia, soralia, or lobules; pseudocyphellae common, frequently elongated and irregularly effigurate (developing from the maculae); **medulla:** white, loosely packed; cell walls containing isolichenan; **photobionts:** primary one a *Treboux-ia*, secondary photobiont absent; **lower surface:** black, attached by simple, furcated or squarrose, black rhizines; cyphellae, pseudocyphellae and tomentum absent; **Ascomata:** apothecial, laminal on thallus, orbicular, cup-shaped, sessile to pedicellate; margin: prominent with thalloid rim; disc: usually pale to dark brown, imperforate; exciple: gray or hyaline, epithecium: brown or brownish yellow; hypothecium: hyaline; **asci:** lecanoral, wall layers thickened; apex: amyloid, with wide, divergent axial body; *c.* 8-spored; **ascospores:** simple, ellipsoid to broadly ellipsoid, 11-15 x 6-9 µm but larger in many Asian species; wall thin, hyaline, not amyloid; **Conidiomata:** absent or present, pycnidia laminal or marginal, immersed or emergent sessile; **conidia:** cylindrical, rarely bifusiform, 5-8 x 1 µm; **Secondary metabolites:** upper cortex atranorin and chloroatranorin (rarely usnic acid accessory); medulla some combination of orcinol depsides or depsidones, ß-orcinol depsides or depsidones or aliphatic acids; **Geography:** predominately temperate/boreal to arctic/alpine; **Substrate:** mostly bark, non-calciferous rock, mosses or humus.

Key to the species of ***Parmelia*** from the Sonoran region:

1. Thallus isidiate 2
1. Thallus sorediate 3

2. Thallus with cylindrical isidia; primarily on rock ..... ***P. saxatilis***
2. Thallus with granular isidia, isintegrating with age; primarily on trees ..... ***P. hygrophila***

3. Soralia mostly laminal, whitish; predominately on trees and frequently rocks ..... ***P. sulcata***
3. Soralia mostly marginal, yellowish; only known from rocks ..... ***P. fraudans***

The Species

Parmelia fraudans (Nyl.) Nyl., Lich. Jap. 28 (1890).

Basionym: *Parmelia saxatilis* (L.) Ach.* *fraudans* Nyl.; Illustrations: Hale (1979), p. 79; Hale (1987), p. 26; Thomson (1984), p. 302.

Thallus: adnate, foliose, 4-16 cm in diam., lobate; **lobes:** sublinear, contiguous to imbricate, elongate, plane, separate, 1-4 mm wide, rather brittle, apices truncate; **upper surface:** gray to yellowish gray, smooth to foveolate, shiny or dull, sometimes white pruinose, becoming cracked along prominent, effigurate pseudocyphellae; **soredia:** coarse to subisidiose, abundant, yellowish, commonly marginal; isidia and pustulae absent; **medulla:** white with continuous algal layer; **lower surface:** black centrally, brown peripherally, rhizinate, rhizines moderately dense, black, simple to furcate; **Apothecia:** rare, laminal, 2-4 mm wide; margin: usually sorediate; disc: dark brown; **asci:** clavate, 8-spored; **ascospores:** ellipsoid, 10-12 x 5-6 µm; **Pycnidia:** not seen; **Spot tests:** upper cortex K+ yellow, C-, KC- (or + orange if usnic acid in high concentration), P+ orange; medulla K+ yellow turning deep red, C-, KC-, P+ yellow; **Secondary metabolites:** upper cortex with atranorin and chloroatranorin and accessory usnic acid (in the soralia); medulla with salazinic acid (ma-

jor), consalazinic and protolichesterinic acids (both minor).

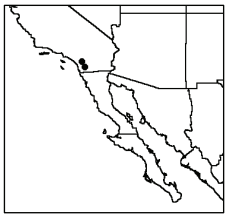
Substrate and ecology: frequent on exposed rocks; **World distribution:** boreal to arctic regions in North American and Europe; **Sonoran distribution:** only known from one scree slope in the upper part of the Chiricahua Mountains, SE Arizona.

Parmelia hygrophila Goward & Ahti, Ann. Bot. Fenn. 20: 9 (1983).

Illustrations: Hale (1987), p. 26; Brodo et al. (2001), p. 482; McCune and Geiser (1997), p. 187.

Thallus: adnate, foliose, 4-10 cm in diam., lobate; **lobes:** sublinear, contiguous, elongate, plane to subconvex, separate, 2-5 mm wide, apices truncate; **upper surface:** whitish gray, smooth to slightly ridged, matt, frequently densely pruinose, becoming cracked along prominent, effigurate pseudocyphellae; **isidia:** granular to subsorediose, laminal, dense; soredia and pustulae absent; **medulla:** white with continuous algal layer; **lower surface:** black, rhizinate; rhizines: moderately dense, black, simple to sparsely furcate; **Apothecia:** rare, laminal, substipitate, 2-4 mm wide; margin: usually isidiate; disc: red brown to dark brown; **asci:** clavate, 8-spored; **ascospores:** broadly ellipsoid, 14-16 x 9-12 µm; **Pycnidia:** not seen; **Spot tests:** upper cortex K+ yellow, C-, KC-, P+ yellow; medulla K+ yellow turning deep red, C-, KC-, P+ orange; **Secondary metabolites:** upper cortex with atranorin and chloroatranorin; medulla with salazinic acid (major) and consalazinic acids (minor).

Substrate and ecology: on trees; **World distribution:** Pacific NW in North America down to southern California; **Sonoran distribution:** only known from a few locations in southern California.

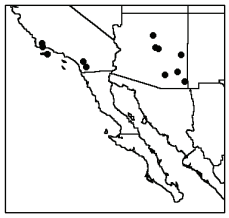


Parmelia saxatilis (L.) Ach, Meth. Lich.: 204 (1803).

Basionym: *Lichen saxatilis* L., Sp. Pl.: 1142 (1753); Illustrations: Hale (1987), p. 37; Wirth (1995), p. 663; McCune and Geiser (1997), p. 187; St. Clair (1999), p. 127; Brodo et al. (2001), p. 483.

Thallus: adnate, foliose, 4-20 cm in diam., lobate; **lobes:** sublinear, contiguous, elongate, plane to subconvex, separate, 2-4 mm wide, apices truncate; **upper surface:** gray (to brown in exposed habitats), smooth to foveolate, shiny, sometimes white pruinose, becoming cracked along prominent, effigurate pseudocyphellae; **isidia:** cylindrical, simple to coralloid, abundant, laminal, dense; soredia and pustulae absent; **medulla:** white with continuous algal layer; **lower surface:** black, rhizinate, rhizines: moderately dense, black, simple to furcate; **Apothecia:** rare, laminal, 2-8 mm wide; margin: usually isidiate; disc: red-brown to dark brown; **asci:** clavate, 8-spored; **ascospores:** ellipsoid, 16-18 x 9-11 µm; **Pycnidia:** not seen; **Spot tests:** upper cortex K+ yellow, C-, KC-, P+ yellow; medulla K+ yellow turning deep red, C-, KC-, P+ orange; **Secondary metabolites:** upper cortex with atranorin and chloroatranorin; medulla with salazinic acid (major) and consalazinic acids (minor).

Substrate and ecology: on rocks in open habitats, rarely on trees; **World distribution:** pantemperate and southern boreal; **Sonoran distribution:** relatively rare on scree rocks in upper montane habitats, Arizona.



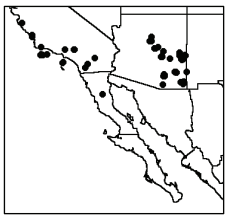
Parmelia sulcata Taylor, Fl. Hibern. 2: 145 (1836).

Illustrations: Hale (1987), p. 37; Wirth (1995), p. 663; McCune and Geiser (1997), p. 191; St. Clair (1999), p. 128; Brodo et al. (2001), p. 485.

Thallus: adnate, foliose, 4-20 cm in diam., lobate; **lobes:** sublinear, contiguous to imbricate, elongate, plane, separate, 2-4 mm wide, apices truncate; **upper surface:** gray, smooth to strongly foveolate, shiny, sometimes white pruinose, becoming cracked along prominent, effigurate pseudocyphellae; **soredia:** granular, abundant, laminal, in linear soralia; isidia, pustulae and dactyls absent; **me-**

dulla: white with continuous algal layer; **lower surface:** black, rhizinate; rhizines moderately dense, black, simple; **Apothecia:** rare, laminal, 2-8 mm wide; margin: usually sorediate; disc: dark brown; **asci:** clavate, 8-spored; **ascospores:** ellipsoid, 11-14 x 6-8 µm; **Pycnidia:** infrequent, immersed; **conidia:** bacilliform, 6-8 x 1 µm; **Spot tests:** upper cortex K+ yellow, C-, KC-, P+ yellow; medulla K+ yellow turning deep red, C-, KC-, P+ orange; **Secondary metabolites:** upper cortex with atranorin and chlorotranorin; medulla with salazinic acid (major) and consalazinic acids (minor).

Substrate and ecology: common on trees in open habitats, occasionally on rocks; **World distribution:** pantemperate and southern boreal; **Sonoran distribution:** relatively common on deciduous and coniferous trees in montane habitats of Arizona, on coastal oaks in California and on rocks in the high mountains of northern Baja California.



PARMELIELLA

by P. M. Jørgensen

Parmeliella Müll.Arg., Mém. Soc. Phys. Genève 16: 376 (1862).

Family: Pannariaceae; Type: *Parmeliella triptophylla* (Ach.) Müll. Arg.; No. species: *c.* 35 world-wide; Selected lit.: Jørgensen (1978 & 2000a & b).

Life Habit: lichenized; **Thallus:** squamulose to ± crustose, sometimes with enlarged peripheral lobes, often resting on a hypothallus of rhizohyphae that may be visible from above; **upper surface:** bluish or brownish, smooth; **photobiont:** primary one a cyanobacterium (*Nostoc*), secondary photobiont absent; **Ascomata:** apothecial, biatorine; proper exciple: distinct cellular, cells rounded to oblong and 15-20 µm wide, thalline margin lacking; hymenium: I+ blue; paraphyses: simple, not or slightly thickened at apices, pigmented externally; **asci:** with apical amyloid tubes (or plug), 8-spored; **ascospores:** simple, colorless, ellipsoid, often apiculate at one or both ends and with a warted or ridged epispore; **Conidomata:** pycnidial, rare; **conidia:** bacilliform; **Secondary metabolites:** none detected; **Geography:** widespread in warm temperate to subtropical, forested habitats; **Substrate:** on soil, rocks and bark in sheltered, humid habitats.

Key to the species of ***Parmeliella*** from the Sonoran region:

1. Thallus with marginal, coralloid isidia 3
1. Thallus with marginal secondary, dorsiventral lobules. 2
   2. Thallus with enlarged, foliose marginal lobes resting on a well-developed hypothallus ..... ***P. pannosa***
   2. Thallus totally crustose-squamulose; hypothallus inconspicuous ..... ***P. miradorensis***
3. Thallus small-squamulose, resting on a thin blackish hypothallus, saxicolous ..... ***P. triptophylla***
3. Thallus with enlaged marginal lobes; hypothallus inconspicuous, corticolous ..... ***P. clavulifera***

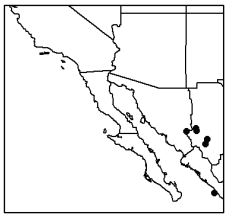
The Species

Parmeliella clavulifera P. M. Jørg., Lichenologist 32: 140 (2000).

Synonym: ?*Parmeliella pannosa* var. *coralloidea* Dodge; Illustration: Jørgensen (2000b), p. 140.

Thallus: squamulose-foliose, forming irregular rosettes up to 4 cm diam., resting on an inconspicuous, thin, blackish hypothallus; **lobes:** somewhat enlarged, up to 3 mm wide and 150 µm thick; **upper surface:** gray-blue to brownish, lobulate, lacking isidia or soredia; **isidia:** coralloid to claviform, marginal; **upper cortex:** paraplectenchymatous, two cells thick; **Apothecia:** rare, up to 1.5 mm wide; disc: brownish, sometimes with adhering isidia; proper exciple: distinctly paraplectenchymatous; hymenium: I+ blue, up to

100 µm high; **asci:** with apical amyloid tubes, 8-spored; **ascospores:** simple, colorless, ellipsoid, smooth, 14-16 x 5-7 µm; **Spot test:** all negative; **Secondary metabolites:** none detected.



Substrate and ecology: on bark, commonest on oaks, about 2000 m; **World distribution:** Central America and Mexico; **Sonoran distribution:** montane oak forests in Mexico (Sonora, Chihuahua and Sinaloa).

Notes: This species is characterized by its numerous claviform isidia, and is much larger and more foliose than *P. triptophylla* which in this region is only found on rocks and at higher altitudes. *Parmeliella pannosa* has flattened lobules and a much more prominent hypothallus, and is mainly found at lower elevation (rarely above 1500 m).

Parmeliella miradorensis Vain., Dansk bot. Arkiv 4 (11): 16 (1926).

Synonym: *Parmeliella nigrocincta* (Mont.) Müll. Arg. var. *brasiliensis* Malme; Illustration: Jørgensen (2000b), p. 143.

Thallus: repeatedly squamulose, occasionally with radiating lobes on smooth bark, forming irregular rosettes up to 5 cm diam., resting on a blackish, variously developed, but mainly inconspicuous hypothallus; **squamules:** up to 3 mm wide and 100 µm thick, leafy, often imbricate; **upper surface:** gray-blue to brownish, lobulate, lacking isidia or soredia; **lobules:** usually gray-blue, occasionally brownish; **upper cortex:** paraplectenchymatous, up to 30 µm and at least two cells thick, **Apothecia:** numerous, up to 1.5 mm diam.; disc: reddish brown; proper margin: distinctly paler, paraplectenchymatous, up to 150 µm thick; hymenium: I+ blue, shallow, up to 90 µm high; **asci:** clavate, with distinct amyloid apical tubes, 8-spored; **ascospores:** simple, colorless, smooth, ellipsoid, 11-17 x 6-8 (-10) µm; **Spot tests:** all negative; **Secondary metabolites:** none detected.

Substrate and ecology: on deciduous trees, mainly oaks in mist forests about 2000 m; **World distribution:** widespread in subtropical parts of South and Central America, the West Indies, Macaronesia, and Japan; **Sonoran distribution:** scattered in the subtropical moist, montane forest of the Sierra Madre Occidental in Sinaloa.

Notes: Previously it was confused with the much more crustose and southern *P. nigrocincta* (Mont.) Müll. Arg., from which it is easily distinguished by its repeatedly squamulose, imbricate, non-waxy lobes. In contrast, *P. nigrocincta* has adpressed, waxy squamules. Also *P. clavulifera* has smaller spores than *P. nigrocincta*.

Parmeliella pannosa (Sw.) Müll. Arg., Flora 64: 86 (1881).

Basionym: *Lichen pannosus* Sw., Nov. Gen. and Spec. plant.:146 (1788); Illustrations: Hale (1979), p. 142; Swinscow and Krog (1988), p. 158; Jørgensen (2000a), p. 697.

Thallus: subfoliose and squamulose centrally, forming orbicular patches, up to 5 cm diam, resting on a conspicuous brownish hypothallus; **lobes:** radiating at the periphery, up to 2 mm wide, with ascending, incised margins; **upper surface:** brownish, smooth or shiny, lobulate, lacking isidia or soredia; **lobules:** covering thallus, sometimes sinuose; **Apothecia:** rare, up to 1.5 mm wide, disc: brown, sometimes obscured by secondary lobules; proper exciple: paler; hymenium: I+ blue; **asci:** clavate with apical amyloid tubes, 8-spored; **ascospres:** simple, colorless, ellipsoid, 15-20 x 7-10 µm; **Spot tests:** all negative; **Secondary metabolites:** none detected.

Substrate and ecology: on bark; **World distribution:** widespread in subtropical regions, particularly of South and Central America; **Sonoran distribution:** rare, possibly because the lowlands are too dry, up to 1900 m in the subtropical, moist montane forests of the Sierra Madre Occidental of Sinaloa.

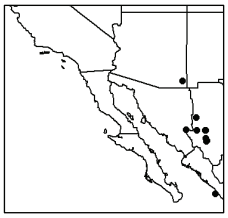
Notes: This species is previously often confused with *Parmeliella mariana* (Fr.) P. M. Jørg. and D. J. Gallow., a species which as yet is not known from the North American continent, but is present in Hawaii and the West Indies. That species has apothecia with distinct thalline margin and lacks secondary squamules on the lobe margins.

Parmeliella triptophylla (Ach.) Müll. Arg., Mém. Soc. Phys. Hist. Genève 16: 376 (1862).

Basionym: *Lecidea triptophylla* Ach., K. Vetensk. Akad. Nya Handl. 29: 272 (1808); Synonym: *Parmeliella corallinoides* sensu Zahlbr., non sensu orig.; Illustrations: Goward et al. (1994), p. 94; Jørgensen (1978), p. 74; Jørgensen (2000a), p. 697; Brodo et al. (2001), p. 485.

Thallus: small-squamulose, resting on a thin blackish hypothallus that contributes to the dark color of this species; **squamules:** rarely more than 1 mm wide, incised, **upper surface:** gray-blue or brown, isidiate but not sorediate; **isidia:** coralloid, digitate but occasionally granular, marginal, sometimes obscuring the squamules; **upper cortex:** paraplechtenchymatous, 25-35 µm thick; **Apothecia:** uncommon, up to 1 mm diam, biatorine; disc: red-brown, often becoming blackish and convex; exciple: paraplectenchymatous, up to 90 µm thick; hymenium: primarily hyaline but brown-black above, I+ persistently deep blue,up to 100 µm high; subhymenium: thick, brownish; **asci:** clavate to subcylindrical, with apical amyloid tubes, 8-spored; **ascospores:** simple, colorless, ellipsoid, without an epispore, 10-17 x 5-8 µm; **Pycnidia:** not seen; **Spot tests:** all negative; **Secondary metabolites:** none detected.

Substrate and ecology: on sheltered, wet montane rocks at fairly high altitudes (2000-3000 m); elsewhere also on bark; **World distribution:** cool-temperate, widespread in the Northern Hemisphere; **Sonoran distribution:** SE Arizona and adjacent Sierra Madre Occidental of Chihuahua and Sonora.



Notes: This species is quite distinctive from *P. clavulifera*, in being smaller, more crustose, and darker with finer isidia. Sometimes flattened lobules are found inbetween the isidia, but the thalli are never just lobulate. Two saxicolous specimens now included in this species were provisionally identified as *P. saxicola* P. M. Jørg. but are now included in this species. Poorly isidiate specimens do resemble *P. saxicola*, a species from northern Venezuela that lacks isidia and has characteristically curved, central squamules.

PARMELINA

by T. H. Nash III and J.A. Elix

Parmelina Hale, Phytologia 28: 481 (1974).

Family: Parmeliaceae**;** Type: *Parmelina tiliacea* (Hoffm.) Hale; No. species: *c.* 10 world-wide; Selected lit.: Hale (1976b), Elix (1993a & 1994i).

Life habit: lichenized; **Thallus:** foliose, ± circular, adnate to tightly adnate, irregularly to rarely dichotomously lobate; **lobes:** flat, sublinear to subirregular; tips: subrotund to rotund, ciliate; cilia: simple, primarily in axils; **upper cortex:** pored epicortex, palisade plectenchymatous; **upper surface:** gray to gray green, rarely yellowish, commonly maculate, with or without soredia, isidia or pustules; pseudocyphellae absent; **medulla:** white or lower medulla yellow-orange; cell walls: containing isolichenan; **photobionts**: primary one a *Trebouxia*, secondary photobiont absent; **lower surface:** black or dark brown, rhizinate; rhizines: black, simple to rarely squarrose; **Ascomata:** apothecial, laminal, sessile to subpedicellate, up to 5 mm diam.; disc: imperforate, brown; exciple: gray or hyaline; epithecium: brown or brownish yellow; hypothecium: hyaline; **asci:** lecanoral; apex: thickened, amyloid, with divergent axial body, 8-spored; **ascospores:** simple, ellipsoid, 8-14 x 5-9 µm; **Conidiomata:** pycnidial, laminal, immersed; **conidia:** cylindrical or bacilliform to weakly fusiform, 3-8 x 1 µm; **Secondary metabolites:** upper cortex with atranorin and chloroatranorin; medulla with orcinol depside or aliphatic acids; **Geography:** pantemperate and relatively cosmopolitan; **Substrate:** on bark, rarely on rock.

Notes: From the original conception of *Parmelina* (Hale 1974c), *Parmelinopsis* was segregated (Elix and Hale 1987) as having apically truncate, emaculate lobes, simple to dichotomously branched rhizines, larger spores and smaller conidia.

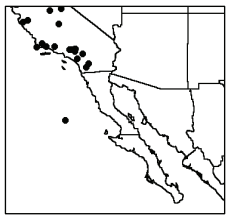
The Species

Parmelina quercina (Willd.) Hale, Phytologia 28: 481 (1974).

Basionym: *Lichen quercinus* Willd., Fl. Berol. Prodr. 353 (1787); Synonyms: *Parmelia quercina* (Willd.) Vain., Illustrations: Hale (1976b), p. 41; Hale (1979) p. 98; Brodo et al. (2001), p. 486.

Thallus: tightly adnate to adnate, foliose, 2-10 cm in diam., irregularly branched, lobate; **lobes:** narrow, sublinear to subirregular, elongate, contiguous to imbricate, plane to convex, 1.5-4 mm wide, lobe tips subrotund, ciliate, cilia simple, up to 0.15 mm long; **upper surface:** whitish gray to pale greenish gray, smooth but cracked with age, dull, sometimes partly pruinose, usually strongly white maculate peripherally, becoming rugulose; soredia, isidia and pustulae absent; **medulla:** white; **lower surface:** black, densely rhizinate; rhizines: black, simple to very rarely squarrose; **Apothecia:** numerous, laminal, 1.5-5 mm diam.; margin: smooth; disc: brown, imperforate; **ascospores:** simple, broadly ellipsoid, 6-12 x 5-9 µm; **Pycnidia:** common, laminal, immersed; **conidia:** bacilliform, 6-8 x 1 µm; **Spot tests:** cortex K+ yellow, C-, KC-, P+ yellow; medulla K-, C+ red, KC+ red, P-; **Secondary metabolites:** upper cortex with atranorin and chloroatranorin; medulla with lecanoric acid (major).

Substrate and ecology: frequent on bark in oak woodlands, rare on rock; **World distribution:** pantemperate region, particularly those with Mediterranean climates, in North Ameica, Europe; Asia and Australasia; **Sonoran distribution:** common in southern California and Guadalupe Island, Baja California.



PARMELINOPSIS

by T. H. Nash III and J.A. Elix

Parmelinopsis Elix & Hale, Mycotaxon 29: 242 (1987).

Family: Parmeliaceae**;** Type: *Parmelinopsis horrescens* (Taylor) Elix & Hale; No. species: *c.* 25 world-wide; Selected lit.: Hale (1976b), Elix (1993a & 1994j), and Elix and Hale (1987).

Life habit: lichenized; **Thallus:** small foliose, *c.* circular in outline, dichotomously to irregularly lobate; **lobes:** narrow, flat, linear to sublinear, elongate; apices: truncate, sometime crenate, ciliate; cilia: simple or rarely branched; **upper cortex:** pored epicortex, palisade plectenchymatous; **upper surface:** gray, commonly emaculate (rarely sparsely maculate), with or without soredia, pustules or isidia, pseudocyphellae absent; **medulla:** white or rarely partly pale yellow, cell walls containing isolichenan; **photobionts**: primary one a *Trebouxia*, secondary photobiont absent; **lower surface:** black or ivory to pale brown, rhizinate; rhizines: concolorous with lower side, simple to sparsely furcated or dichotomous; **Ascomata:** apothecial, laminal, sessile or subpedicellate, imperforate; exciple: gray or hyaline; epithecium: brown or brownish yellow; hypothecium: hyaline, **asci:** lecanoral, wall layers apex thickened, apex amyloid, axial body divergent towards apex, 8-spored; **ascospores:** simple, broadly ellipsoid, 9-20 x 6-14 µm; **Conidiomata:** pycnidial, laminal, immersed; **conidia:** cylindrical to bacilliform or bifusiform, 3-8 x 0.5-1 µm; **Secondary metabolites:** upper cortex with atranorin and chloroatranorin; medulla with some combination of orcinol depsides and ß-orcinol depsidones; **Ge-**

ography: pantemperate, subtropical and tropical; **Substrate:** on bark and rocks.

Note: From the original conception of *Parmelina* (Hale 1974c), *Parmelinopsis* was segregated (Elix and Hale 1987) on the basis of having apically truncate, emaculate lobes, simple to dichotomously branched rhizines, larger spores and smaller conidia.

Key to the species of ***Parmelinopsis*** in the Sonoran region:

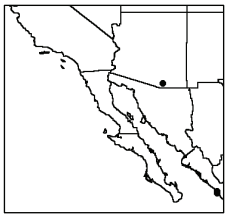
1. Isidia in part procumbent and flattened-lobulate, apically ciliate; medulla C-, K-, P-, KC+ rose (hiascic acid complex) ..... ***P. horrescens***
1. Isidia erect, cylindrical, finer, apically eciliate; medulla K- or faint yellow, P-, C+ and KC+ rose (gyrophoric acid, major) ..... ***P. minarum***

The Species

Parmelinopsis horrescens (Taylor) Elix & Hale, Mycotaxon 29: 242 (1987).

Basionym: *Parmelia horrescens* Taylor, Fl. Hibern. 2: 144 (1836); Synonyms: *Parmelina horrescens* (Tayl.) Hale, *Hypotrachyna horrescens* (Taylor) Krog & Swinscow; Illustrations: Hale (1976b), p. 41, and Hale (1979), p. 93, both as *Parmelina horrescens*; Elix (1994j), p. 133; Brodo et al. (2001), p. 487.

Thallus: tightly adnate to adnate, foliose, 2-6 cm in diam.; subdichotomously lobate; **lobes:** narrow, sublinear,, contiguous and often imbricate, elongate, plane, 0.5-2 mm wide; apices: subrotund, often lacinate, ciliate; cilia: simple, up to 0.8 mm long; **upper surface:** whitish to greenish gray, smooth, shiny, epruinose, emaculate, densely isidiate, **isidia:** cylindrical or slightly flatted and becoming lobulate-coralloid, apically spinulose to short-ciliate; soredia and pustulae absent; **medulla:** white; **lower surface:** black with a narrow, naked brown zone peripherally, densely rhizinate, rhizines black, simple to rarely squarrose or dichotomous; **Apothecia:** rare, laminal, sessile, 1.5-4 mm diam.; margin: isidiate; disc: brown; **ascospores:** simple, broadly ellipsoid, 16-18 x 10-12 µm; **Pycnidia:** rare, laminal, immersed; **conidia:** cylindrical, 3-5 x 0.5 µm; **Spot tests:** cortex K+ yellow, C-, KC-, P+ yellow; medulla K-, C+ rose, KC+ red, P-; **Secondary metabolites:** upper cortex with atranorin and chloroatranorin; medulla with 3-methoxy-2,4-di-*O*-methylgyrophoric acid (major), gyrophoric, 2,4-di-*O*-methylgyrophoric, 5-*O*-methylhiascic, lecanoric and umbilicaric acids (all minor) and hiascic, 2-*O*-methylhiasic, 2,4,5-tri-*O*-methylhiascic, 4,5-di-*O*-methylhiascic, 3-hydroxyumbilicaric, 3-hydroxygyrophoric, 3-methoxyumbilicaric and 4-*O*-methylgyrophoric acids (all trace).



Substrate and ecology: frequent on bark, rocks or mosses over rock in forests; **World distribution:** pantemperate and montane pantropical; **Sonoran distribution:** mountains of SE Arizona and Sinaloa in the Sierra Madre Occidental.

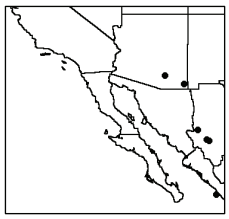
Parmelinopsis minarum (Vain.) Elix & Hale, Mycotaxon 29: 242 (1987).

Basionym: *Parmelia minarum* Vain., Acta Soc. Fauna Fl. Fenn. 7: 48 (1890); Synonyms: *Parmelia dissecta* Nyl., *Parmelina dissecta* (Nyl.) Hale, *Hypotrachyna minarum* (Vain.) Krog & Swinscow and see Hale (1976b) under *Parmelina dissecta*; Illustrations: Hale (1976b), p. 24, and Hale (1979), p. 93, both as *Parmelina dissecta*; Elix (1994j), p. 133; Brodo et al. (2001), p. 488.

Thallus: adnate, foliose, 2-7 cm in diam.; lobate; **lobes:** narrow, sublinear, elongate, contiguous to imbricate, plane, 1-3 mm wide; apices: subrotund, ciliate; cilia: simple, up to 0.7 mm long; **upper surface:** whitish to pale greenish gray, smooth, shiny, epruinose, emaculate, isidiate; **isidia:** cylindrical to branched, eciliate; soredia and isidia absent; **medulla:** white; **lower surface:** black, densely rhizinate, rhizines black, simple to sparingly furcate; **Apothecia:** very rare, laminal, sessile, 1-4 mm diam.; margin: crenate, isidiate; disc: brown; **ascospores:** simple, broadly ellipsoid, 12-17 x 8-10 µm; **Pycnidia:** rare, laminal, immersed; **conidia:** cylindrical, 3-5 x 0.5

µm; **Spot tests:** cortex K+ yellow, C-, KC-, P+ yellow; medulla K-, C+ rose, KC+ red, P-; **Secondary metabolites:** upper cortex with atranorin and chloroatranorin; medulla with gyrophoric acid (major), 5-*O*-methylhiascic, lecanoric and umbilicaric acids (all minor), 4,5-di-*O*-methylhiascic and 2,4,5-tri-*O*-methylhiascic acids (both trace).

Substrate and ecology: frequent on bark in woodlands, rare on rock; **World distribution:** pantemperate in North Ameica, Europe; Asia and Australasia; **Sonoran distribution:** SE Arizona and in the Sierra Madre Occidental region of Chihuahua and Sinaloa.



PARMELIOPSIS

by B. D. Ryan

Parmeliopsis (Nyl.) Nyl., Lich. Lapp. Orient. 121 (1866).

Family: Parmeliaceae; Type: *Parmeliopsis ambigua* (Wulfen) Nyl., *typ. cons.*; No. species. four world-wide. Selected lit.: Meyer (1982) and Hinds (1999).

Life habit: lichenized; **Thallus:** foliose, rosette-forming (with ± centrifugal growth), to 6 (-10) cm diam., adnate, closely adpressed; **lobes:** linear (strap-shaped) to sublinear, ± radiating, discrete and divaricate, or contiguous to overlapping; 0.2-1 (-1.5) mm wide, thin; tips: incised, eciliate; **upper surface:** pale greenish- to grayish- yellow or whitish gray to bluish or slightly greenish, generally dull in center and shiny at lobe margins, without pseudocyphellae or distinct maculae; **soralia:** present, round, laminal or terminal, 10-20 µm thick; **upper cortex:** palisade plectenchmatous, covered by pored epicortex; **medulla:** white, of densely interwoven hyphae; cell walls: containing isolichenan; **photobiont:** primary one a *Trebouxia*, secondary photobiont absent; **lower cortex:** paraplectenchymatous, 5-20 µm thick; **lower surface** whitish to pale or dark brown to black, rhizinate; rhizines: moderately dense, usually concolorous with lower surface (to darker), simple or sparsely furcated; **Ascomata:** rare, apothecial, laminal, sessile or somewhat elevated (shortly pedicellate), with a prominent thalline exciple concolorous with the thallus; disc: concave, becoming plane or convex, imperforate, mostly light brown, rarely to dark brown; true exciple: gray or hyaline; epithecium: 5-30 µm ("pseudoepithecium") pale brown or ochraceous-yellowish; hymenium: hyaline, very gelatinous, 30-50 (-60) µm high, with indistinct, simple paraphyses; hypothecium: hyaline; **asci:** clavate, *Lecanora*-type, *c.* 8-spored; **ascospores:** simple, slightly to strongly curved, reniform to allantoid, obtuse at the poles, or rarely ellipsoid, with one end more pointed, (6-) 7-12 (-15) x (2) 3-4 (-6) µm; walls: hyaline, smooth, without distinct endospore thickening, not amyloid; **Conidiomata:** pycnidial, black, laminal, immersed; conidiophores *Psora*-type (= type II of Vobis); **conidia:** borne terminally (acrogenously) from joints of conidiogenous hyphae, curved, falcate (sickle-shaped), 15-18 (-30) x (0.5-) 1 (-1.5) µm; **Secondary metabolites:** some combination of a ß-orcinol para-depside, orcinol depside and/or usnic acid; **Geography:** boreal-temperate to warm-temperate in the Northern Hemisphere; **Substrate:** on bark or wood, rarely rock, lowland to montane or alpine.

Notes: This genus is distinguished from most other genera of Parmeliaceae by the conidiophore type (which in most other Parmeliaceae is type V of Vobis, with pleurogenously formed conidia). It differs from its segregate genus *Imshaugia* in having larger and distinctly curved ascospores, and immersed and always laminal pycnidia with long, falcate conidia; *Parmeliopsis* also has a palisade plectenchymatous upper cortex, consistently has soredia and lacks isidia, contains isolichenan rather than lichenan in the cell walls, and has divaricatic acid (P-) rather than thamnolic acid (P+) in the medulla (with the cortex often containing usnic acid, which is absent from *Imshaugia*), and most species have a darkening lower

surface. See Hinds (1999) for a summary of the nomenclatural and taxonomic history of *Parmeliopsis* (syn. *For aminella*) and *Imshaugia*; which has contributed to confusing and/or contradictory descriptions in both genera.

Key to species of ***Parmeliopsis*** in the Sonoran region:

1. Upper side mineral-gray to whitish gray or blue-gray, K+ yellowish, KC- (atranorin) ..... ***P. hyperopta***
1. Upper side greenish yellow, K-, KC+ yellow (usnic acid major, ± atranorin) ..... ***P. ambigua***

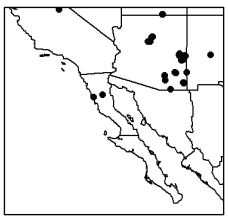
The Species

Parmeliopsis ambigua (Wulfen) Nyl., Lich. Lapp. Orient. 121 (1866) [preprint from Not. Sällsk. Fauna Fl. Fenn. Förh. 8: 121 (1882)].

Basionym: *Lichen ambiguus* Wulfen, in Jacq., Collect. Bot. 4: 239: tab. 4, fig. 2 (1790); Synonym: *Foraminella ambigua* (Wulfen) S. F. L. Mey. and see Hinds (1999); Illustrations: Brodo et al. (2001), p. 489; Hale and Cole (1988), pl. 7c; McCune and Goward (1995), p. 133, McCune and Geiser (1997), p. 192; Flenniken (1999), pl. 16-H; Hinds (1999), fig. 1; Wirth (1995), p. 671.

Thallus: foliose, orbicular, often forming rosettes, 1-3 cm diam. or irregularly expanded to 6 (-10) cm, often contiguous with adjacent thalli closely adnate and appressed; **lobes:** generally radiating and contiguous (to partly overlapping centrally, or ± discrete at margins, only occasionally much reduced, flat to ± concave, 0.5-0.8 (-1.5) mm wide, short sublinear; irregularly dichotomously branched; margins: sparingly indented; tips: usually closely appressed; **upper surface:** pale greenish yellow to yellow (becoming straw-colored in herbarium), rarely gray-green or with dead parts becoming black, often brownish at margins and lobe tips, dull, smooth, continuous or weakly maculate, flat and roughened near periphery, becoming rugose towards thallus center; **soredia:** powdery, yellowish green to green, paler or concolorous with thallus, in ± discrete, well-delimited soralia; soralia: laminal (often on ridges) or subterminal (pedicillate, at the tips of short lobes), orbicular, eroded, flat or occasionally ± convex and forming mounds, rarely capitate, sometimes ± contiguous to form a continuously sorediate crust in older (central) parts of thallus; **upper cortex:** 10-20 µm thick; **medulla** white, loose, sometimes poorly developed, 10-20 µm thick, of 2-4 µm thick hyphae; algal layer: continuous; **lower cortex:** well developed, composed of hyphae ± parallel to the surface; **lower surface:** gradually darkening from narrow brown zone at the margins to dark brown or black towards center (only occasionally uniform light brown to brown), shiny; rhizines: moderately abundant, to the margins and often extending beyond the lobe edges, concolorous with lower surface, simple (to sparsely branched); **Apothecia:** rare, occasional on lignicolous specimens, sessile to shortly pedicillate, up to 1-2 mm diam.; thalline margin: yellow or brownish, entire or becoming sorediate; disc: chestnut brown or red-brown, dull, at first concave, becoming flat or convex, epruinose; ephymenium: 8-12 µm pale brown or yellowish, smooth, with a covering of amorphous material; hymenium: hyaline, 50-60 µm high; **ascospores:** ellipsoid or one end more pointed, 6.5-13.0 x 1.5-5 µm; **Pycnidia:** rare; **conidia** falcate, 12-18 (-22) x 0.5-1 µm; **Spot tests:** upper cortex K- or + faintly yellow, C-. KC+ yellow, P-, UV-; medulla P-, K-, KC-, C-, UV+ white; **Secondary metabolites:** cortex with usnic acid (major) and sometimes atranorin (minor or trace); medulla with divaricatic acid (major) and nordivaricatic acid (minor).

Substrate and ecology: common on bark of conifers, old wood, stumps and logs, rare on broad-leaved trees, sandstone and mosses over rocks; often on or near tree bases, below the snowpack, only occasionally on twigs or small branches. In open to shady forests or woodlands, occurring with *P. hyperopta*, but more tolerant of dry conditions; **World distribution:** circumpolar, arctic to mid-boreal and higher elevations in the south; North America, Europe, northern Asia and Australasia; **Sonoran distribution:** common in Arizona in spruce-fir zone, 1740-3535 m, occasional in Baja California (2800 m, on *Abies*) and in mountains north of southern California.



Notes: In western North America this species is easily recognized in the field by the very narrow, closely

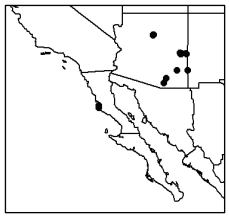
appressed greenish yellow lobes, usually with abundant roundish soralia. *Xanthoparmelia mougeotii* is superficially similar but is collected only on rocks and has a generally shiny upper surface throughout and a K+ yellow, P+ orange medulla (stictic acid). Related species in eastern North America are *Parmeliopsis subambigua* Gyeln., which has diffuse laminal soralia arising from pustules and is restricted to the southeastern coastal plain, and *P. capitata* R. C. Harris, which has mostly capitate soralia on the tips of upturned narrow lobes, and a consistently pale lower surface. The illustration in Hale (1979) labeled as *P. ambigua* is actually of *P. capitata* (Hinds 1999).

Parmeliopsis hyperopta (Ach.) Arnold, Verh. Zool.-Bot. Gesell. Wien 30: 117 (1880).

Basionym *Parmelia hyperopta* Ach., Syn. Lich.: 208 (1814); Synonyms: *Foraminella hyperopta* (Ach.) S. F. L. Meyer and see Hinds (1999); Illustrations: Thomson (1984), p. 326; Flenniken (1999), Pl. 16-I); Hinds (1999), fig. 4; Wirth (1995), p. 671; Brodo et al. (2001), p. 490.

Thallus foliose, orbicular, tightly adnate to adnate, 2-7 (-8) cm diam., closely appressed, deeply lobed; **lobes:** sublinear, ± irregularly dichotomous, generally contiguous to overlapping, 5-15 mm long, 0.3-1 mm wide; tips: broadened, rounded or crenate; **upper surface:** whitish to light or ashy or sometimes dark gray, brownish at the tips, dull or shining; **soredia:** granular (to somewhat powdery), white to white-gray or blue-gray, in well-delimited, round, capitate, and ± convex soralia; soralia: laminal (scattered to contiguous) or subterminal (at the tips of short, adnate or somewhat ascending lobes); **upper cortex** brownish, 16-20 µm thick; **medulla** white, loose, of 4 µm thick hyphae; algal layer: continuous or interrupted; **lower cortex:** 16-20 µm thick; **lower surface** tan to dark brown, becoming black towards center; rhizines: short, simple, dark, up to the margins; **Apothecia:** very rare, laminal or marginal, slightly pedicillate, up to 2 mm diam.; thalline margin: whitish or brown, crenulate, sometimes becoming sorediate; disc: pale or dark brown, shiny, flat or becoming convex, epruinose; epihymenium: 14-30 µm brown or yellow-brown; hymenium: hyaline or yellowish; **ascospores** short ellipsoid or bacilliform with the ends rounded, 8-15 x 1.5-5 µm; **Pycnidia:** rare, on lobe tips; **conidia:** falcate, 16-22 x 0.5-0.8 µm; **Spot tests:** upper cortex K+ yellow, C-, KC-, P- or + pale yellow, UV-; medulla K-, C-, KC- or faintly purplish, P-, UV+ white; **Secondary metabolites:** upper cortex with atranorin and chloroatranorin, medulla with divaricatic acid.

Substrate and ecology: common on conifers (especially *Pseudotsuga*) and old stumps, burned logs, old wood, rare on acid rocks, often on or near the bases of trees, below the snowpack; in open to shady moist forests, often with *P. ambigua*; **World distribution:** circumpolar; North America, Europe and northern Asia; also in South America; **Sonoran distribution:** common in Arizona at high elevations (2900-3535 m) in pine-fir and spruce-fir forests; also found in Baja California.



Notes: As pointed out by Hinds (1999), although *P. hyperopta* has been considered as differing from *P. ambigua* mainly in chemistry (cortex with atranorin rather than usnic acid, reflected in the color of the upper surface), it also differs somewhat morphologically, e.g., in having more often terminal, capitate soralia and on the average somewhat longer ascospores, and also perhaps (Thomson 1984) a thicker pigmented layer in the upper part of the hymenium. *Parmeliopsis hyperopta* can be distinguished from sorediate *Physcia* spp. (most of which occur on rocks at lower elevations in the Sonoran region) by the somewhat shiny upper surface near the lobe tips, presence of divaricatic acid in the medulla, and occurrence over acidic bark. Similar species in eastern North America include *Physcia americana* (which is white below and has a K+ yellow medulla). Essentially all other gray, sorediate parmelioids in the Sonoran region are larger, more robust and more loosely adnate; a few *Hypotrachynae* are closest, but they have dichotomous rhizines.

PARMOTREMA

by T. H. Nash III and J. A. Elix

Parmotrema A. Massal., Atti Reale Ist. Veneto Sci. Lett.. Arti, ser 3, 5: 248 (1860).

Family: Parmeliaceae; Type: *Parmotrema perforatum* (Ach.) A. Massal.; No. species: over 300 world-wide; Selected lit.: Elix (1993a & 1994k) and Hale (1965).

Life habit: lichenized; **Thallus:** adnate to loosely adnate, large foliose, lobate; **lobes:** usually subirregular to irregular, sometimes imbricate; apices: typically rotund, flat (to subconvex), ciliate or not; **upper surface:** gray or rarely yellow green, smooth, plane to rugulose, shiny or dull, sometimes white maculate, usually epruinose, epseudocyphellate, with or without soredia, isidia or pustules; **upper cortex:** pored epicortex, palisade plechenchymatous; **medulla:** usually white, sometimes pigmented in whole or part; cell walls: containing *Cetraria*-type lichenan; **photobiont**: primary one a *Trebouxia*, secondary photobiont absent; **lower surface:** black, broad brown (or mottled white and brown) zone peripherally, plane to sometimes wrinkled, attached by simple (rarely branched) rhizines, lacking tomentum; **Ascomata:** apothecial, laminal, orbicular, cup-shaped, pedicellate; margin: prominent, with thalloid rim; disc: imperforate or commonly perforate; exciple: gray or hyaline; epithecium: brown or brownish yellow; hypothecium hyaline; **asci:** lecanoral, apically with thickened wall layers and divergent axial body; apex: amyloid; 8-spored; **ascospores:** simple, ellipsoid, 8-35 x 5-18 µm (typically at the larger end of the range); wall: thick, hyaline; **Conidiomata:** pycnidial, laminal or marginal, immersed; **conidia:** sublageniform (3-10 x 1 µm) or filiform (8-20 x 1 µm); **Secondary metabolites:** some combination of orcinol depsides, orcinol depsidones, ß-orcinol depsides [and atranorin], ß-orcinol depsidones, (higher) aliphatic acids, pulvinic acid derivatives, anthraquinones, xanthones, and dibenzofurans [and usnic acids]; **Geography:** although cosmopolitan, predominately tropical,; **Substrate:** mostly on bark or acidic rocks, rarely on compacted soil.

Notes: Until the 1970's (Hale 1974) *Parmotrema* was usually treated as the section *Amphigymnia* of *Parmelia*, although it had been proposed as a separate genus over 100 years earlier. Nevertheless, it has received widespread acceptance in recent years. The circumscription given here follows Elix (1994h) and Hale, and is slightly less inclusive than the circumscription used by Krog and Swinscow (1981). Key characters for the genus include large thalli with broad, rotund lobe apices, broad naked marginal zones on the lower surface, frequent occurrence of marginal cilia, simple rhizines, thick-walled ellipsoid spores, and sublageniform or filiform conidia.

Key to the species of ***Parmotrema*** in the Sonoran region:

1. Thallus yellow green (usnic acid or secalonic acids) .. 2
1. Thallus gray (atranorin major in upper cortex) 4

2. Thallus sorediate; upper cortex fragile, ± flaking off; secalonic acids present ..... ***P. xanthopustulatum***
2. Thallus isidiate; upper cortex coriaceous, intact; lacking secalonic acids 3

3. Medulla C+ red (gyrophoric acid major) ... ***P. aberrans***
3. Medulla C- (gyrophoric acid absent) ..... ***P. xanthinum***

4. Upper cortex fragile, ± flaking off; medulla strongly yellow ..... ***P. xanthopustulatum***
4. Upper cortex coriaceous, intact; medulla usually white (rarely lightly pigmented or mottled) 5

5. Thallus neither isidiate or sorediate 6
5. Thallus isidiate or sorediate 9

6. Thallus lobes relatively narrow (<5 mm wide), tips subtruncate ..... ***P. moreliense***
6. Thallus lobes broad (>5 mm wide), tips rotund 7

7. Lower surface margin mottled white and brown; medulla K+ yellow turning orange (norstictic acid major) ..... ***P. perforatum***
7. Lower surface margin uniformly brown; medulla K+ yellow turning deep red (salazinic acid major) 8

8. Thallus margin ciliate and dentate lacinate .... ***P. eurysacum***
8. Thallus margin eciliate and lacking lacinae ..... ***P. latissimum***

9. Thallus isidiate 10
9. Thallus sorediate (not isidiate) 12

10. Medulla K+ yellow turning orange (stictic acid) .... ***P. crinitum***
10. Medulla K- (stictic acid absent) 11

11. Medulla C+ red (lecanoric acid major), UV- .... ***P. tinctorum***
11. Medulla C-, UV+ white ..... ***P. mellissii***

12. Thallus lobes relatively narrow (generally <5 mm wide), tips subtruncate ..... ***P. paramoreliense***
12. Thallus lobes broad (generally >5 mm wide), tips rotund 13

13. Medulla K+ yellow, turning orange or deep red 14
13. Medulla K- (stictic, norstictic or salazinic acids absent) 18

14. Underside uniformly brown peripherally 15
14. Underside mottle white and brown peripherally . 17

15. Medulla K+ yellow, turning orange (stictic acid major) ..... ***P. chinense***
15. Medulla K+ yellow, turning deep red (salazinic acid major) 16

16. Cilia short, less than 0.2 mm long; spores, if present 22-30 µm long ..... ***P. cristiferum***
16. Cilia long, up to 2.0 mm long; spores, if present 12-17 µm long ..... ***P. stuppeum***

17. Medulla with stictic acid major ..... ***P. hypoleucinum***
17. Medulla with norstictic acid major ..... ***P. hypotropum***

18. Medulla P+ red (protocetraric acid major) 19
18. Medulla P- (protocetraric acid lacking) 20

19. Underside uniformly brown peripherally; medulla with fatty acids (minor) ..... ***P. gardneri***
19. Underside mottled white and brown peripherally; medulla with echinocarpic acid (minor) ..... ***P. dilitatum***

20. Medulla C+ red (lecanoric acid major) .... ***P. austrosinense***
20. Medulla C- (lecanoric acid absent) 21

21. Medulla UV+ white (alectoronic acid major) 22
21. Medulla UV- (alectoronic acid absent) 23

22. Thallus lobes <10 mm wide; thallus surface strongly white maculate ..... ***P. louisianae***
22. Thallus lobes >10 mm wide; thallus surface emaculate (or weakly so) ..... ***P. arnoldii***

23. Thallus margin ciliate; medulla with norlobaridone (major) ..... ***P. hababianum***
23. Thallus margin eciliate; medulla with fatty acids (lacking norlobaridone) 24

24. Underside uniformly brown; medulla with caperatic acid (major); on rocks ..... ***P. mordenii***
24. Underside mottled white and brown peripherally; medulla with praesorediosic and protopraesorediosic acids (major), commonly on bark .... ***P. praesorediosum***

The Species

Parmotrema aberrans (Vain.) Abbayes, Phytologia 28: 334 (1974).

Basionym: *Parmelia xanthina* f. *aberrans* Vain., Bull. Inst. Fr. Afr. Noire, ser A 20: 22 (1959).

Thallus: loosely adnate, foliose, 3-15 cm in diam., lobate; **lobes:** subirregular, elongate, slightly imbricate, plane, separate, 10-15 mm wide; apices: rotund, becoming crenate and dissected with age, ciliate; cilia: up to 3.0 mm long; **upper surface:** yellow green with some blackened areas, smooth, dull to shiny, epruinose, emaculate, finely reticulately cracked with age; **isidia:** simple to coralloid branched, sometimes apically ciliate, common, laminal; soredia and pustulae: absent; **medulla:** pale orange yellow with continuous algal layer; **lower surface:** black with brown naked zone peripherally, centrally rhizinate; rhizines: simple; **Apothecia:** rare, substipitate, up to 4 mm in diam.; margin: sparsely sorediate; disc: brown, imperforate; **ascospores:** broadly ellipsoid, 10-16 x 7-10 µm; **Pycnidia:** not seen; **Spot tests:** upper cortex K+ yellow, C-, KC-, P-; medulla K-, C+ red, KC+ red, P-; **Secondary metabolites:** upper cortex with usnic acid (major), atranorin and chloroatranorin (trace); medulla with gyrophoric acid (major).

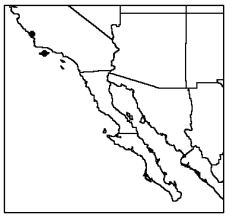
Substrate and ecology: usually on trees in open habitats, rarely on rocks; **World distribution:** neotropics from Mexico to Paraguay; **Sonoran distribution:** on pines in the pine-oak forests of the Sierra Madre Occidental of Sinaloa.

Parmotrema arnoldii (Du Rietz) Hale, Phytologia 28: 335 (1974).

Basionym: *Parmelia arnoldii* Du Rietz, Nyt. Mag. Naturvid. 62: 80 (1924); Illustrations: Hale (1979), p. 62; McCune and Geiser (1997), p. 195; Brodo et al. (2001), p. 492.

Thallus: foliose, adnate to loosely adnate, 3-20 cm in diam., lobate; **lobes:** subirregular, elongate, slightly imbricate, plane, separate, 10-20 mm wide; apices: rotund, often ascending and wavy, ciliate; cilia: up to 5 mm long; **upper surface:** gray with some blackened areas, smooth, dull to shiny, faintly white maculate; **soredia:** granular, common, in linear, marginal to submarginal soralia; isidia and pustulae: absent; **medulla:** white with continuous algal layer; **lower surface:** black with brown to mottled white naked zone peripherally, centrally rhizinate; rhizines: scattered, simple; **Apothecia:** rare, substipitate, up to 10 mm in diam.; margin: crenulate; disc: brown, often perforate; **ascospores:** ellipsoid to broadly ellipsoid, 15-22 x 9.5-12 µm; **Pycnidia:** laminal, immersed; **conidia:** 10.5-11.5 µm long; **Spot tests:** upper cortex K+ yellow, C-, KC-, P-; medulla K-, C-, KC+ red or orange, P-; **Secondary metabolites:** upper cortex with atranorin and chloroatranorin; medulla with alectoronic acid (major) and α-collatolic acid (minor).

Substrate and ecology: on hardwood trees (often among mosses) in relatively exposed positions; **World distribution:** neotropics and extending well into temperate regions to the north and south, Macaronesia, throughout Europe and New Zealand; **Sonoran distribution:** common on live oaks in woodlands of southern California, especially the Channel Islands.

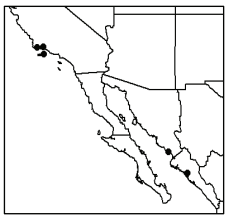


Parmotrema austrosinense (Zahlbr.) Hale, Phytologia 28: 335 (1974).

Basionym: *Parmelia austrosinense* Zahlbr. Symb. Sin. 3: 192 (1930); Synonyms: see Hale (1965) under *Parmelia austrosinense*; Illustrations: Hale (1979), p. 65; Swinscow and Krog (1988), p. 169; Brodo et al. (2001), p. 493.

Thallus: foliose, loosely adnate, 3-10 cm in diam., lobate; **lobes:** subirregular, elongate, slightly imbricate, plane, separate, 10-30 mm wide; apices: rotund, often ascending, elacinate and eciliate; **upper surface:** gray with some blackened areas, smooth, dull to shiny, usually weakly white maculate; **soredia:** granular, common, in linear, submarginal or marginal soralia; isidia and pustulae: absent; **medulla:** white with continuous algal layer; **lower surface:** black with brown to mottled white naked zone peripherally, centrally rhizinate; rhizines: scattered, simple; **Apothecia:** rare, substipitate, up to 10 mm in diam.; margin: sparsely sorediate; disc: brown, often perforate; **ascospores:** ellipsoid to broadly ellipsoid, 12-18 x 7-10 µm; **Pycnidia:** not seen; **Spot tests:** upper cortex K+ yellow, C-, KC-, P-; medulla K-, C+ red, KC+ red, P-; **Secondary metabolites:** upper cortex with atranorin and chloroatranorin; medulla with lecanoric acid (major).

Substrate and ecology: usually on trees in open habitats, rarely on rocks; **World distribution:** pantropical and extending into some adjacent temperate areas; **Sonoran distribution:**.coastal areas of California, Sonora and Sinaloa.

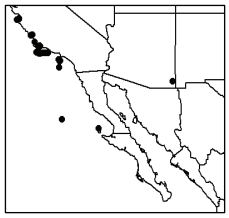


Parmotrema chinense (Osbeck) Hale & Ahti, Taxon 35: 133 (1986).

Basionym: *Lichen chinensis* Osbeck Dagb. Ostind. Resa 221 (1757); Synonyms: *Lichen perlatus* Huds.; *Parmelia perlata* (Huds.) Ach., *Parmotrema perlatum* (Huds.) M. Choisy and see Elix (1994); Illustrations: Wirth (1995), p. 673; McCune and Geiser (1997), p. 196; Brodo et al. (2001), p. 493.

Thallus: foliose, adnate to loosely adnate, 3-20 cm in diam., lobate; **lobes:** subirregular, elongate, often imbricate, plane, separate, 4-15 mm wide; apices: rotund, sometimes deeply crenate, sometimes ascending, elacinate, ciliate; cilia: frequent, up to 2.0 mm long; **upper surface:** gray, sometimes with some blackened areas, smooth, dull to shiny, emaculate to faintly white maculate; **soredia:** granular, common, in linear, marginal to submarginal soralia that often erode large areas and causing the margin to become revoute; isidia and pustulae: absent; **medulla:** white, with continuous algal layer; **lower surface:** black with brown naked zone peripherally, centrally rhizinate; rhizines: scattered, simple, black; **Apothecia:** very rare, substipitate, up to 7 mm in diam.; margin: sparsely sorediate; disc: brown, imperforate; **ascospores:** ellipsoid to broadly ellipsoid, 22-30 x 13-18 µm; **Pycnidia:** not seen; **Spot tests:** upper cortex K+ yellow, C-, KC-, P-; medulla K+ yellow turning orange, C-, KC-, P+ orange; **Secondary metabolites:** upper cortex with atranorin and chloroatranorin; medulla with stictic acid (major) and constictic acid (minor), norstictic, menegazziaic and cryptostictic acids (trace).

Substrate and ecology: usually on hardwood trees in open habitats, occasionally on rocks; **World distribution:** widespread in temperate region of the Northern and Southern Hemispheres; **Sonoran distribution:** common on oaks and other trees and shrubs in coastal woodlands of California and Baja California, much rarer inland in Arizona and Sonora.

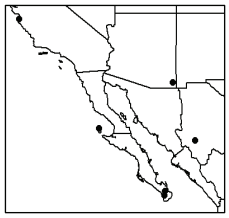


Parmotrema crinitum (Ach.) M. Choisy, Bull. Mens. Soc. linn. Lyon 21: 175 (1952).

Basionym: *Parmelia crinita* Ach. Syn, Meth. Lich. 196 (1814); Synonyms: see Elix (1994); Illustrations: Elix (1994), p. xviii; Wirth (1995), p. 675; McCune and Geiser (1997), p. 197; Brodo et al. (2001), p. 494.

Thallus: foliose, adnate to loosely adnate, 3-15 cm in diam., lobate; **lobes:** subirregular, elongate, slightly imbricate, plane, separate, 5-20 mm wide; apices: rotund, becoming crenate and dissected with age, sometimes ascending, ciliate; cilia: up to 3.0 mm long; **upper surface:** gray with some blackened areas, smooth, dull to shiny, epruinose, emaculate, finely reticulately cracked with age; **isidia:** simple to coralloid branched, sometimes disintegrating with age, often apically ciliate, common, laminal and marginal; soredia and pustulae: absent; **medulla:** white with continuous algal layer; **lower surface:** black with brown naked zone peripherally, centrally rhizinate, rhizines simple, black; **Apothecia:** rare, substipitate, up to 8 mm in diam.; margin: sparsely isidiate; disc: brown, imperforate; **ascospores:** ellipsoid, 21-35 x 11-18 µm; **Pycnidia:** not seen; **Spot tests:** upper cortex K+ yellow, C-, KC-, P-; medulla K+ yellow turning orange, C-, KC-, P+ orange; **Secondary metabolites:** upper cortex with atranorin and chloroatranorin; medulla with stictic acid (major) and constictic acid (minor), menegazziaic acid (trace).

Substrate and ecology: usually on hardwood trees in open habitats, rarely on rocks or soil; **World distribution:** pantropical and pantemperate; **Sonoran distribution:** SE Arizona southwards along the Sierra Madre Occidental in Chihuahua, Baja California and in the mountains of southern Baja California Sur.



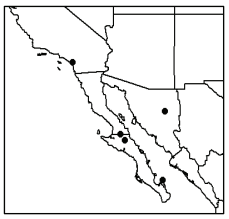
Parmotrema crisiferum (Taylor) Hale, Phytologia 28: 335 (1974).

Basionym: *Parmelia cristifera* Taylor, London J. Bot. 6: 165 (1847); Synonyms: see Hale (1965) under *Parmelia cristifera*; Illustrations: Hale (1979), p. 64; Krog and Swinscow (1981), p. 174; Brodo et al. (2001), p. 495.

Thallus: foliose, adnate to loosely adnate, 3-15 cm in diam., lobate; **lobes:** subirregular, elongate, slightly imbricate, plane, separate, 4-20 mm wide; apices: rotund, sometimes deeply crenate, elacinate, ciliate; cilia: sparse to frequent, 0.3-2.0 mm long; **upper surface:** gray, smooth, dull, emaculate; **soredia:** granular, common, in linear, submarginal soralia that are often on lateral, subascending lobes; isidia and pustulae: absent; **medulla:**

white with continuous algal layer; **lower surface:** black with brown naked zone peripherally, centrally rhizinate; rhizines: scattered, simple; **Apothecia:** very rare, substipitate, up to 7 mm in diam.; margin: sparsely sorediate; disc: brown, imperforate; **ascospores:** ellipsoid, 22-30 x 13-15 µm; **Pycnidia:** not seen; **Spot tests:** upper cortex K+ yellow, C-, KC-, P-; medulla K+ yellow turning deep red, C-, KC-, P+ orange; **Secondary metabolites:** upper cortex with atranorin and chloroatranorin; medulla with salazinic acid (major) and consalazinic acids (minor).

Substrate and ecology: usually on trees in open habitats, rarely on rocks; **World distribution:** pantropical and pantemperate; **Sonoran distribution:** southern California, Baja California Sur and Sonora.



Parmotrema dilatatum (Vain.) Hale, Phytologia 28: 335 (1974).

Basionym: *Parmelia dilatata* Vain., Acta Soc. Fauna Fl. Fenn. 7: 32 (1890); Synonyms: see Hale (1965) under *Parmelia dilatata*; Illustrations: Hale (1979), p. 61; Brodo et al. (2001), p. 496.

Thallus: foliose, adnate to loosely adnate, 3-20 cm in diam., lobate; **lobes:** subirregular, elongate, slightly imbricate, plane, separate, 10-20 mm wide; apices: rotund, ecilliate or short cilia developing in the axils of the lobes; **upper surface:** gray with some blackened areas, smooth, usually shiny, emaculate to faintly white maculate, reticulately cracked with age; **soredia:** granular, common, marginal, in linear soralia that sometimes develop on marginal lacinae; isidia and pustulae: absent; **medulla:** white or pigmented pale yellowish pink, with continuous algal layer; **lower surface:** black with brown to mottled ivory naked zone peripherally, centrally rhizinate; rhizines: scattered, simple; **Apothecia:** rare, substipitate, up to 10 mm in diam.; margin: sparsely sorediate; disc: brown, imperforate; **ascospores:** ellipsoid, 18-22 x 8-10 µm; **Pycnidia:** not seen; **Spot tests:** upper cortex K+ yellow, C-, KC-, P-; medulla K-, C-, KC-, P+ red; **Secondary metabolites:** upper cortex with atranorin and chloroatranorin; medulla with protocetraric acid (major), echinocarpic and conechinocarpic acids (minor or trace), secalonic acid A (± trace).

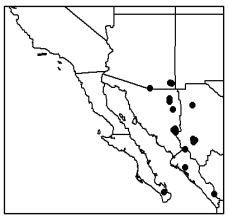
Substrate and ecology: usually on trees in open habitats, rarely on rocks; **World distribution:** pantropical and SE USA and SW Europe; **Sonoran distribution:** Sinaloa, in the Sierra Madre Occidental.

Parmotrema eurysacum (Hue) Hale, Phytologia 28: 336 (1974).

Basionym: *Parmelia eurysaca* Hue, Nouv. Arch. Mus. Hist. Nat., sér. 4: 1 (1899); Illustration: Hale (1979), p. 71.

Thallus: foliose, adnate to loosely adnate, 3-20 cm in diam., lobate; **lobes:** subirregular, elongate, slightly imbricate, plane, separate, 8-15 mm wide; apices: rotund, margin becoming dentate lacinate with age; lacinae: 5-10 x 1-2 mm; margin: ciliate; cilia: sparse, up to 4.0 mm long; **upper surface:** ashy white to gray, smooth, dull to rather shiny, emaculate to white maculate, becoming reticulately cracked with age; soredia, isidia and pustulae: absent; **medulla:** white, with continuous algal layer; **lower surface:** black with brown naked zone peripherally, centrally rhizinate; rhizines: scattered, simple; **Apothecia:** common, substipitate, up to 15 mm in diam.; margin: rugose, white maculate; disc: brown, often perforate; **ascospores:** broadly ellipsoid, 9-16 x 6-10; **Pycnidia:** common; **conidia:** bacilliform to short-filiform, 8-10 x 1 µm; **Spot tests:** upper cortex K+ yellow, C-, KC-, P-; medulla K+ yellow turning deep red, C-, KC-, P+ orange; **Secondary metabolites:** upper cortex with atranorin and chloroatranorin; medulla with salazinic acid (major) and consalazinic acids (minor).

Substrate and ecology: usually on trees and rocks in open habitats in canyons at intermediate elevations; **World distribution:** Mexico and SW U.S.A.; **Sonoran distribution:** SE Arizona and adjacent Sierra Madre Occidental of Chihuahua, Sonoran and Sinaloa and southern Baja Cali-



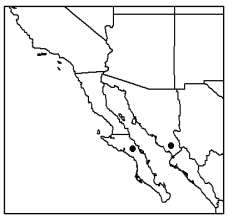
fornia Sur.

Parmotrema gardneri (C. W. Dodge) Sérus., Bryologist 87: 5 (1984).

Basionym: *Parmelia gardneri* C. W. Dodge, Ann. Missouri Bot. Gard. 46: 179 (1959); Illustration: Swinscow and Krog (1988), p. 177.

Thallus: foliose, adnate to loosely adnate, 3-10 cm in diam., lobate; **lobes:** subirregular, elongate, slightly imbricate, plane, separate, 8-15 mm wide; apices: rotund, subascending, eciliate or short cilia developing in the axils of the lobes; **upper surface:** gray with some blackened areas, smooth, usually shiny, emaculate, reticulately cracked with age; **soredia:** granular, common, in linear to subcapitate, marginal soralia that sometimes develop on marginal lacinae; isidia and pustulae: absent; **medulla:** white with continuous algal layer; **lower surface:** black with brown naked zone peripherally, centrally rhizinate; rhizines: scattered, simple; **Apothecia:** rare, substipitate, up to 5 mm in diam.; margin: sparsely sorediate; disc: brown, imperforate; **ascospores:** ellipsoid, 18-22 x 8-10 µm; **Pycnidia:** rare, punctiform, **conidia:** sublageniform, 6-7 x 1 µm; **Spot tests:** upper cortex K+ yellow, C-, KC-, P-; medulla K-, C-, KC-, P+ red; **Secondary metabolites:** upper cortex with atranorin and chloroatranorin; medulla with protocetraric acid (major), unknown fatty acid (major, minor or ± trace).

Substrate and ecology: usually on trees in open habitats; **World distribution:** pantropical; **Sonoran distribution:** southern lowlands of Sonora, Baja California del Sur.



Parmotrema hababianum (Gyeln.) Hale, Phytologia 28: 336 (1974).

Basionym: *Parmelia hababiana* Gyeln., Reprium nov. Spec. Regni veg. 29: 288 (1931); Synonyms: see Hale (1965) under *Parmelia hababiana*; Illustration: Hale (1965), plate 15 as *Parmelia hababiana*.

Thallus: foliose, adnate to loosely adnate, 3-15 cm in diam., lobate; **lobes:** subirregular, elongate, slightly imbricate, plane, separate, 5-15 mm wide; apices: rotund, subascending, ciliate; cilia: up to 4 mm long; **upper surface:** gray, smooth, usually shiny, faintly white maculate, reticulately cracked with age; **soredia:** granular, common, in linear to subcapitate, marginal soralia that sometimes develop on marginal lacinae; isidia and pustulae: absent; **medulla:** white with continuous algal layer; **lower surface:** black with brown and mottled white naked zone peripherally, centrally rhizinate; rhizines: scattered, simple; **Apothecia:** rare, substipitate, up to 5 mm in diam.; margin: often sorediate; disc: brown, perforate, **ascospores:** ellipsoid, 13-20 x 8-10 µm; **Pycnidia:** rare, punctiform; **conidia:** sublageniform, 6-8 x 1 µm; **Spot tests:** upper cortex K+ yellow, C-, KC-, P-; medulla K-, C-, KC+ purple, P-; **Secondary metabolites:** upper cortex with atranorin and chloroatranorin; medulla with norlobaridone (major), loxodin (± trace), protolichesterinic acid (trace).

Substrate and ecology: usually on trees in open habitats, rarely on rocks; **World distribution:** pantropical and some adjacent temperate areas; **Sonoran distribution:** SE Arizona and the Sierra Madre Occidental region of Sonora and Sinaloa.

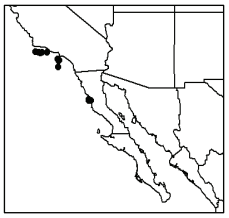
Parmotrema hypoleucinum (Steiner) Hale, Phytologia 28: 336 (1974).

Basionym: *Parmelia hypoleucina* Steiner, Österr. Bot. Zeitschr. 67: 282 (1918).

Thallus: foliose, adnate to loosely adnate, 3-15 cm in diam., lobate; **lobes:** subirregular, elongate, slightly imbricate, plane, separate, 8-15 mm wide; apices: rotund, ciliate; cilia: sparse, 0.3-2.0 mm long; **upper surface:** gray with some blackened areas, smooth, dull to shiny, sometimes white pruinose, usually white maculate; **soredia:** granular, common, in linear, marginal to submarginal soralia; isidia and pustulae: absent; **medulla:** white with continuous algal layer; **lower surface:** black with brown to mottled white naked zone peripherally, centrally rhizinate; rhizines: scattered, simple; **Apothecia:** not seen; **Pycnidia:** not seen; **Spot tests:** upper cortex K+ yellow,

C-, KC-, P-; medulla K+ yellow turning orange, C-, KC-, P+ orange; **Secondary metabolites:** upper cortex with atranorin and chloroatranorin; medulla with stictic acid (major) and constictic and norstictic acids (minor).

Substrate and ecology: usually on trees in open habitats, rarely on rocks; **World distribution:** pantropical and pantemperate; **Sonoran distribution:** southern, coastal regions of California and the western fringe of Baja California.

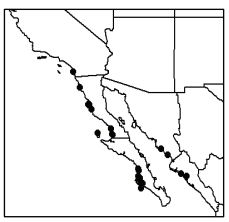


Parmotrema hypotropum (Nyl.) Hale, Phytologia 28: 337 (1974).

Basionym: *Parmelia hypotropa* Nyl., Syn. Meth. Lich. 378 (1860); Synonyms: see Hale (1965) under *Parmelia hypotropa*; Illustrations: Hale (1979), p. 60; Brodo et al. (2001), p. 497.

Thallus: foliose, adnate to loosely adnate, 3-15 cm in diam., lobate; **lobes:** subirregular, elongate, slightly imbricate, plane, separate, 8-15 mm wide; apices: rotund, ciliate; cilia: sparse, 0.3-2.0 mm long; **upper surface:** gray with some blackened areas, smooth, dull to shiny, sometimes white pruinose, usually white maculate; **soredia:** granular, common, in linear, marginal to submarginal, soralia; isidia and pustulae: absent; **medulla:** white with continuous algal layer; **lower surface:** black with brown to mottled white naked zone peripherally, centrally rhizinate; rhizines: scattered, simple; **Apothecia:** very rare, substipitate, up to 5 mm in diam.; margin: sparsely sorediate; disc: brown, imperforate; **ascospores:** ellipsoid, 22-30 x 13-16 µm; **Pycnidia:** not seen; **Spot tests:** upper cortex K+ yellow, C-, KC-, P-; medulla K+ yellow turning orange, C-, KC-, P+ orange; **Secondary metabolites:** upper cortex with atranorin and chloroatranorin; medulla with norstictic acid (major) and connorstictic acid (minor).

Substrate and ecology: usually on trees in open habitats, rarely on rocks; **World distribution:** eastern USA and NW Mexico; **Sonoran distribution:** southern, coastal regions of California and Baja California, Baja California Sur, Sonora and Sinaloa.



Notes: Culberson (1973) proposed a new taxonomy based on the assumption that chemical evolution had occurred prior to morphological differentiation. The result is that *P. hypoleucinum*, *P. hypotropum* and *P. louisianae* are all morphological nearly identical. The species have not yet been investigated from a molecular perspective.

Parmotrema latissimum (Fée) Hale, Phytologia 28: 337 (1974).

Basionym: *Parmelia latissima* Fée; Illustration: Awasthi (1976), plate 4, fig. 3.

Thallus: foliose, loosely adnate, 3-25 cm in diam., lobate; **lobes:** subirregular, elongate, becoming somewhat imbricate, plane, separate, 8-20 mm wide; apices: rotund, eciliate; **upper surface:** gray, smooth to rugulose, dull, emaculate, becoming reticulately cracked with age; soredia, isidia and pustulae: absent; **medulla:** white with continuous algal layer; **lower surface:** black with brown naked zone peripherally, centrally rhizinate; rhizines: scattered, simple, black; **Apothecia:** common, substipitate, up to 10 mm in diam.; margin: crenulate, emaculate; disc: brown, perforate; **ascospores:** ellipsoid, 28-32 x 14-16 µm; **Pycnidia:** not seen; **Spot tests:** upper cortex K+ yellow, C-, KC-, P-; medulla K+ yellow turning deep red, C-, KC-, P+ orange; **Secondary metabolites:** upper cortex with atranorin and chloroatranorin; medulla with salazinic acid (major) and consalazinic acids (minor).

Substrate and ecology: montane usually on trees in open habitats; **World distribution:** neotropics and India; **Sonoran distribution:** Sonora, in the Sierra Madre Occidental.

Parmotrema louisianae (Hale) Hale, Phytologia 28: 337 (1974).

Basionym: *Parmelia louisianae* Hale, Phytologia 22: 92 (1971).

Thallus: foliose, adnate to loosely adnate, 3-15 cm in diam., lobate; **lobes:** subirregular, elongate, slightly imbricate, plane, separate, 5-10 mm wide; apices: rotund, crenate, ciliate; cilia: sparse, up to 2.0 mm long; **upper surface:** gray with some blackened areas, smooth, dull to shiny, usually white maculate; **soredia:** granular, common, in linear, marginal to submarginal soralia that often occur on revolute lobes; isidia and pustulae: absent; **medulla:** white with continuous algal layer; **lower surface:** black with brown to mottled white naked zone peripherally, centrally rhizinate; rhizines: scattered, simple; **Apothecia:** not seen; **Pycnidia:** occasional, punctiform; **conidia:** filiform, 10-12 x 1 µm; **Spot tests:** upper cortex K+ yellow, C-, KC-, P-; medulla K-, C-, KC+ red or orange, P-; **Secondary metabolites:** upper cortex with atranorin and chloroatranorin; medulla with alectoronic acid (major) and α-collatolic acid (± trace).

Substrate and ecology: usually on trees in open habitats, rarely on rocks; **World distribution:** SE U.S.A. and Mexico; **Sonoran distribution:** Sonora, in the Sierra Madre Occidental.

Parmotrema mellissii (C. W. Dodge) Hale, Phytologia 28: 337 (1974).

Basionym: *Parmelia mellissii* C. W. Dodge, Ann. Missouri Bot. Gard. 46: 146 (1959); Synonyms: see Hale (1965) under *Parmelia mellissii*; Illustration: Hale (1979), p. 67.

Thallus: foliose, loosely adnate, 3-10 cm in diam., lobate; **lobes:** subirregular, elongate, slightly imbricate, plane, separate, 6-12 mm wide; apices: rotund, crenate, ascending, ciliate; cilia: up to 4 mm long; **upper surface:** gray with some blackened areas, smooth, dull, sometimes white pruinose, usually white maculate; **isidia:** simple to coralloid, common, laminal to submarginal; tips: sometimes ciliate, becoming eroded and subsorediate; soredia and pustulae: absent; **medulla:** white with patches of yellow to orange brown, particularly in lower layers, continuous algal layer; **lower surface:** black with brown to tan or mottled white naked zone peripherally, centrally rhizinate; rhizines: scattered, simple; **Apothecia:** rare, substipitate, up to 5 mm in diam.; margin: sparsely sorediate; disc: brown, imperforate; **ascospores:** broadly ellipsoid, 16-22 x 10-14 µm; **Pycnidia:** not seen; **Spot tests:** upper cortex K+ yellow, C-, KC-, P-; medulla K-, C-, KC+ red or orange, P-; **Secondary metabolites:** upper cortex with atranorin and chloroatranorin; medulla with alectoronic acid (major), α-collatolic acid (minor) and skyrin (accessory).

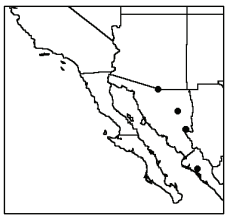
Substrate and ecology: usually on trees in open habitats, rarely on rocks; **World distribution:** pantropical and southern USA; **Sonoran distribution:** Sonora and Sinaloa, in the Sierra Madre Occidental.

Parmotrema mordenii (Hale) Hale, Phytologia 28: 337 (1974).

Basionym: *Parmelia mordenii* Hale, Smith. Contr. Bot. 4: 18 (1971); Illustration: Hale (1971), p. 19.

Thallus: foliose, adnate, 2-8 cm in diam., lobate; **lobes:** subirregular, elongate, slightly imbricate, plane, separate, 5-8 mm wide; apices: rotund, eciliate; **upper surface:** gray with some blackened areas, smooth, shiny, sometimes white pruinose, conspicuously white maculate; **soredia:** granular, common, in linear to orbicular, laminal or marginal soralia; isidia and pustulae: absent; **medulla:** white with continuous algal layer; **lower surface:** black with brown, naked zone peripherally, centrally rhizinate; rhizines: scattered, simple; **Apothecia:** not seen; **Pycnidia:** not seen; **Spot tests:** upper cortex atranorin K+ yellow, C-, KC-, P-; medulla K-, C-, KC-, P-; **Secondary metabolites:** upper cortex with atranorin and chloroatranorin; medulla with caperatic acid (major), protolichesterinic acid (minor).

Substrate and ecology: on rocks in open habitats; **World distribution:** neotropics and SW USA; **Sonoran distribution:** lower montane of SE Arizona southwards through the thorn forests of Sonora and Sinaloa.

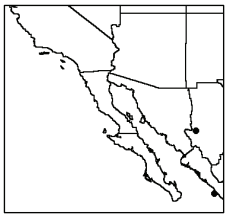


Parmotrema moreliense (de Lesd.) W. L Culb & C. F. Culb., Bryologist 84: 310 (1981).

Basionym: *Parmelia moreliense* de Lesd., Lich. Mexique 5 (1914); Synonym: *Everniastrum moreliense* (de Lesd.) Hale; Illustration: Culberson and Culberson (1981), p. 310.

Thallus: foliose, loosely adnate, 4-15 cm in diam., lobate; **lobes:** linear, elongate, loosely imbricate, convex, separate, 2-5 mm wide; apices: subtruncate, ciliate; cilia: common, to 10 mm long, simple; **upper surface:** gray with some blackened areas, smooth, shiny, sometimes white pruinose, conspicuously white maculate; isidia, soredia and pustulae: absent; **medulla:** white with continuous algal layer; **lower surface:** black to brown at the tips, rhizinate (except tips); rhizines: scattered, simple to rarely branched; **Apothecia:** common, laminal on thallus, 2-10 mm wide, stipitate; margin: smooth; disc: red brown to dark brown, becoming perforate with age; **ascospores:** ellipsoid, 16-20 x 8-10 µm; **Pycnidia:** punctiform; **conidia:** 16-21 x 1 µm; **Spot tests:** upper cortex K+ yellow, C-, KC-, P-; medulla K+ yellow turning deep red, C- or C+ pink, KC- or KC+ pink, P+ orange; **Secondary metabolites:** upper cortex with atranorin and chloroatranorin; medulla with salazinic acid (major); consalazinic acids (minor); gyrophoric, protocetraric, norstictic and protolichesterinic acids (accessory).

Substrate and ecology: usually on trees in open habitats, rarely on rocks; **World distribution:** central to southern Mexico; **Sonoran distribution:** Sierra Madre Occidental region of Chihuahua and Sinaloa.



Parmotrema paramoreliense W. L. Culb. & C. F. Culb., Bryologist 84: 311 (1981).

Illustration: Culberson and Culberson (1981), p. 310.

Thallus: foliose, loosely adnate, 2-10 cm in diam., lobate; **lobes:** linear, elongate, slightly imbricate, convex, separate, 2-7 mm wide; apices: subtruncate, ciliate; cilia: sparse, up to 5 mm long, simple; **upper surface:** gray with some blackened areas, smooth, shiny, sometimes white pruinose, conspicuously white maculate; **soredia:** farinose to granular, common, in globose, terminal or marginal soralia that are irregularly erumpent; isidia and pustulae: absent; **medulla:** white with continuous algal layer; **lower surface:** black to brown at the tips, rhizinate (except tips); rhizines: scattered, simple to rarely branched; **Apothecia:** not seen; **Pycnidia:** not seen; **Spot tests:** upper cortex K+ yellow, C-, KC-, P-; medulla K+ yellow turning deep red, C- or C+ pink, KC- or KC+ pink, P+ orange; **Secondary metabolites:** upper cortex with atranorin and chloroatranorin; medulla with salazinic acid (major); consalazinic acids (minor); gyrophoric and protocetraric acids (accessory).

Substrate and ecology: usually on hardwood trees or pines in open habitats, rarely on rocks or soil; **World distribution:** Mexico, Central America and Chile; **Sonoran distribution:** Sierra Madre Occidental region of Sinaloa.

Parmotrema perforatum (Jacq.) A. Massal., Atti Reale Lst Veneto Sci. Lett. Arti, 248 (1860).

Basionym: *Lichen perforatus* Jacq., Coll. Bot. III, 1: 116, pl. 3 (1786) ; Synonyms: *Parmelia perforata* (Jacq.) Ach. and see Hale (1965) under *Parmelia perforata*; Illustrations: Hale (1965), plate 2 as *Parmelia perforata*; Hale (1979), p. 70; Brodo et al. (2001), p. 498.

Thallus: foliose, loosely adnate, 3-15 cm in diam., lobate; **lobes:** subirregular, elongate, slightly imbricate, plane, separate, 10-20 mm wide, margin becoming lacerate to lacinate with age; apices: rotund, ciliate; cilia: up to 4 mm wide; **upper surface:** gray with some blackened areas, smooth to rugulose, shiny, epruinose, strongly white maculate, becoming reticulately cracked with age; soredia, isidia and pustulae: absent; **medulla:** white with continuous algal layer; **lower surface:** black with brown with a mottled ivory (rarely tan) naked zone peripherally, centrally rhizinate; rhizines: scattered, simple; **Apothecia:** common, substipitate, up to 20 mm in diam.; margin: rugose, white maculate; disc: brown, perforate; **ascospores:** broadly ellipsoid, 12-16 x 7-9 µm; **Pycnidia:** not seen; **Spot tests:** upper cortex K+ yellow, C-, KC-, P-; medulla K+ yellow turning orange, C-, KC-, P+ orange; **Secon-**

dary metabolites: upper cortex with atranorin and chloroatranorin; medulla with norstictic acid (major) and connorstictic acid (minor).

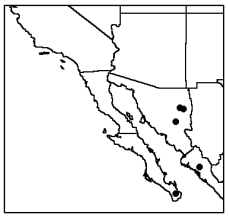
Substrate and ecology: usually on trees in open habitats, rarely on rocks; **World distribution:** Mexico, eastern USA, southern Africa and Ireland; **Sonoran distribution:** Sierra Madre Occidental region of Chihuahua.

Parmotrema praesorediosum (Nyl.) Hale, Phytologia 28: 338 (1974).

Basionym: *Parmelia praesorediosa* Nyl., Sert. Lich. Trop. Labuan Singapore 18 (1891); Synonyms: see Hale (1965) under *Parmelia praesorediosa*; Illustrations: Hale (1979), p. 64; Elix (1994k), p. 193; Brodo et al. (2001), p. 499.

Thallus: foliose, adnate, 3-10 cm in diam., lobate; **lobes:** subirregular, elongate, slightly imbricate, plane, separate, 4-10 mm wide; apices: rotund, often suberect, eciliate; **upper surface:** gray, smooth, dull, emaculate to faintly white maculate, becoming cracked with age; **soredia:** granular, common, in linear to crescent-shaped, marginal or submarginal soralia; isidia and pustulae: absent; **medulla:** white with continuous algal layer; **lower surface:** black with brown to mottled ivory naked zone peripherally, centrally rhizinate; rhizines: scattered, simple; **Apothecia:** rare, substipitate, up to 10 mm in diam.; margin: sorediate; disc: brown, imperforate; **ascospores:** ellipsoid, 15-21 x 7-10 µm; **Pycnidia:** rare, punctiform; **conidia:** sublageniform, 7-8 x 1 µm; **Spot tests:** upper cortex K+ yellow, C-, KC-, P-; medulla K-, C-, KC-, P-; **Secondary metabolites:** upper cortex with atranorin and chloroatranorin; medulla with protopraesorediosic and praesorediosic acids (major), unknown fatty acids (minor).

Substrate and ecology: on rocks and trees in open habitats; **World distribution:** pantropical and pantemperate; **Sonoran distribution:** thorn forests of Sonora, Sinaloa and southern Baja California Sur.



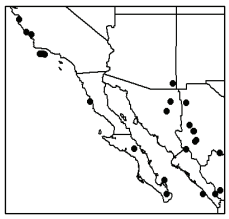
Note: Originally the species was reported to have caperatic acid (Hale 1965), but subsequent investigation has shown the fatty acids to be unique (Elix 1994k).

Parmotrema stuppeum (Taylor) Hale, Phytologia 28: 339 (1974).

Basionym: *Parmelia stuppea* Taylor, Lond. J. Bot. 6: 175 (1847); Synonyms: *Parmelia maxima* Hue and see Hale (1965) under *Parmelia stuppea*; Illustrations: Brodo et al. (2001), p. 500; Hale (1965), plate 9 as *Parmelia stuppea*; Hale (1979), p. 62.

Thallus: foliose, adnate to loosely adnate, 2-20 cm in diam., lobate; **lobes:** subirregular, elongate, slightly imbricate, plane, separate, 4-8 mm wide; apices: rotund, ciliate; cilia: up to 2.0 mm long; **upper surface:** gray, smooth, dull, emaculate; **soredia:** granular, common, in linear to orbicular, laminal or marginal soralia; isidia and pustulae: absent; **medulla:** white with continuous algal layer; **lower surface:** black with brown, naked zone peripherally, centrally rhizinate; rhizines: scattered, simple, black; **Apothecia:** rare, substipitate, up to 30 mm in diam.; margin: crenulate; disc: brown, imperforate; **ascospores:** ellipsoid, 12-17 x 6-9 µm; **Pycnidia:** common, punctiform; **conidia:** sublageniform, 4-6 x 1 µm; **Spot tests:** upper cortex K+ yellow, C-, KC-, P-; medulla K+ yellow turning deep red, C-, KC-, P+ orange; **Secondary metabolites:** upper cortex with atranorin and chloroatranorin; medulla with salazinic acid (major) and consalazinic acids (minor).

Substrate and ecology: usually on trees in open habitats, rarely on rocks; **World distribution:** pantropical and pantemperate; **Sonoran distribution:** SE Arizona, southern California, Sierra Madre Occidental region of Chihuahua, Sonora and Sinaloa Baja Califoria and southern mountains of Baja California Sur.



Parmotrema tinctorum (Nyl.) Hale, Phytologia 28: 339 (1974).

Basionym: *Parmelia tinctoria* Nyl., Flora 55: 547 (1872); Synonyms: see Hale (1965) under *Parmelia tinctoria*; Illustrations: Hale (1979), p. 66; Swinscow and Krog (1988), p. 194; Brodo et al. (2001), p. 502.

Thallus: foliose, loosely adnate, 3-30 cm in diam., lobate; **lobes:** subirregular, elongate, slightly imbricate, plane, separate, 10-20 mm wide; apices: rotund, becoming crenate and dissected with age, ciliate; cilia: up to 2.0 mm long; **upper surface:** gray, smooth, dull centrally, shiny marginally, emaculate, finely reticulately cracked with age; **isidia:** simple to coralloid branched, frequently very dense, sometimes apically ciliate, common, laminal to marginal; soredia and pustulae: absent; **medulla:** white with continuous algal layer; **lower surface:** black with brown naked zone peripherally, centrally rhizinate; rhizines: simple; **Apothecia:** rare, substipitate, up to 8 mm in diam.; margin: sparsely isidiate; disc: brown, usually imperforate; **ascospores:** ellipsoid to broadly ellipsoid, 13-16 x 7-10 µm; **Pycnidia:** rare, punctiform; **conidia:** filiform, 12-16 x 1 µm; **Spot tests:** upper cortex K+ yellow, C-, KC-, P-; medulla K-, C+ red, KC+ red, P-; **Secondary metabolites:** upper cortex with atranorin and chloroatranorin; medulla with lecanoric acid (major), orsellinic acid (trace).

Substrate and ecology: usually on trees in open habitats, rarely on rocks; **World distribution:** pantropical and adjacent temperate regions; **Sonoran distribution:** coastal plain to mountains of southern Baja California Sur and Sinaloa.

Parmotrema xanthinum (Müll. Arg.) Hale, Phytologia 28: 339 (1974).

Basionym: *Parmelia proboscidea* var. *xanthina* Müll. Arg., Flora 67: 616 (1884); Synonym: *Parmelia xanthina* (Müll. Arg.) Vain., *Parmelia madagascariacea* (Hue) des Abb. and *Parmotrema madagascariaceum* (Hue) Hale and see Hale (1965) under *Parmelia xanthina*; Illustration: Brodo et al. (2001), p. 503.

Thallus: foliose, loosely adnate, 3-20 cm in diam., lobate; **lobes:** subirregular, elongate, slightly imbricate, plane, separate, 8-12 mm wide; apices: rotund, becoming crenate and dissected with age, ciliate; cilia: up to 2.5 mm long; **upper surface:** yellow green, smooth, dull, epruinose, emaculate, finely reticulately cracked with age; **isidia:** simple to coralloid branched, often apically ciliate, common, initially laminal but becoming submarginal to marginal with age; soredia and pustulae: absent; **medulla:** pale orange yellow with continuous algal layer; **lower surface:** black with brown naked zone peripherally, centrally rhizinate; rhizines: simple; **Apothecia:** not seen; **Pycnidia:** not seen; **Spot tests:** upper cortex K+ yellow, C-, KC-, P-; medulla K-, C-, KC+ red or KC-, P-; **Secondary metabolites:** upper cortex with usnic acid (major) atranorin (trace); medulla with protolichesterinic acid (major).

Substrate and ecology: trees or rocks in open habitats; **World distribution:** pantropical and southern Africa; **Sonoran distribution:** oak and pine forests of the Sierra Madre Occidental in Sinaloa.

Parmotrema xanthopustulatum, Elix & T. H. Nash, **sp. nov.**

Diagnosis: *Thallus ut in Parmotrema enteroxanthum sed lobis elobulatis et acidum salazinicum noncontinente differt.*

Type: Mexico: Chihuahua, Parque Nacional Cumbres de Majalca, 50 km NW of Chihuahua City, 28º48'N, 106º 28'W, *c.* 1900 m, on acidic rock in pinyon pine-juniper-oak woodland, 20 May 1992, T. H. Nash 31211 (holotype in ASU; isotypes in ANUC, MEXU and US).

Further specimens examined: MEXICO: Chihuahua, along E bank of Río Sirupa, adjacent a secondary dirt road, *c.* 32 km W of Ciudad Madera, 29º11'N, 108º19'25"W, *c.* 1340 m, on acidic rock in in pasture with scattered oaks, 20 July 1994, T. H. Nash 36608 (ASU); Durango, Sierra Madre Occidental, 47 km W of Durango, E-facing hillside above creek, 23º56'N, 104º57'30"W, *c.* 2215 m, on rhyolite, 26 May 1992, T. H. Nash 31,100 (ASU).

Thallus: foliose, moderately to loosely adnate, ± circular, 4-10 cm diam., fragile and easily breaking apart, irregularly lobate; **lobes:** irregular, 3-10 mm wide, sinuous in the axils, continguous to slightly imbricate; apices: rotund; margin: entire, eciliate; **upper surface:** pale yellowish greenish or bluish gray (whitish gray in herbarium) with pale yellow patches where the cortex has disintegrated, dull to shiny in younger portions, smooth but becoming strongly rugulose submarginally, in part white pruinose; **soredia:** granular, arising from coarse dactyls which break open apically forming pustules; isidia: absent; **medulla:** pale yellow to yellow-orange with a ± continuous algal layer; **lower surface:** black, smooth to rugulose, moderately to sparsely rhizinate; rhizines: simple to sparsely furcated, with a narrow, brown, erhizinate marginal zone; **Apothecia:** not seen; **Pycnidia:** not seen; **Spot tests:** cortex: K+ yellow, C-, KC-, P-; medulla: K-, C-, KC-, P- or pigmented area turning darker yellow in K; **Secondary metabolites:** cortex with atranorin (major), chloroatranorin (minor); usnic acid (minor/trace), medulla with secalonic acid A (minor), secalonic acid B (minor), secalonic acid C (minor), butlerin F (minor), unknown secalonic acid derivatives (minor).

Substrate and ecology: on acidic rocks (including rhyolite) in moist to somewhat open oak-conifer forests; **World** and **Sonoran distribution:** along the Sierra Madre Occidental from SW Chihuahua to SW Durango adjacent Sinaloa.

Notes: *Parmotrema xanthopustulatum* closely resembles the Venezuelan species, *Parmotrema enteroxanthum* Hale, as both have a yellow medulla and develop similar pustules or open dactyls with an intense yellow or yellow-orange interior. However, *P. enteroxanthum* differs in developing lobulate-dissected margins, in being sparingly ciliate and in containing medullary salazinic acid whereas *P. xanthopustulatum* has entire margins, lacks lobules, cilia and salazinic acid. *Parmotrema xanthopustulatum* could also be confused with *Parmotrema flavomedullosum* Hale, as the latter species has a much more robust, coriaceous thallus, coarse, irregular, submarginal soralia rather than open dactyls and contains medullary gyrophoric acid.

PAULIA

by M. Schultz and M. Tretiach

Paulia Fée, Linnaea 10: 471 (1836).

Family: Lichinaceae; Type: *Paulia perforata* (Pers.) Asahina; No. species: *c.* 12 world-wide; Selected lit.: Henssen (1986b), Schultz et al. (1999), and Tretiach and Henssen (1996).

Life habit: lichenized; **Thallus:** umbilicate-rosette shaped, squamulose, subfruticose, fruticose, gelatinous when wet; **surface:** black, rarely grayish pruinose, smooth, uneven, sometimes tessellate; **anatomy:** ecorticate, homoiomerous, composed of a loose hyphal network surrounding large photobiont cells; **photobionts:** primary one a chroococcoid cyanobacterium, secondary photobiont absent; **Ascomata:** apothecial, laminal on thallus or terminal, orbicular, immersed to semi-immersed; margin: thalloid, indistinct to distinct; **ontogeny:** hemiangiocarpous, ascogonia arising in a tangle of generative hyphae beneath the thallus surface; **anatomy:** exciple: absent; epithecium: hyaline or brownish yellow; hypothecium: hyaline; **asci:** prototunicate, wall thin, nonamyloid, 8-spored; **ascospores:** simple, ellipsoid, broadly ellipsoid to globose; 9.5-21.5 x 6-14 µm; walls: thick with age, hyaline; **Conidiomata:** pycnidial, laminal, immersed; **conidia:** ellipsoid or bacilliform, *c.* 3-5 x 1 µm; **Secondary metabolites:** none detected; **Geography:** world-wide in arid, semi-arid to semi-humid regions, rarely in warm temperate regions; **Substrate:** mainly limestone, but also siliceous rock.

Notes: Species of *Phylliscum*, *Phyllisciella* and *Anema* are similar in anatomy and external appearance, but their

ascomata arise beneath pycnidia and they have a thin exciple. In *Phyllisciella* the conidia are filiform. Species of the *Phylliscum demangeonii* group lack paraphyses and have tapered ascus tips. In *Anema* the apothecia have a prominent thalline margin.

Key to the species of ***Paulia*** from the Sonoran region:

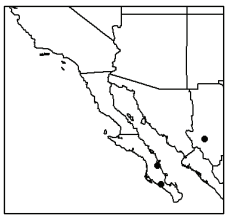
1. Thallus forming small, flat, umbilicate rosette-shaped squamules, up to 4.5 mm wide, surface regularly tessellate with angular "areoles"; margin effigurate .... ***P. myriocarpa***
1. Thallus larger, fruticose, up to 10 mm high and 20 mm wide, caespitosely branched, lobules terete, apically densely aggregated and then the surface may appear irregularly tessellate; margin never effigurate .... ***P. caespitosa***

The Species

Paulia caespitosa Tretiach & Henssen, Mycotaxon 57: 360 (1996).

Illustrations: Schultz et al. (2000b), p. 30; Tretiach and Henssen (1996), p. 363.

Thallus: fruticose, stalked, caespitose, roundish to irregular in outline, *c.* 5-20 mm in diam., lobules terete, richly branched; **surface:** black; **attachment:** by thick compact rhizoidal strand that forms a stalk; **Apothecia:** rare, immersed to semi-immersed, lecanorine, small, up to 0.2 mm wide; disc: immersed, flat, reddish brown, with thick smooth persisiting thalline margin; exciple**:** lacking; hymenium: 150-200 µm high, hyaline, non-amyloid; paraphyses: distinctly septate, branched and anastomosing, apical cells indistinctly thickened; **asci:** 8-spored; **ascospores:** simple, hyaline, globose to broadly ellipsoid, (9-) 12.5-15 x 7.5-10 (-12.5) µm; old ascospore walls: 2.5 (-5) µm thick; **Pycnidia:** immersed, simple, pyriform, up to 0.15 mm high and 0.075 mm wide; **conidia:** cylindrical, hyaline, 3-5 x 1 µm; **Spot tests:** all negative; **Secondary metabolites:** none detected.



Substrate and ecology: on limestone or calcareous volcanic rock, often on steep rock faces; coastal to montane; **World distribution:** SW North America, Australia; **Sonoran distribution:** SW Chihuahua and Baja California Sur.

Notes: This species is very distinct because of its caespitose branching pattern. In juvenile thalli terete lobules do not develop and the thallus surface appears ± tessellate. Such small, juvenile thalli resemble *Paulia myriocarpa*, but that species always has a distinctly effigurate margin while *Phloeopeccania* that has small, roundish to angular fungal cells.

Paulia myriocarpa (Zahlbr.) Henssen, Lichenologist 22: 142 (1990).

Basionym: *Thyrea myriocarpa* Zahlbr., Annls. Mycol. 19: 233 (1921); Synonym: *Paulia tessellata* Henssen; Illustrations: Henssen (1986b), pp. 206 & 208; and Fig. 69 below.

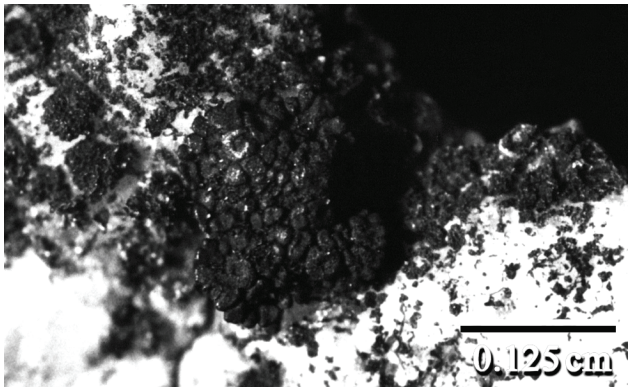


Fig. 69. *Paulia myriocarpa*, photo by M. Schultz.

Thallus: umbilicate, rosette-shaped, squamules roundish in outline, up to 4.5 mm wide; **"areoles":** 0.06-0.25 mm wide, margin effigurate, marginal lobules 0.1-0.4 mm long; **surface:** black, regularly tessellate, **Apothecia:** immersed to semi-immersed, lecanorine, 1-3 per squamules, small, up to 0.2 mm; disc: blackish, flat, with persisting thalline margin; exciple: lacking; epihymenium: yellow-

ish brown; hymenium: 80-160 µm high, hyaline, iodine reaction variable; paraphyses: distinctly septate, sparingly to richly branched and anastomosing, apical cells slightly enlarged, up to 3.5 µm wide; **asci:** 8-spored; **ascospores:** simple, hyaline, broadly ellipsoid, 11-15 x 7.5-9 µm wide; old spores: with thick (-3 µm) wall; **Pycnidia:** immersed, broadly pyriform, *c.* 0.1 mm wide; **conidia:** cylindrical, hyaline, *c.* 3.5 x 1 µm; **Spot tests:** all negative; **Secondary metabolites:** none detected.

Substrate and ecology: on volcanic, calcareous or siliceous rocks, mainly on vertical or inclined, sheltered rock faces or along seepage tracks; mainly coastal or island habitats, rarely inland; **World distribution:** SW North America, the neotropics and Socotra Island (Indian Ocean); **Sonoran distribution:** southern Baja California Sur.

Notes: This is a small but very distinct species because of its regularly tessellate thallus surface with its effigurate margin.

PELTULA

by B. Büdel and T. H. Nash III

Peltula Nyl., Ann. Sci. Nat. Bot. 20: 316 (1853) and Mém. Soc. Sci. Nat. Cherbourg 2: 322 (1853).

Family: Peltulaceae; Type: *Peltula radicata* Nyl.; No. species: *c.* 40 world-wide; Selected lit.: Wetmore (1970), Büdel (1987), and Egea (1989).

Life habit: lichenized; **Thallus:** peltate, crustose, squamulose, or suffruticose (rarely cylindrical); margins: entire, minutely lobate to sometimes effigurate; **upper surface:** olive green to olive brown, rarely black; with or without soredia; **upper cortex:** usually absent but with an epinecral layer; **medulla:** white, with numerous airspaces, composed of globose or elongated hyphae; **photobionts:** primary one an unicellular cyanobacterium (*Chroococcidiopsis* or *Myxosarcina*), secondary photobiont absent; **lower cortex:** normally well developed, pseudoparenchymatous; **lower surface:** usually paler than the upper surface, attached by an umbilicus, rhizohyphal weft or rhizines; **Ascomata:** apothecial, lecanorine, completely immersed or with a raised rim; disc: punctiform or widely opened; hymenium: 90-300 µm high; paraphyses: sometimes anastomosing, rarely branched, 1-3.5 µm thick; subhymenium: 16-70 µm; **asci:** clavate to obclavate, unitunicate-rostrate (lecanoralean type), 60-170 x 10-30 µm; walls: red or blue in iodine (blue after K pretreatment); 16->100-spored; **ascospores:** simple, hyaline, globose to ellipsoid, 3-12 x 2-6 µm; **Conidiomata:** pycnidial, solitary to cerebriform, immersed; **conidia:** oval to fusiform, hyaline, 1.5-4.3 x 0.5-2.5 µm; **Secondary metabolites:** none detected in North American material; **Geography:** predominately in arid and semi-arid regions of the world, but occurring wherever arid microclimates are found; **Substrate:** acidic or calcareous rocks or soil.

Key to the species of ***Peltula*** from the Sonoran region:

1. Thallus sorediate 2
1. Thallus not sorediate 5

2. Thallus peltate 3
2. Thallus areolate centrally, effigurate marginally ..... ***P. placodizans***

3. Thallus up to 2 mm diam.; margin strongly undulate .... ***P. bolanderi***
3. Thallus larger, up to 22 mm diam.; margin not strongly undulate 4

4. Upper surface smooth, olive to olive-brown, epruinose; thalli up to 12 mm in diam. ..... ***P. euploca***
4. Upper surface rough, grayish, pruinose; thalli up to 22 mm in diam. ..... ***P. farinosa***

5. Thallus with effigurate squamules marginally 6
5. Thallus without effigurate squamules marginally 7

6. Apothecial disc usually punctiform; spores 4.5-8 x 3-4.5 µm ..... ***P. placodizans***

6. Apothecial disc usually expanded; spores 3.5-4.8 (-7) x 2.4-3.5 (-4) µm ..... ***P. impressa***

7. Thallus peltate 8
7. Thallus squamulose, subfoliose or suffruticose 10

8. Thallus up to 2.5 mm diam., blackish-brown, almost hemispherical ..... ***P. omphaliza***
8. Thallus larger, bright olive or olive-brown colored, much wider than thick 9

9. Thalli usually < 4 mm wide; usually sterile (typical sorediate thalli often found nearby) .... ***P. euploca*** (young thalli)
9. Many thalli > 4 mm wide; usually with several punctiform to slightly expanded apothecia ..... ***P. sonorensis***

10. Lobes with a clearly visible rim along the margin, giving the lobes an ear-shaped appearance .... ***P. auriculata***
10. Lobes without a rim along the margin, not ear-shaped 11

11. Thallus suffruticose; lobes upright 12
11. Thallus squamulose; lobes (if present) horizontal ... 13

12. Upper surface olive black to black; lobes club-shaped, 0.5-1.5 mm long, usually not branched (if branched then usually at the base); medulla often hollow ..... ***P. clavata***
12. Upper surface olive-brown to olive-green; lobes flattened, up to 8 mm (rarely -15 mm) long, richly branched lobes; medulla not hollow ..... ***P. tortuosa***

13. Growing on rock 14
13. Growing on soil (only very rarely on soil over rock or on soil in rock crevices) 17

14. Squamules inflated at the top; apothecia remaining punctiform, 1-8 per squamule .... ***P. zahlbruckneri***
14. Squamules not swollen or inflated; apothecia becoming expanded, 1 (rarely 2) per squamule 15

15. Epihymenium K+ red .... ***P. obscurans*** var. ***obscurans***
15. Epihymenium K- 16

16. Sqaumules usually lobate; often on acidic rocks .... ***P. obscurans*** var. ***hassei***
16. Squamules usually not lobate; often on limestone (or caliche) ..... ***P. obscurans*** var. ***deserticola***

17. Squamules always less than 2 mm wide, solitary or forming small patches (1-2 cm wide) 18
17. Squamules usually more than 2 mm wide, usually forming large patches (several cm wide) 20

18. Epihymenium K+ red ***P. obscurans*** var. ***obscurans***
18. Epihymenium K- 19

19. Squamules deeply concave ..... ***P. michoacanensis***
19. Squamules plane ..... ***P. obscurans*** var. ***hassei***

20. Squamule margin with a prominent raised rim .... ***P. patellata***
20. Squamule margin not raised 21

21. Squamules up to 6 (-10) mm wide; apothecial discs up to 3 (-5) mm wide; epithecium K+ red violet .... ***P. richardsii***
21. Squamules up to 4 mm wide; apothecial discs up to 1 mm wide; epithecium: usually K- .... ***P. psammophila***

The Species

Peltula auriculata Büdel, M. Schultz & Gröger, Plant Biology 2: 484 (2000).

Illustrations: Schultz et al. (2000a), fig. 1(a-i).

Thallus: squamulose to subfoliose, sometimes peltate, lobate; **lobes:** with a clearly visible rim along the margins giving it an ear-like shape, 0.75-1.5 mm wide and up to 2.5 mm long; **upper surface:** olive brown, sometimes grayish, not sorediate; **upper cortex:** in some parts poorly developed (0-5 µm thick), composed of globose hyphal cells (2.5-5 µm in diam.); epinecral layer: sometimes developed (up to 5 µm thick); **medulla:** 50-75 (-250) µm thick, composed of loosely interwoven with numerous air spaces, sometimes prosoplectenchymatous hyphae (2.5 µm thick); **lower cortex:** well developed, 50-60 (-75) µm thick, paraplectenchymatous with globose hyphal cells (7.5-10 µm diam.); **lower surface:** paler than the upper surface, attached by an umbilicus; **Apothecia:** rare, laminal, adnate, lecanorine, up to 3 per squamule; disc: red, up to 0.5 mm in diam.; epihymenium: reddish brown, K-; hymenium: I+ blue but turning wine-red and constantly blue after pretreatment with K; **asci:** clavate, I+ blue but turning wine-red and constantly blue after pretreatment

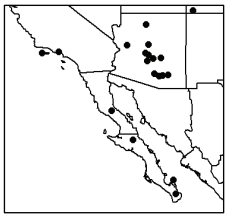
with K, >100-spored; **ascospores:** globose, 3-4 (-5) x 3-4 µm; **Pycnidia:** immersed, flask-shaped with a single chamber, conidiophores simple; **conidia:** ellipsoid, 2.5 x 1 µm; **Spot tests:** all negative; **Secondary metabolites:** none detected.

Substrate and ecology: so far only known from acidic rocks in deserts and other open, arid habitats; **World distribution:** Venezuela, Guyana and Mexico; **Sonoran distribution:** Baja California Sur.

Peltula bolanderi (Tuck.) Wetmore, Ann. Mo. Bot. Gard. 57: 168 (1971).

Basionym: *Pannaria bolanderi* Tuck., Gen. Lich. 51, footnote (1872); Synonyms: *Endocarpiscum bolanderi* (Tuck.) Tuck., *Heppia bolanderi* (Tuck.) Vain., *Pannariella bolanderi* (Tuck.) Gyeln.; Illustrations: Wetmore (1970), p. 180; Büdel (1987), figs. 84-88.

Thallus: peltate, scattered or in irregular patches, individual thalli up to 2 mm diam.; margin: often strongly undulated; **upper surface:** dark olive green to olive brown; **soredia:** farinose, black, marginal, in linear to orbicular soralia; **upper cortex:** lacking but with a yellow to brownish epinecral layer (up to 10 µm thick); **medulla:** with a poorly delimited algal layer in the upper third, composed of loosely interwoven hyphae with elongated (2.5 µm wide) or globose (7 µm in diam.) cells; **lower cortex:** 20-75 µm thick, pseudoparenchymatous, with globose hyphal cells (7-8 µm in diam.); **lower surface:** paler than the upper surface, attached by an umbilicus; **Apothecia:** rare, one to several, adnate, with a raised rim when mature; epihymenium: light yellow, K-; hymenium: I+ wine-red, 150-170 µm high; **asci:** clavate to obclavate; ascal wall: I+ orange but blue after pretreatment with K, >100-spored; **ascospores:** globose to ellipsoid, 5-7.6 x 3-4.5 µm; **Pycnidia:** spherical, up to 150 µm diam.; **Conidia:** fusiform, 3.1-3.7 x 1.2 µm; **Spot tests:** all negative; **Secondary metabolites:** none detected.



Substrate and ecology: usually on acidic rocks but occasionally on calcareous ones in deserts and other open, arid habitats; **World distribution:** SW North America, Australasia and southern Africa; **Sonoran distribution:** desert areas of Arizona, southern California, Sonora, Baja California and Baja California Sur.

Peltula clavata (Kremp.) Wetmore, Ann. Mo. Bot. Gard. 57: 181 (1971).

Basionym: *Heterina clavata* Kremp., Flora 59: 56 (1876); Synonym: *Heppia clavata*; Illustrations: Büdel (1987), figs. 106-111; Büdel and Elix (1997), figs. 7-8.

Thallus: suffruticose, in patches up to 3 cm in diam.; **squamules:** up to 1.5 mm long, club-shaped; **upper surface:** dark olive-black to black; **isidia:** sometimes present, minute, laminal; not sorediate; **upper cortex:** lacking but with a yellow to brownish epinecral layer (3-6 µm thick); **medulla:** almost completely hollow; hyphae: peripheral, 1.5-2 µm thick, elongated, loosely interwoven; algal layer: delimited to the 30-50 µm thick outer part; **lower cortex:** not developed; **Apothecia:** (only known from Australian material) 1-3, immersed; disc: punctiform, up to 0.2 mm in diam.; **asci:** clavate, I+ wine-red but blue after pretreatment with K, >64-spored; **ascospores:** globose, 3.5-4.7 µm diam.; **Pycnidia:** no data available; **conidia:** fusiform, 3.7-4.3 x 1.2-1.8 µm; **Spot tests:** all negative; **Secondary metabolites:** none detected.

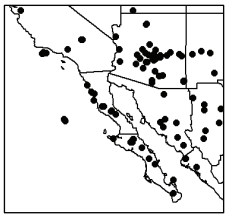
Substrate and ecology: on acidic rocks in arid woodlands; **World distribution:** SW North America, NE Brazil, southern Africa and northern Australia; **Sonoran distribution:** desert transition areas of SE Arizona.

Peltula euploca (Ach.) Poelt, Acta Rer. Nat. Mus. Slov. 13: 8 (1967).

Basonym: *Lichen euplocus* Ach., Lich. Suec. Prod. Lin. 141 (1798); Synonym: *Heppia euploca*; Illustrations: Wetmore (1970), p. 183; Büdel (1987), figs. 125-148; Brodo et al. (2001), p. 524; Swinscow and Krog (1988), p. 206.

Thallus: peltate, scattered individually, sometimes lobed (rarely polyphyllous), up to 12 mm in diam.; margins: downrolled, not undulate; **upper surface:** tan-olive-green to dark olive-brown, dull to shiny; **soredia:** farinose, black, marginal (rarely laminal), in elongated soralia; **upper cortex:** lacking but with a yellow to brownish epinecral layer (5-10 µm thick); **medulla:** composed of loosely interwoven hyphae (cells: elongated, 1.5-3 µm thick); algal layer: clearly delimited, 70-150 µm thick; **lower cortex:** 18-90 µm thick, proso- to paraplectenchymatous, hyphae often anticlinally arranged; cells: globose to elongated, 3-8 µm thick; **lower surface:** paler than the upper surface, attached by an umbilicus; **Apothecia:** rare, many per squamule, immersed; disc: punctiform to widely expanded, 0.1-0.9 mm diam.; epihymenium: yellowish brown or pinkish, K-; hymenium: I+ wine-red, 105-220 µm high; **asci:** clavate to obclavate; wall: I+ slightly blue and more strongly blue after pretreatment with K, 32-100-spored; **ascospores:** ellipsoid to bacilliform, 6-9 x 3-4.8 µm; **Pycnidia:** immersed, chambered, up to 150 µm diam.; **conidia:** fusiform, 3-3.5 x 1-1.5 µm; **Spot tests:** all negative; **Secondary metabolites:** none detected.

Substrate and ecology: on acidic rocks in deserts and other open, arid habitats; **World distribution:** throughout arid and semi-arid regions on all continents and extending into temperate regions of North America, Eurasia and Australasia; **Sonoran distribution:** desert to mountain areas of Arizona, southern California, Sonora, Sinaloa, Chihuahua Baja California and Baja California Sur.

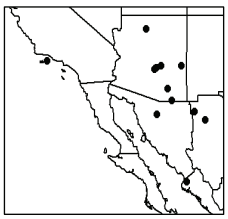


Peltula farinosa Büdel, Crypt. Bot. 4: 263 (1994).

Illustrations: Büdel and Lange (1994), pp. 264-266.

Thallus: peltate, scattered, individual thalli up to 22 mm in diam., often lobate; margin: undulate; **upper surface:** gray, pruinose, spot-like; **soredia:** farinose, black, marginal, rarely occurring; **upper cortex:** with numerous air spaces, 4.5-13 µm thick and with an epinecral layer (7-18 µm thick); **medulla:** composed of loosely interwoven hyphae with elongated cells (2-3.6 µm thick); algal layer: clearly delimited above, 55-100 µm thick; **lower cortex:** paraplectenchymatous, 24-37 µm thick, composed of 3 (rarely 4) rows of hexagonal cells (4.5-7.5 µm in diam.), in 4-5 rows; **lower surface:** pale orange-brown, attached by an umbilicus; **Apothecia:** rare (only one found in material from Sinaloa), one to presumably several, immersed with an orange colored; disc: slightly protruding when mature; **asci:** obclavate, I- (but the material was to scanty to be sure!); **ascospores:** numerous (>64) in asci, ellipsoid to bacilliform, 4.4-8 x 2.9-4.4 µm; **Pycnidia:** not observed; **Spot tests:** all negative; **Secondary metabolites:** none detected.

Substrate and ecology: on acidic rocks and drainage areas where calcium may accumulate in secondary deposits; **World distribution:** South Africa, Pakistan, SW North America; **Sonoran distribution:** desert and other semiarid areas of Arizona, California, Sonora, Chihuahua and Sinaloa.



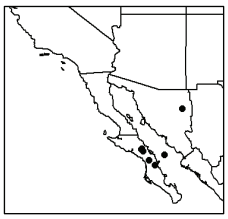
Peltula impressa (Vain.) Swinscow & Krog, Norw. J. Bot. 26: 219 (1979).

Basionym: *Heppia impressa* Vain., Beibl. Hedwigia 37: 43 (1898); Illustrations: Büdel (1987), figs. 150-155.

Thallus: squamulose, ± placodioid, overall *c.* 1-2 cm diam.; **central squamules:** obconical to clavate or cylindrical, convex or flattened at top, 0.2-0.5 mm wide 0.4-0.8 mm long; **marginal squamules:** effigurate, sometimes almost ribbon-like; **upper surface:** olive brown, smooth, not sorediate; **upper cortex:** not developed but with a yellow epinecral layer (6-12 µm thick); **medulla:** composed of densely interwoven hyphae with globose to elongated cells (2.5-3 µm thick), with an poorly delimited algal layer in the upper part; **lower cortex:** 15-24 µm thick, paraplectenchymatous with globose hyphal cells, 5-8 µm diam.; **lower surface:** paler than the upper surface, **Apothecia:** 1-2 (-3) per squamule, only occurring on central squamules, immersed; disc: red-brown to black, usually expanded (0.1-0.3 mm in diam.); epihymenium: red-

brown to black; hymenium: I+ wine-red or weakly blue, 170-250 µm high; **asci:** clavate to obclavate; wall: I+ red-brown but blue after pretreatment with K, >64-spored; **ascospores:** globose to ellipsoid, 3.5-5 (-7) x 2.4-3.5 (-4) µm; **Pycnidia:** only one immature seen, spherical; **conidia:** not known; **Spot tests:** all negative; **Secondary metabolites:** none detected.

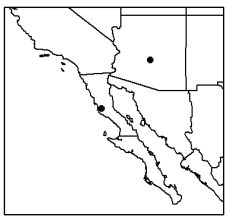
Substrate and ecology: mainly on acidic rocks in deserts and other open, arid habitats; **World distribution:** SW North America, Australasia, southern and East Africa; **Sonoran distribution:** desert areas of Sonora and Baja California Sur.



Peltula michoacanensis (de Lesd.) Wetmore, Ann. Mo. Bot. Gard. 57: 187 (1971).

Basionym: *Heppia michoacanensis* de Lesd., Lich. Mexique 10 (1914); Illustration: Wetmore (1970), p. 188.

Thallus: squamulose, widely scattered; **squamules:** concave and cone shaped, 1-2 mm in diam., shallowly or deeply lobed; margins: ascending; **upper surface:** tan-olive, not sorediate; **upper cortex:** not developed but with a yellowish epinecral layer (up to 12 µm thick); **medulla:** composed of loosely to densely interwoven hyphae of elongated cells; algal layer: indistinctly delimited above; **lower cortex:** 25-50 µm thick, 3-5 layers of globose hyphal cells; **lower surface:** paler than the upper surface, attached by a central branched umbilicus; **Apothecia:** one per squamule, immersed in the center of concave squamules; disc: light brown, according to Wetmore (1970), 0.5-1 mm in diam.; epihymenium: light brown, K-; hymenium: I+ wine-red (probably due to the reaction of ascus walls), 150-220 µm high, >100-spored; **ascospores:** ellipsoid to bacilliform, 6.1-7.7 x 3.4-4.6 µm; **Pycnidia:** immersed, chambered; **conidia:** fusiform, 3.1-3.7 x 1.2-1.8 µm; **Spot tests:** all negative; **Secondary metabolites:** none detected.

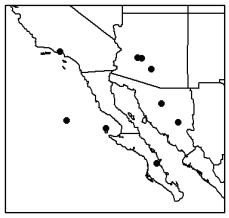


Substrate and ecology: on soil over acidic or calcareous rocks in deserts and other open, arid habitats; **World distribution:** SW North America to central Mexico and India; **Sonoran distribution:** desert areas of southern California.

Peltula obscurans (Nyl.) Gyeln., Rep. Spec. Nov. Regn. Veg. 38: 308 (1935).

Basionym: *Endocarpiscum obscurans* Nyl., Bull. Soc. Linn. Normand. 2: 309 (1872); Synonym: *Heppia obscurans* (Nyl.) Nyl. and see Wetmore (1970).

Substrate and ecology: usually on acidic rocks, occasionally calcareous one and soil in deserts and other open, arid habitats; **World distribution:** southern Europe, South America, SW North America, Africa, Asia, Australia and Papua New Guinea; **Sonoran distribution:** Arizona, California, Baja California, Baja California Sur, and Sonora.



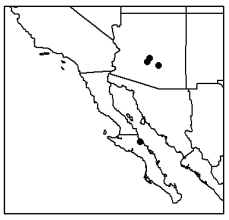
Peltula obscurans var. **obscurans**

Basionym: *Endocarpiscum obscurans* Nyl., Bull. Soc. Linn. Normand. 2: 309 (1872); Synonym: *Heppia obscurans* (Nyl.) Nyl. and see Wetmore (1970).

Thallus: squamulose, often widely scatted but in aggregate sometimes rosette-shaped; **squamules:** lightly or deeply lobed, flat to convex, up to 2 mm diam.; **upper surface:** olive-brown to brown, not sorediate; **upper cortex:** not developed but with a yellowish epinecral layer (11-13 µm thick); **medulla:** consisting of loosely interwoven hyphae and partly paraplectenchymatous; algal layer: 90-180 µm thick; **lower cortex:** usually present but not distinguishable from medulla; **lower surface:** paler than the upper surface, attached by a branched umbilicus; **Apothecia:** one per squamule (extremely rarely 2-3), adnate, with a raised rim when mature; disc: red to yellow-brown, 0.5-1 mm in diam.; epihymenium: yellowish

brown, K+ red-violet; hymenium: I+ wine-red, 70-150 µm high; **asci:** clavate to obclavate; wall: I+ orange but blue after pretreatment with K, >100-spored; **ascospores:** ovoid to ellipsoid, 4.5-7.6 x 3 µm; **Pycnidia:** immersed; **conidia:** ovoid-fusiform, 3.1-3.7 x 1.2 µm; **Spot tests:** all negative; **Secondary metabolites:** none detected.

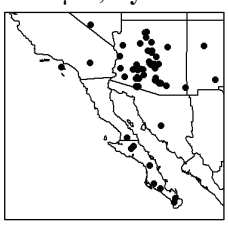
Substrate and ecology: usually on rocks, occasionally on soil in deserts and other open, arid habitats; **World distribution:** southern Europe, South America, SW North America to Mexico; **Sonoran distribution:** in desert areas of Arizona, southern California, Sonora, Baja California and Baja California Sur.



Peltula obscurans var. **deserticola** (Zahlbr.) Wetmore, Ann. Mo. Bot. Gard. 57: 190 (1971).

Basionym: *Heppia deserticola* Zahlbr., Bull. Torrey Bot. Cl. 35: 300 (1908); Illustration: Wetmore (1970), p 188.

Thallus: squamulose, usually widely scattered; **squamules:** orbicular, not lobed, flat to convex at top, 0.5-1.2 mm diam.; **upper surface:** olive-brown, not sorediate; **upper cortex:** not developed but with a yellowish epinecral layer; **medulla:** partly consisting of loosely interwoven hyphae and partly paraplectenchymatous; algal layer: 60-120 µm thick; **lower cortex:** poorly developed or not present; **lower surface:** paler than the upper surface, attached by rhizines or an umbilicus, **Apothecia:** one or two per squamule, immersed and finally filling the whole squamule, leaving the squamule margin as the rim; disc: yellowish brown, 0.3-1.2 mm diam.; epihymenium: yellowish brown, K-; hymenium: I+ wine-red, 105-140 µm high; **asci:** clavate to obclavate, >100-spored; **ascospores:** ovoid to ellipsoid, 4.6-7.7 x 3-4.6 µm; **Pycnidia:** no data; **conidia:** fusiform, 3.1-3.7 x 1.2-1.8 µm; **Spot tests:** all negative; **Secondary metabolites:** none detected.



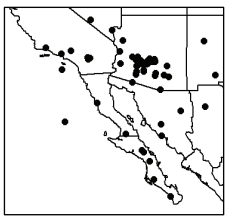
Substrate and ecology: primarily on calcareous rocks, including secondary deposits of caliche and along pebble edges in deserts and other open, arid habitats; **World distribution:** SW North America to central Mexico; **Sonoran distribution:** desert areas of Arizona, southern California, Sonora and Baja California and Baja California Sur.

Peltula obscurans var. **hassei** (Zahlbr.) Wetmore, Ann. Mo. Bot. Gard. 57: 191 (1971).

Basionym: *Heppia hassei* Zahlbr., Beih. Bot. Centrbl. 13: 157 (1902); Illustrations: Wetmore (1970), fig. 23; Büdel (1987), figs. 174-178; Brodo et al. (2001), p. 524.

Thallus: squamulose, scattered or sometimes forming rosette-shaped patches; **squamules:** shallowly or deeply lobed, flat to convex, up to 2 mm diam.; **upper surface:** olive-brown to brown, not sorediate; **upper cortex:** not developed but with a yellowish epinecral layer (11-13 µm thick); **medulla:** partly consisting of loosely interwoven hyphae and partly paraplectenchymatous (cells: elongated, 1-1.5 µm thick); algal layer: 45-100 µm thick; **lower cortex:** proso- to paraplectenchymatous, 15-26 µm thick; cells: globose, up to 6.5 µm in diam.; **lower surface:** paler than the upper surface, attached by a tuft of rhizines or a branched umbilicus; **Apothecia:** one per squamule (extremely rarely 2-3), adnate, with a raised rim when mature; disc: red to yellow-brown, 0.5-1 mm in diam.; epihymenium: yellow-brown, K-; hymenium: I+ blue, 120-150 µm high; **asci:** clavate to obclavate; wall: I+ orange but blue after pretreatment with K, >100-spored; **ascospores:** subglobose to ellipsoid, 5-8 x 2-4 µm; **Pycnidia:** no data available; **conidia:** ovoid-fusiform, 3.1-4.3 x 1.8-2.4 (-3.1) µm; **Spot tests:** all negative; **Secondary metabolites:** none detected.

Substrate and ecology: commonly on soil and acidic rocks, occasionally on calcareous rocks in deserts and other open, arid habitats; **World distribution:** SW North America, southern and West Africa, Europe, Asia, Australia; **Sonoran distribution:** desert areas of Arizona, southern California, Sonora, Sinaloa, Baja California and Baja California Sur.

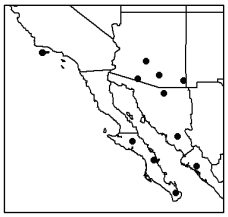


Peltula omphaliza (Nyl.) Wetmore, Ann. Mo. Bot. Gard. 57: 194 (1971).

Basionym: *Heppia omphaliza* Nyl., Bull. Torrey Bot. Cl. 16: 106 (1889), Illustrations: Wetmore (1970), fig. 24; Büdel and Mies (1993), fig. 3; Filson (1988), fig. 7.

Thallus: peltate, often widely scattered, orbicular convex, up to 2 mm diam.; margins: smooth, entire to slightly lobed, **upper surface:** dull greenish-olive, brown to black, not sorediate; **upper cortex:** not developed but with a yellowish epinecral layer; **medulla:** composed of loosely interwoven hyphae; algal layer: 90-120 µm thick; **lower cortex:** 24-36 µm thick, 3-5 layers of cells; **lower surface:** paler than the upper surface, attached by a central umbilicus; **Apothecia:** 5-20 per squamule, immersed; disc: initially punctiform, later slightly expanded, 0.1-0.2 mm diam.; epihymenium: yellow to yellowish brown, K+ red-violet or K-; hymenium: I+ wine-red or blue; **asci:** clavate to obclavate, >100-spored; **ascospores:** ellipsoid to bacilliform, 5-7 x 3 µm; **Pycnidia:** immersed, spherical; **conidia:** fusiform, 2.4-3.1 x 1.2 µm; **Spot tests:** all negative; **Secondary metabolites:** none detected.

Substrate and ecology: on both acidic and calcareous rocks in deserts and other open, arid habitats; **World distribution:** SW North America to southern Mexico, Australia, and the Cape Verde Islands; **Sonoran distribution:** rare in desert areas of Arizona, southern California, Sonora and Baja California Sur.



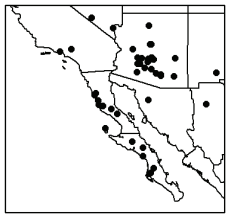
Notes: Wetmore (1970) reported specimens of *P. omphaliza* reaching a size of up to 4 mm diameter. However, we have not observed such large specimens of that species. All the material we saw, including the type material, never was larger than 2 mm in diameter. We suspect, therefore, that his circumscription of *P. omphaliza* included the more recently described *P. sonorensis*, which can reach or exceed 4 mm in size. Although young thalli of *P. sonorensis* may easily be mistaken as *P. omphaliza* based on size alone, *P. sonorensis* is always a very shiny spcecies and *P. omphaliza* is quite dull.

Peltula patellata (Bagl.) Swinscow & Krog, Norw. J. Bot. 26: 221 (1979).

Basionym: *Acarospora patellata* Bagl., Nuov. Giorn. Bot. Ital. 7: 245 (1875); Synonym: *Peltula polyspora* (Tuck.) Wetmore; *Heppia polyspora* Tuck. and see Wetmore (1970) under *Peltula polyspora*; Illustrations: Wetmore (1970), fig. 26 (as *P. polyspora*); Swinscow and Krog (1979), fig. 6 (legend mismatched with fig. 7); Filson (1988) fig. 8; Upreti and Büdel (1990), fig. 4; Brodo et al. (2001), p. 525.

Thallus: squamulose, often occurring in patches of squamules several cm wide; **squamules:** orbicular to somewhat angulate or lobulate, up to 4 mm diam.; margins: smooth, thickened and upturned; **upper surface:** pale to olivaceous brown or grayish green, dull, not sorediate; **upper cortex:** not developed but with a well developed epinecral layer, often with numerous airspaces (thus giving the thallus a grayish appearance); **medulla:** paraplectenchymatous; algal layer: 60-120 µm thick; **lower cortex:** 30-40 µm thick, of 2-8 layers of isodiametric or globose cells; **lower surface:** paler than the upper surface, attached by a tuft of hyphae; **Apothecia:** immersed, 1-20 per squamule, with a raised rim when mature; disc: yellowish to reddish brown, up to 1 mm in diam.; epihymenium: yellowish brown, K+ red-violet or rarely K-; hymenium: I+ blue-green, becoming wine-red; **asci:** obclavate; wall: I+ orange but blue after pretreatment with K, >100-spored; **ascospores:** globose to subglobose, 3-8 (-9) x 3-6 µm; **Pycnidia:** no data; **conidia:** fusiform, 3.7-4.3 x 1.2-2.8 µm; **Spot tests:** all negative; **Secondary metabolites:** none detected.

Substrate and ecology: on soil, frequently with a high calcium content in deserts and other open, arid habitats; **World distribution:** SW and north central North America to central Mexico, India, Australia, southern Europe, Africa, and the Cape Verde Islands; **Sonoran dis-**



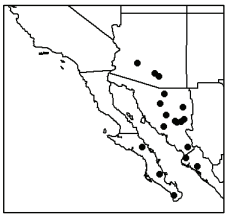
tribution: desert areas of Arizona, southern California, Sonora, Baja California, Baja California Sur, Sonora and Chihuahua.

Peltula placodizans (Zahlbr.) Wetmore, Ann. Mo. Bot. Gard. 57: 196 (1971).

Basionym: *Heppia placodizans* Zahlbr., Bull. Torrey Bot. Cl. 35: 299 (1908); Illustrations: Wetmore (1970), fig. 25; Büdel (1987), figs. 179-184; Filson (1988), Fig. 4.

Thallus: squamulose, ± placodioid, areolate in center, lobate at margins; **central squamules:** upright, cylindrical, roundish, flat or convex, 0.1-0.5 in diam., **marginal lobes:** 0.2-0.5 mm wide and up to 1.3 mm long; **upper surface:** brownish to olive-green; **soredia:** farinose, black, in capitate soralia (often on top of the central squamules; **upper cortex:** not developed but with a yellow epinecral layer (8-15 µm thick); **medulla:** composed of loosely interwoven hyphae with globose cells and numerous air spaces; algal layer: 50-90 µm thick; **lower cortex:** poorly developed, 20-40 µm thick, paraplectenchymatous with globose hyphal cells (3-8 µm in diam.); **lower surface:** paler than the upper surface, **Apothecia:** rare, normally one per squamule, restricted to central squamules, immersed with punctiform discs; disc: yellowish brown to blackish brown, up to 0.3 mm diam.; epihymenium: yellowish brown, K+ red-violet or K-; hymenium: I+ wine-red, 90-120 µm high; **asci:** clavate to obclavate; hymenium: wine red in iodine; wall: I+ orange but blue after pretreatment with K, >64-spored; **ascospores:** globose to ellipsoid, 4.5-8 x 3-4.5 µm; **Pycnidia:** immersed, simple, spherical; **conidia:** fusiform, 3.5 x 1.5 µm; **Spot tests:** all negative; **Secondary metabolites:** none detected.

Substrate and ecology: on acidic rocks, frequently in places that receive some shade in deserts and other open, arid habitats; **World distribution:** South America, SW North America, Africa, Australia and Europe; **Sonoran distribution:** desert areas and lower elevation forests of Arizona, southern California, Sonora, Sinaloa, and Baja California Sur.



Peltula psammophila (Nyl.) Egea, Bibliotheca Li chenologica 31: 101 (1989).

Basionym: *Heppia psammophila* Nyl., Flora 61: 339 (1879); Illustation: Fig. 70 below.

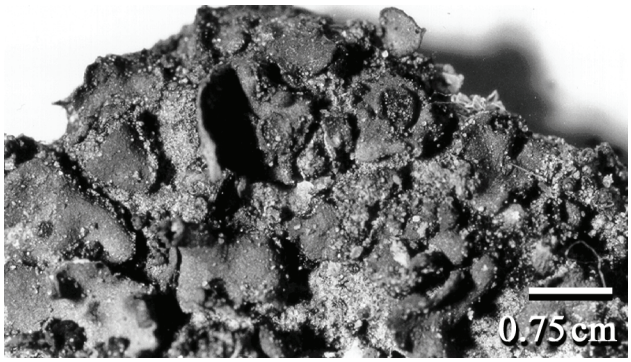


Fig. 70. *Peltula psammophila*, photo by M. Schultz.

Thallus: squamulose, often in patches of multiple squamules several cm wide; **squamules:** orbicular flat or concave on top, often angulate or lobulate, up to 4 mm diam. and 0.7 mm high; **upper surface:** olive-brown to dark brown, rugose and fissured, not sorediate; **upper cortex:** not developed but with an epinecral layer (10-30 µm thick); **medulla:** composed of loosely interwoven hyphae; algal layer: 140-200 µm thick; **lower cortex:** paraplectenchymatous, 10-50 µm thick, composed of 4-7 layers of isodiametric cells; **lower surface:** paler than the upper surface, attached by a tuft of hyphae; **Apothecia:** one or two per squamule, centrally immersed, with slightly raised rim when mature; disc: dark red to almost black, expanded, up to 1 mm in diam.; epihymenium: K- or rarely K+ red-violet, >100-spored; **ascospores:** globose, 5-8 µm diam.; **Pycnidia:** not observed; **Spot tests:** all negative; **Secondary metabolites:** none detected.

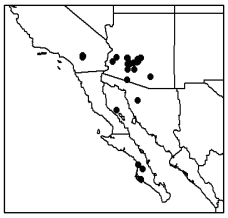
Substrate and ecology: on poor or sandy soils and on detritus in rock fissures in deserts and other open, arid habitats; **World distribution:** North Africa, SW North America; **Sonoran distribution:** so far only known from Maricopa County, Arizona.

Notes: This species was not separated from *P. polyspora* (= *P. patellata*) by Wetmore (1970), but was subsequently separated from that species by Egea (1989) on the basis of differences in thallus structure. The squamules of *P. patellata* are somewhat smaller and usually half as thin as those of *P. psammophila*. In addition, *P. psammophila* has a thicker epinecral layer and a more lax medulla than *P. patellata*. Perhaps the best separating character is the fact that the epithecium is almost always K- in *P. psammophila* and K+ red in *P. patellata*.

Peltula richardsii (Herre) Wetmore, Ann. Mo. Bot. Gard. 57: 202 (1971).

Basionym: *Heppia richardsii* Herre, Bryologist 53: 297 (1950); Illustrations: Wetmore (1970), fig. 27; Brodo et al. (2001), p. 525.

Thallus: squamulose, often in patches of multiple squamules several cm wide; **squamules:** 2-6 (-10) mm diam., round, concave or rarely convex; **upper surface:** brown-olive, smooth and shiny, not sorediate; **upper cortex:** not developed but with a yellowish epinecral layer (30-45 µm thick); **medulla:** composed of loosely interwoven hyphae; algal layer: 75-105 µm thick; **lower cortex:** absent or only poorly developed (2-3 rows of globose cells); **lower surface:** paler than the upper surface, attached centrally by large rhizines; **Apothecia:** one per squamule (very rarely 2-3), immersed; disc: expanded, 0.5-3 (-5) mm in diam., red to yellow-brown; epihymenium: yellow-brown, K+ red-violet; hymenium: I+ wine-red, 165-170 µm high, >100-spored; **ascospores:** globose, 6.6-8.3 µm diam.; **Pycnidia:** no data available; **conidia:** fusiform, 3.1-3.7 x 1.2 µm; **Spot tests:** all negative; **Secondary metabolites:** none detected.

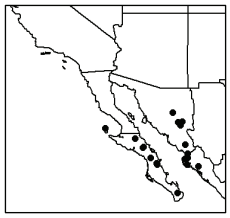


Substrate and ecology: on soil with high calcium levels, particularly in places particularly in places where water runs across the surface during heavy storms; **World distribution:** SW North America to central Mexico; **Sonoran distribution:** desert areas of Arizona, southern California, Sonora, Baja California and Baja California Sur.

Peltula sonorensis Büdel & T. H. Nash, Lichenol. 25: 280 (1993).

Illustrations: Büdel and Nash (1993), pp. 280 & 281.

Thallus: peltate, scattered, up to 9 mm diam., margin: sometimes undulate, downcurved, entire; **upper surface:** olive to yellowish green, smooth, shiny, not sorediate; **upper cortex:** poorly developed, 18-20 µm thick, with a pale yellow epinecral layer (9-16 µm thick); **medulla:** loosely interwoven hyphae (2-2.5 µm thick, short celled), below with numerous air spaces; algal layer: 100-225 µm thick; **lower cortex:** 18-30 µm thick, composed of anticlinally arranged, short-celled hyphae (3-5 µm wide) in 4-5 rows; **lower surface:** paler than the upper surface, attached by a central umbilicus; **Apothecia:** numerous, completely immersed; disc: yellow-brown, punctiform when young, later up to 0.8 mm wide; epihymenium: yellow-brown; hymenium: I+ blue, 160-240 µm high; **asci:** clavate to obclavate; wall: I+ blue, >100-spored; **ascospores:** bacilliform, 4-8.5 x 2-4 µm; **Pycnidia:** immersed, spherical, chambered; **conidia:** fusiform, 3-4 x 1 µm; **Spot tests:** all negative; **Secondary metabolites:** none detected.



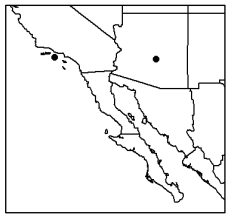
Substrate and ecology: on acidic rock in deserts and other open, arid habitats; **World distribution:** only known from NW Mexico; **Sonoran distribution:** desert and thorn forest areas of Sonora, Sinaloa, Baja California and Baja California Sur.

Peltula tortuosa (Nees) Wetmore, Ann. Mo. Bot. Gard. 57: (1971).

Basionym: *Dufourea tortuosa* Nees, Horae Phys. Berol. 43: Pl 5, f. 2 (1820); Illustrations: Büdel (1987), figs. 201-206; Upreti and Büdel (1990), fig. 5.

Thallus: suffruticose, often forming a tuff of aggregated thalli, lobate; **lobes:** upright, flattened, somewhat branched, often twisted, occasionally partially terete, lobes up to 8 (-15) mm long and 0.4-1 mm wide at top; **upper surface:** dark olive-brown to olive-green, smooth, not sorediate; **upper cortex:** not developed in the upper part of the lobes but surrounded by a yellow-brown epinecral layer (5–12 µm thick), forming a rudimentary cortex (consisting of several layers of globose cells) at the base of the lobes; **medulla:** paraplectenchymatous, composed of loosely interwoven hyphae with large air spaces, giving the impression of a hollow thallus lobes; algal layer: indistinctly delimited, scattered throughout; **lower surface:** paler than the upper surface, attached by an umbilicus; **Apothecia:** very rare, one the sides or in swollen ends of the lobes, several per lobe, immersed and punctiform; disc: slightly enlarging when mature; epihymenium: yellowish brown, K-; hymenium: I+ wine-red, >100-spored; **ascospores:** globose to subglobose, 4.5 x 3-4.5 µm; **Pycnidia:** immersed, spherical, on the sides or in swollen ends of lobes; **conidia:** fusiform, 3.1-3.7 x 1.2 µm; **Spot tests:** all negative; **Secondary metabolites:** none detected.

Substrate and ecology: on granitic rocks in deserts and other open, arid habitats; **World distribution:** India, southern North America, Venezuela, and southern and tropical Africa; **Sonoran distribution:** desert areas of Arizona, California.

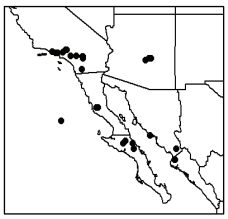


Peltula zahlbruckneri (Hasse) Wetmore, Ann. Mo. Bot. Gard. 57: 205 (1971).

Basionym: *Heppia zahlbruckneri* Hasse, Bryologist 14: 100 (1911); Illustrations: Wetmore (1970), fig. 28; Filson (1988), fig. 10.

Thallus: typically areolate-squamulose but sometimes minutely suffruticose, in loosely aggregated patches; **squamules:** swollen, somewhat angulate to lobate, convex, often with flattened tops (especially when young), 0.5-3 mm wide; **upper surface:** tan to dark brownish olive, dull, not sorediate; **upper cortex:** not developed but with a yellow epinecral layer; **medulla:** composed of loosely interwoven hyphae with many hollow areas; algal layer: 75-150 µm thick; **lower cortex:** paraplectenchymatous, 30-56 µm thick, with 3-6 layers of globose cells; **lower surface:** paler than upper surface, attached by short stalk and an umbilicus; **Apothecia:** 1-7 (or more) per squamule, immersed; disc: punctiform, enlarging with age, reddish-brown; epihymenium: brownish, K-; hymenium: I+ wine-red, 105-150 µm high, >100-spored; **ascospores:** globose to subglobose, 4.5-7.6 x 3-4.5 µm; **Pycnidia:** immersed, spherical, up to 400 µm diam.; **conidia:** fusiform, 3.5-4.5 x 1.5 µm; **Spot tests:** all negative; **Secondary metabolites:** none detected.

Substrate and ecology: on acidic rocks, including granites in deserts and other open, arid habitats; **World distribution:** SW North America, West Africa, India, central Australia, **Sonoran distribution:** desert areas of Arizona, southern California, Sonora, Baja California and Baja California Sur.



PERIDIOTHELIA

by A. Aptroot

Peridiothelia D. Hawksw., Bull. Brit. Mus. (Nat. Hist.), Bot. 14: 120 (1985).

Family: Pleomassariaceae; Type: *Peridiothelia fuliguncta* (Norman) D. Hawksw.; No. species: three world-wide; Selected lit.: Aptroot (1995a), and Hawksworth (1985b).

Life habit: non-lichenized, saprophytic; **Thallus:** crustose, mostly within the substrate; **photobiont:** absent; **Ascomata:** perithecial; **involucrellum:** absent; **ascomatal wall:** black, cellular, not continuous below the hamathecium; **hamathecium:** branched pseudoparaphyses,

anastomosing above the asci, amyloid; **asci:** bitunicate, clavate, with tholus, non-amyloid; **ascospores:** medium to golden brown, clavate to pyriform, 1-septate with an euseptum, 16-35 x 7-13 µm; walls: ornamented with tiny warts; **Conidiomata:** unknown; **Secondary metabolites:** none detected; **Geography:** mostly temperate; **Substrate:** only on bark.

Notes: The genus is characterized by the 1-septate, medium to golden brown, conspicuously ornamented ascospores.

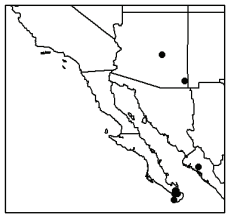
The Species

Peridiothelia fuliguncta (Norman) D. Hawksw., Bull. Brit. Mus. (Nat. Hist.), Bot. 14: 121 (1985).

Basionym: *Microthelia fuliguncta* Norman, Oefvers. Förh. Kongl. Svenska Vetensk.-Akad. 41 (8): 36 (1884); Synonyms: *Mycomicothelia fuliguncta* (Norman) D. Hawksw. *Microthelia macula* auct.; Illustrations: Hawksworth (1985b), pp. 122 & 123.

Thallus: absent or continuous, smooth, immersed in the substrate, whitish; **photobiont:** absent; **Perithecia:** hemispherical, black, superficial on the substrate, 0.2-0.4 mm diam.; **ascomatal wall:** black, absent below the hamathecium; **hamathecium:** branched pseudoparaphyses, anastomosing above the asci; filaments: *c.* 2 µm wide, not inspersed with oil droplets; **asci:** clavate, *c.* 60-75 x 15-20 µm, with 8, irregularly arranged ascospores; **ascospores:** medium to golden brown, clavate to pyriform, 1-septate with a supramedian euseptum, (16-) 17-22 (-25) x (6-) 7-9 (-10) µm; walls: soon becoming ornamented with warts, without or with a *c.* 2 µm wide gelatinous sheath; **Spot tests:** all negative, UV negative; **Secondary metabolites:** none detected.

Substrate and ecology: on bark of various woody plants, e.g. *Bursera, Lysiloma* and *Prunus*; **World distribution:** primarily north temperate, previously only known from Europe and Canada; **Sonoran distribution:** rather commonly collected in southern Arizona, Baja California Sur and Sinaloa.



Notes: Although it was previously reported to be restricted to *Tilia* (Hawksworth 1985b), it has subsequently also been found on other tree species (Aptroot 1995 & 1997). The collections from *Bursera*, *Lysiloma* and *Prunus* are additional host records.

PERTUSARIA

by H. T. Lumbsch and T. H. Nash III

Pertusaria DC., in Lam. & DC., Fl. Franç., ed. 3, 2: 319 (1805), nom. cons.

Family: Pertusariaceae; Type: *Pertusaria pertusa* (Weigel) Tuck.; No. species: *c.* 350 world-wide; Selected lit.: Dibben (1980), and Lumbsch et al. (1999).

Life habit: lichenized; **Thallus:** crustose, superficial, moderately thick or thin and immersed in substrate, continuous to rimose-cracked, fissured-areolate or warted; **upper surface:** gray, gray-green, or yellow; smooth or rugulose, dull or shiny; soredia or isidia: present or absent; **upper cortex:** present but often poorly developed, paraplectenchymatous in better developed specimens but often composed of little more than a thin, gelatinous epinecral layer; **medulla:** white; of irregularly interwoven hyphae, quite variable in thickness from almost neglible to quite thick in robuster specimens; **photobiont:** primary photobiont a *Trebouxia*, secondary photobiont absent; algal layer: horizontally continuous; algal cells 7-18 µm in diam.; **lower cortex:** absent; **lower surface:** not distinguishable from the substrate, attached by bundles of hyphae penetrating the substrate; **Ascomata:** apothecioid, either sessile with an expanded, open disc or almost

closed and perithecial like and one to several immersed within a wart; disc: sometimes covered with granular soredia and appearing soralia-like or pruinose; hymenium: hyaline; hamathecium: lax, branched and richly anastomosing paraphysoids, 1.5-2.0 µm thick; **asci:** ± broadly cylindrical, apex with a broad ocular chamber, thick-walled, outer sheath K/I+ blue, otherwise K/I-, with an inner extensible layer, *Pertusaria*-type, 1-8-spored; **ascospores:** non-septate, thick walled, 1- or 2-layered, wall uniform or at times radiated canals to the surface, or ornamented; 60-250 x 20-80 µm; **Conidiomata:** pycnidial, rare; **conidia:** straight, acicular or bacilliform, 15-25 x 1-2 µm; **Secondary metabolites:** some combination of xanthones, ß-orcinol depsides, ß-orcinol depsidones, depsones or fatty acids; **Geography:** world-wide, particularly in subtropics and temperate regeions; **Substrate:** soil, moss, detritus, rocks or bark.

Notes: There is a stratification in the development of secondary metabolites; thiophanic acid and other xanthones, which partially screen incoming solar radiation, are best developed near the surface; the depsides, depsidones, depsones and fatty acids, in the medulla below the surface. Thus, in thick specimens the spot tests should be applied on a piece of the upper surface and on an exposed section of the medulla. The xanthones in general react C+ orange and are strongly fluorescent (yellow to orange) in long-wave UV. Specimens can thus be rapidly screened for xanthones with UV light with the caution that specimens with low xanthone concentrations will not necessarily be fluorescent. In short, a UV- specimen may still have low xanthone concentrations (e.g. *P. consocians*) whereas a UV+ specimen always has xanthones. Because many specimens have very thin medullas, it is not practical to differentiate upper surface and medullary reactions among the spot test given with each species description below.

In general the spot test in *Pertusaria* occur in both the cortex and medulla with the exception of the xanthones (C+) that are often restricted to the cortex. Thus the descriptions do not distinguish between cortex and medulla.

Brown spored species, sometimes treated as the genus *Melanaria*, will be treated in vol. II.

Key to the species of ***Pertusaria*** from the Sonoran region:

1. Saxicolous 2
1. Corticolous 14

2. Thallus sorediate or isidiate 3
2. Thallus lacking soredia or isidia 7

3. Thallus isidiate, containing norstictic acid, lacking xanthones ..... ***P. pseudocorallina***
3. Thallus sorediate, norstictic acid present or not 4

4. Thallus whitish, containing lichexanthone or lacking xanthones 5
4. Thallus yellowish, containing thiophaninic acids 6

5. Thallus UV + yellow, containing lichexanthone and haemathamnolic acid ..... ***P. moreliensis***
5. Thallus UV -, containing picrolichenic acid .. ***P. amara***

6. Thallus containing stictic acid .... ***P. flavicunda***, sorediate morphotype
6. Thallus containing confluentic and planaic acids .... ***P. tejocotensis***, sorediate morphotype

7. Ascospores remaining hyaline, K- or pale purple 8
7. Ascospores becoming brown when mature, K+ purple .. .. "***Melanaria"*** (Vol. II)

8. Thallus UV + yellow or orange, containing xanthones 9
8. Thallus UV - or slightly gray, lacking xanthones, containing norstictic acid 12

9. Thallus whitish, containing lichexanthone and 2-*O*-methylperlatolic acid, apothecia poriform ..... ***P.mariae***
9. Thallus yellowish, containing thiophaninic acid, apothecia poriform or disciform 10

10. Apothecia disciform, asci containing 2 spores, thallus with stictic acid ..... ***P. flavicunda***
10. Apothecia poriform, asci containing 4 spores, thallus with norstictic acid or depsides 11

11. Thallus with confluentic and planaic acids .... ***P. tejocotensis***
11. Thallus with norstictic acid ..... ***P. wulfenoides***

12. Apothecia disciform, asci containing 2-8 spores . 13
12. Apothecia poriform, asci containing 1-2 spores .... ***P. californica***

13. Asci containing 8 spores, thallus containing stictic acid ..... ***P. chiodectonoides***
13. Asci containing 2-4 spores, thallus containing norstictic acid ..... ***P. brattiae***

14. Thallus sorediate 14
14. Thallus lacking soredia 19

15. Thallus UV + yellow or orange, containing xanthones. 16
15. Thallus UV -, lacking xanthones 17

16. Thallus yellowish, K + yellow turning red, C -, containing thiophaninic and norstictic acids; soralia are not sorediate verrucae, lacking asci and ascospores ..... ***P. azulensis***
16. Thallus whitish or gray, K -, C + red, containing lichexanthone and lecanoric acid; soralia are in fact sorediate verrucae, containing asci and ascospores .. .. ***P. velata***

17. Thallus containing picrolichenic acid, with a bitter taste ..... ***P. amara***
17. Thallus lacking phenolic substances, not bitter 18

18. Verrucae small (up to 1,2 mm in diam.), apothecial margins crenulate, black apothecial disc usually visible, often fertile ..... ***P. ophthalmiza***
18. Verrucae large (up to 4.5 mm in diam.), apothecial margins smooth, black disc rarely seen, usually sterile ..... ***P. albescens***

19. Asci with single ascospores or 2-spored 20
19. Asci 4-8-spored, sometimes asci with fewer ascospores occur, but then 4-8-spored asci occur as well 28

20. Apothecia poriform 21
20. Apothecia disciform 24

21. Thallus containing norstictic acid and thiophaninic acid ..... ***P. neolecanina***
21. Thallus containing stictic acid and xanthones 22

22. Thallus whitish gray, containing 4,5-dichloroliche-xanthone, UV- or gray ..... ***P. consocians***
22. Thallus yellowish, containing xanthones, UV + yellow to orange 23

23. Thallus yellowish, containing thiophaninic acid .... ***P. xanthodes***
23. Thallus yellowish green, containing 2-chloro-6-*O*-methylnorlichexanthone ..... ***P. pustulata***

24. Thallus yellowish, containing norstictic and thiophaninic acids ..... ***P. lecanina***
24. Thallus whitish gray to brown, lacking chlorinated xanthones 25

25. Apothecial discs pruinose or sorediate 26
25. Apothecial discs epruinose 27

26. Thallus containing lecanoric acid and often also lichexanthone ..... ***P. velata***
26. Thallus lacking phenolic substances ***P. ophthalmiza***

27. Epithecium and spore walls K+ violet, thallus containing 2-*O*-methylconfluentic acid ..... ***P. saximontana***
27. Only epithecium K+ violet, thallus lacking secondary metabolites ..... ***P. stenhammarii***

28. Thallus yellowish, containing thiophaninic acid (UV + orange) 29
28. Thallus whitish gray to brown, containing 4,5-dichlorolichexanthone (UV – or gray) 32

29. Thallus containing norstictic acid 30
29. Thallus lacking norstictic acid, containing stictic or gyrophoric acids 31

30. Asci 8-spored, epithecium K+ violet ... ***P. rubefacta***
30. Asci usually 4-spored, epithecium K- .... ***P. wulfenoides***

31. Epithecium K+ violet, ostioles dilating to form pseudolecanorate discs when mature ..... ***P. hymenea***
31. Epithecium K-, ostioles small and non-dilating .... ***P. texana***

32. Ascospores subglobose to broadly ellipsoid, 16-48 µm long, epithecium K+ violet, asci 8-spored .... ***P. sommerfeltii***
32. Ascopores ellipsoid to fusiform, longer, epithecium K-, asci 4- to 8-spored 33

33. Thallus containing 2'-*O*-methylperlatolic acid and 4, 5-dichlorolichexanthone ..... ***P. mesotropa***
33. Thallus containing stictic acid and 4,5-dichloroliche-xanthone 34

34. Inner spore wall smooth, verrucae center pink .... ***P. leioplaca***
34. Inner spore wall rough, verrucae center brown .....

..... ***P. tetrathalamia***

The Species

Pertusaria albescens (Huds.) M. Choisy & Werner, in Werner, Cavanillesia 5: 165 (1932).

Basionym: *Lichen albescens* Huds., Fl. Angl., ed. 1: 445 (1762); Synonyms*:* see Dibben (1980), Erichsen (1936) and Laundon (1963); Illustrations*:* Dibben (1980), p. 138; Lumbsch et al. (1999), p. 219.

Thallus: continuous to fissured, with thin to moderately thick verrucae; margins: definite, entire to zoned; **upper surface:** whitish gray to yellowish gray, epruinose; **soredia:** in verrucae, 0.5-4.5 mm in diam., lecanorate; **Apothecia:** no fertile specimens seen; **Pycnidia:** not seen; **Spot tests:** K-, C-, KC-, P-, UV-; **Secondary metabolites:** allopertusaric (major) and dihydropertusaric (minor) acids.

Substrate and ecology*:* on hardwoods or conifers, such as *Pseudotsuga*, at 2000 to 2600 m; **World distribution:** widely distributed in the Northern Hemisphere, very common in Europe, restricted in North America to the SW and central Mexico; **Sonoran distribution:** restricted to montane areas of southern California.

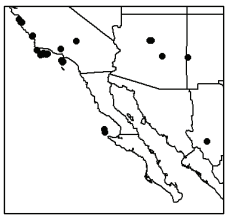
Notes: This species is readily identified by the large disciform soralia, the thick thallus often with zonate margins and the lack of phenolic compounds. The soralia are in fact sorediate verrucae, but these are very rarely fertile, and no material from the study area examined contained spores or asci. *Pertusaria albescens* may be confused with *P. amara* when poorly developed. However, the two species are easily distinguished by the bitter taste or KC + violet reaction of the thallus due to the presence of picrolichenic acid in the latter species.

Pertusaria amara (Ach.) Nyl., Bull. Soc. Linn. Normandie, sér. 2, 6: 288 (1872).

Basionym: *Variolaria amara* Ach., Kongl. Vet.-Acad. Nya Handl. 30: 163 (1809); Synonyms: see Dibben (1980) and Erichsen (1936); Illustrations: Dibben (1980), p. 138; Lumbsch et al. (1999), p. 219; Wirth (1995), p. 699; Brodo et al. (2001), p. 527.

Thallus: continuous to fissured, with thin to moderately thick verrucae; margin: definite, often zonate; **upper surface:** whitish gray to greenish gray, margins entire to weakly zoned, epruinose; **soredia:** farinose, restricted to verrucae or coalescing and spreading onto ruptured thallus surface; **Apothecia:** no fertile specimens seen; **Pycnidia:** not seen; **Spot tests:** K- or K+ yellow to red, C-, KC+ rose-violet, P- or + yellow to red, UV-; **Secondary metabolites:** picrolichenic and ± protocetraric acids (both major); ± conprotocetraric and subpicrolichenic acid (both minor).

Substrate and ecology: on deciduous trees, such as *Aesculus, Quercus* or conifers, and also occasionally on siliceous rocks in shady places; **World distribution:** widely distributed in the Northern Hemisphere; **Sonoran distribution:** in coastal areas of southern California and Baja California and scattered in inland mountains up to 1800 m in Arizona and Chihuahua.



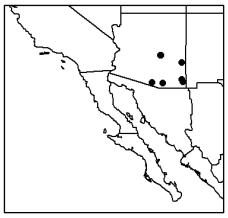
Notes: *Pertusaria amara* is characterized by small, but coalescing soralia with farinose soredia, a relatively thin, grayish thallus and the presence of the picrolichenic acid chemosyndrome and thus a bitter taste. It is hardly confused with any other *Pertusaria* species occurring in western North America, except *P. albescens.* The distinction of both species is discussed above.

Pertusaria azulensis de Lesd., Lichens du Mexique, 17 (1914).

Illustration: Lumbsch et al. (1999), p. 219.

Thallus: verrucose, with moderately thick verrucae, margins: indefinite, unzoned to seldom zoned; **upper surface:** yellow-green to sulfur yellow, smooth to rugose, dull to slightly glossy, epruinose to slightly grayish pruinose; **soredia:** whitish green to whitish gray, often with a bluish glimmer, in orbicular soralia, 0.5-2.0 mm in diam.; **Apothecia:** no fertile specimens seen; **Pycnidia:** not seen; **Spot tests:** K+ yellow to red, C+ orange, KC-, P+ yellow to orange, UV+ orange-red; **Secondary metabolites:** norstictic and thiophaninic acids (both major), connorstictic acid, 2-chloro-6-*O*-methylnorlichexanthone and 4-chloro-6-*O*-methylnorlichexanthone (all minor).

Substrate and ecology: *Pertusaria azulensis* grows on dead wood, and sometimes on *Pinus* bark; **World distribution:** endemic to North America from central Mexico to SW USA; **Sonoran distribution:** restricted to mountainous areas of Arizona at 1900 to 2800 m.



Notes: This species is easily identified by the yellowish thallus, the definite, orbicular soralia and the presence of the norstictic and thiophaninic acids chemosyndromes. It is hardly confusable with any other *Pertusaria* species in North America.

Pertusaria brattiae Lumbsch & T. H. Nash, Bryologist 102: 218 (1999).

Illustration: Lumbsch et al. (1999), p. 219.

Thallus: rimose- to verrucose-areolate, with thin to moderately thick verrucae; margins: indefinite, unzoned; **upper surface:** whitish gray to reddish gray, smooth, dull, epruinose; lacking soredia or isidia; **fertile verrucae:** concolorous with thallus, lecanorate, numerous, *c.* 0.5-1.7 mm in diam; **Apothecia:** 1-2 per fertile verruca; discs: gray-brown to blackish brown, grayish pruinose; epithecium: dark brown to red-brown; hypothecium: hyaline; **asci:** cylindrical, 215-400 x 45-74 µm, 2-4-spored; **ascospores:** hyaline, ellipsoid, 75-110 x 33-45 µm; spore walls *c.* 8-13 µm thick, apices up to 18 µm thick, 2-layered; outer spore wall: *c.* 1-3 µm thick; inner spore wall: 7-11 µm thick; **Pycnidia:** not seen; **Spot tests**: medulla K+ yellow to red, C-, KC-, P+ orange, UV-; **Secondary metabolites:** norstictic acid (major), connorstictic and subnorstictic acids and unknowns (minors).

Substrate and ecology: occurring on coastal, siliceous rocks at 0-300 m; **World distribution**: endemic to the western coast of North America; **Sonoran distribution:** coastal, southern California and the adjacent NW Baja California.

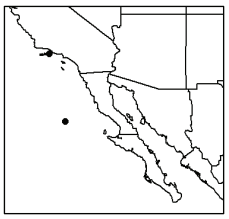
Notes: *Pertusaria brattiae* is characterized by the apothecioid ascomata, 2-4-spored asci and the presence of norstictic acid and related substances. The species is similar to *P. chiodectonoides* which, however, is readily distinguished by 8-spored asci and the presence of stictic acid. *Pertusaria flavicunda* is another species, which might be confused with *P. brattiae*. This taxon differs in containing thiophaninic and stictic acids.

Pertusaria californica Dibben, Millwaukee Publ. Mus., Publ. Biol. Geol. 5: 86 (1980).

Illustrations: Lumbsch et al. (1999), p. 219; Dibben (19 80), p. 140.

Thallus: areolate, with moderately thick verrucae; margins: entire, zoned; **upper surface:** ash gray to dark gray, smooth, shiny, epruinose, lacking soredia or isidia; **fertile verrucae:** concolorous with thallus, pertusariate, hemispherical to flat-topped, numerous, rarely fused, *c.* 0.8-2.0 mm in diam.; ostioles: 1 or 2-10 per verruca; **Apothecia:** 1-10 per verruca, 0.4-0.8 mm in diam.; epithecium: dark brown to black, K-; hypothecium: hyaline to yellowish; **asci:** cylindrical, 300-500 x 60-90 µm, (1-) 2-spored; **ascospores:** hyaline, ellipsoid, 145-270 x 50-80 µm, 2-layered; outer spore wall: *c.* 4-10 µm thick, inner spore wall: 10-20 µm thick; **Pycnidia:** immersed; **conidia:** bacilliform, 5-8 x 0.5-1.0 µm; **Spot tests:** K+ yellow to red, C-, KC-, P+ yellow to orange, UV-; **Secondary metabolites:** norstictic (major) and connorstictic (minor) acids.

Substrate and ecology: The species grows on siliceous rocks at the coast and in coastal mountains; **World distribution:** endemic to the west coast of North America; **Sonoran distribution:** restricted to coastal California and Baja California.



Notes: *Pertusaria californica* is characterized by the gray thallus with large pertusariate verrucae that have several dark ostioles, two- to single-spored asci, and the presence of norstictic acid. The relationships of *P. californica* were discussed in detail by Dibben (1980). *Pertusaria californica* may be confused with poorly developed specimens of *P. brattiae* which, however, differs in having disciform apothecia and can further be distinguished by smaller ascospores and the presence of stictic acid.

Pertusaria chiodectonoides Bagl. *ex* A. Massal., Misc. Lich.: 26 (1856).

Synonyms*:* see Erichsen (1936); Illustration: Dibben (1980), p. 140.

Thallus: fissured to fissured-areolate, with thin to moderately thick verrucae; margins: entire, unzoned; **upper surface:** gray to dark gray, smooth, dull or shiny, epruinose to gray-white pruinose; lacking soredia or isidia; **fertile verrucae:** concolorous with thallus, lecanorate, numerous, *c.* 0.5-1.5 mm in diam.; **Apothecia:** 1-3 per verruca; discs: black, sunken, grayish pruinose; epithecium: dark brown to blackish brown; hypothecium: yellowish to hyaline; **asci:** cylindrical, 120-250 x 20-45 µm, 8-spored; **ascospores:** hyaline, ellipsoid to fusiform, 25-50 x 14-24 µm; spore wall: *c.* 2-5 µm thick, smooth, 1-layered; **Pycnidia:** immersed; **conidia:** bacilliform, 7-10 x 0.5-1.0 µm; **Spot tests:** K- or + pale yellow, C-, KC-, P- or + yellow to orange, UV-; **Secondary metabolites:** stictic acid (major), constictic and norstictic acids (both minor).

Substrate and ecology: on siliceous rocks in coastal mountains; **World distribution:** western North American and disjunct in the Mediterranean region; **Sonoran distribution:** restricted to coastal California.

Notes: *Pertusaria chiodectonoides* is characterized by a generally dark gray thallus with lecanorate verrucae with pruinose, blackish discs, a K+ violet epithecium, 8-spored asci, and the presence of stictic acid. It may be confused with *P. brattiae* which contains norstictic acid and has 2-4-spored asci. No recent collections of *P. chiodectonoides* from North America are known.

Pertusaria consocians Dibben, Millwaukee Publ. Mus. Publ. Biol. Geol. 5: 87 (1980).

Illustrations: Lumbsch et al. (1999), p. 219; Dibben (1980), p. 141.

Thallus: continuous to weakly fissured, with thin to moderately thick verrucae; margins: entire, unzoned; **upper surface:** whitish gray to ash gray, smooth, shiny, epruinose; lacking soredia or isidia; **fertile verrucae:** concolorous with thallus, ampliariate or pertusariate, numerous, often fused, *c.* 0.5-2.2 mm in diam; ostioles: 1-8 per verruca, blackish brown, sunken; **Apothecia:** 1-7 per verruca; epithecium: dark brown to red-brown, K+ violet; hypothecium: yellowish; **asci:** cylindrical, 250-450 x 45-90 µm, (1-) 2-spored; **ascospores:** hyaline, ellipsoid to fusiform, 95-210 x 35-55 µm; spore wall: 2-layered; outer spore wall: c. 1-5 µm thick; inner spore wall: *c.* 2-12 µm thick; **Pycnidia:** not seen; **Spot tests:** K+ yellow, C-, KC-, P+ yellow to orange, UV- or + orange-pink; **Secondary metabolites:** stictic acid and 4, 5-dichlorolichexanthone (both majors) and constictic acid (minor).

Substrate and ecology: *Pertusaria consocians* grows primarily on conifers (including *Abies*); **World distribution:** endemic to North America, where it is relatively common in the East; **Sonoran distribution:** coastal mountains of southern California.

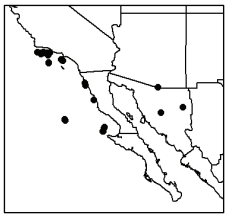
Notes: *Pertusaria consocians* is a gray lichen with ampliariate or pertusariate verrucae with dark ostioles, 2-spored asci, ellipsoid to fusiform ascospores, and stictic acid and 4,5-dichlorolichexanthone. It is very similar to the European *P. pertusa* (Weigel) Tuck. and the differences between these taxa have been discussed by Dibben (1980).

Pertusaria flavicunda Tuck., Proc. Amer. Acad. Arts & Sci. 12: 176 (1877).

Illustrations: Dibben (1980), p. 142; Lumbsch et al. (1999), p. 222; Brodo et al. (2001), p. 529.

Thallus: fissured to fissured-areolate, with thin to moderately thick verrucae; margins: entire, unzoned; **upper surface:** green-yellow to sulfur-yellow, smooth to tuberculate or rugose-plicate, dull, slightly pruinose; lacking soredia or isidia or superficially sorediate; **fertile verrucae:** concolorous with thallus, lecanorate, numerous, often fused, *c.* 0.5-1.8 mm in diam.; **Apothecia:** 1 (-2) per verruca; disc: brown to blackish brown, sunken, yellowish pruinose; epithecium: yellow-brown to brown, K+ violet; hypothecium: yellowish to brown; **asci:** cylindrical, 150-300 x 50-70 µm, 2 (-4)-spored; **ascospores:** hyaline, ellipsoid to fusiform or oval, 50-115 x 25-60 µm; spore wall: *c.* 8-28 µm thick, 1-layered; **Pycnidia:** not seen; **Spot tests:** K+ yellow, C+ orange, KC-, P+yellow to orange, UV+ orange-red; **Secondary metabolites:** stictic and thiophaninic acids (both major), constictic acid, 2-chloro-6-*O*-methylnorlichexanthone, and 4-chloro-6-*O*-methylnorlichexanthone (all minor).

Substrate and ecology: The species grows on siliceous rocks at the coast and the coastal mountains at 0 -200 m and some specimens were collected at an elevation of up to 750 m; **World distribution:** endemic to western North America; **Sonoran distribution:** coastal southern California and Baja California and at scattered inland locations in southern Arizona and Sonora.



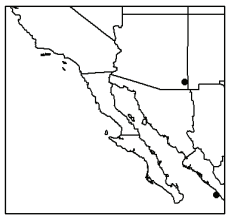
Notes: This taxon can easily be recognized by the yellowish thallus, large lecanorate verrucae with pruinose discs, ± 2-spored asci, and the presence of stictic and thiophaninic acids. Some morphotypes of *P. tejocotensis* may be similar, but this species is distinguishable by poriform apothecia, 4-spored asci, and the presence of depsides instead of stictic acid. *Pertusaria flavicunda* is generally a uniform species, but some populations differ in producing soralia instead or in addition to apothecia. The sorediate morphotypes do not differ in any other morphological or chemical characters.

Pertusaria hymenea (Ach.) Schaer., Lich. Helv. Spic. 1 (7): 353 (1836).

Basionym: *Lichen hymeneus* Ach., Lich. Suec. Prodr.: 80 (1798); Synonyms: see Dibben (1980) and Erichsen (1936); Illustrations: Dibben (1980), p. 143; Lumbsch et al. (1999), p. 222.

Thallus: continuous to irregularly fissured, with thin to moderately thick verrucae; margins: entire, zoned or unzoned; **upper surface:** gray to yellow-gray or greenish gray, smooth or rugose-plicate, shiny or dull, epruinose; lacking soredia or isidia; **fertile verrucae:** concolorous with thallus, pertusariate to falsely lecanorate, numerous, crowded and locally fused (2-4) in mutually deformed groups, *c.* 0.4-3.0 mm in diam.; ostioles: 1-8 per verruca, well sunken, soon dilating to form a pseudolecanorate disc, blackish brown, grayish pruinose; **Apothecia:** 1-4 per verruca; epithecium: dark brown to black; hypothecium: hyaline or yellowish; **asci:** clavate, 270-450 x 40-100 µm, (6-) 8-spored; **ascospores:** hyaline, ellipsoid or fusiform, 60-130 x 25-50 µm.; spore wall: 2-layered; outer spore wall: *c.* 1-4 µm thick; inner spore wall: 2-10 µm thick; apices: up to 28 µm thick; **Pycnidia:** immersed; **conidia:** bacilliform, 7-15 x 0.5-1.0 µm; **Spot tests:** K- or + yellow, C- or + yellow, KC+ orange, P-, UV+ orange-red; **Secondary metabolites:** thiophaninic acid (major), gyrophoric acid (minor).

Substrate and ecology: on *Quercus* or *Pinus* bark; **World distribution:** temperate Europe and western North America; **Sonoran distribution:** widely scattered, SE Arizona and coastal Sinaloa, at *c.* 500 - 2300 m.



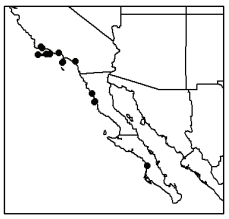
Notes: *Pertusaria hymenea* is characterized by a moderately thick yellowish thallus, poriform ascomata with sunken ostiola which soon dilate and fuse to form a blackish pseudolecanorate disc, a K+ violet epithecium, 8-spor-

ed asci and the presence of thiophaninic and gyrophoric acids. A very similar species is *P. rubefacta* which is best separated by the presence of the norstictic acid chemosyndrome.

Pertusaria lecanina Tuck., Gen. Lich.: 127 (1872).

Illustrations: Dibben (1980), p. 144; Lumbsch et al. (1999), p. 222.

Thallus: fissured, with thin to moderately thick verrucae; margins: entire, unzoned; **upper surface:** yellowish gray to ash gray or green-gray, smooth to tuberculate, dull, slightly pruinose; lacking soredia or isidia; **fertile verrucae:** concolorous with thallus, lecanorate, numerous, *c.* 0.7-1.2 mm in diam.; **Apothecia:** 1 (-2) per verruca; disc: brown to blackish brown, level to sunken, whitish pruinose; epithecium: yellow-brown to blackish brown, K-; hypothecium: hyaline to yellowish; **asci:** clavate, 170-350 x 45-85 µm, (1-) 2-spored; **ascospores:** hyaline, ellipsoid to cylindrical, 75-150 x 35-75 µm; spore wall: *c.* 5-20 µm thick, smooth, 1-layered; **Pycnidia:** not seen; **Spot tests:** K+ yellow to red, C- or red, KC- or red, P+ yellow, UV+ orange-red; **Secondary metabolites:** norstictic and thiophaninic acids (both major), connorstictic acid, 2-chloro-6-*O*-methylnorlichexanthone, 4-chloro-6-*O*-methylnorlichexanthone, and ± gyrophoric acid (all minors).



Substrate and ecology: bark of different phorophytes, most commonly collected on *Quercus* in mountainous regions; **World distribution:** endemic to North America; **Sonoran distribution:** along the west coast from central California to Baja California and Baja California Sur at 200-600 m.

Notes: *Pertusaria lecanina* has a yellowish gray thallus with lecanorate verrucae with dark, but heavily whitish gray pruinose, discs. It is further characterized by 2-spored asci and the presence of norstictic and thiophaninic acids. It may superficially resemble *P. xanthodes* when poorly developed, but this species is readily distinguished by the poriform ascomata and the presence of stictic acid. Another somewhat similar species is *P. neolecanina*, the differences of these two species are discussed under the latter.

Pertusaria leioplaca DC., in Lam. & DC., Fl. Franc. ed. 3, 6: 173 (1815).

Synonyms: *Pertusaria leucostoma* (Bernh.) A. Massal.; further synonymy see Erichsen (1936); Illustrations: Dibben (1980), p. 144; Wirth (1995), p. 698.

Thallus: continuous to superficially fissured, with thin to very thin verrucae; margins: entire, unzoned; **upper surface:** ash gray to yellow-gray or green-gray, smooth to tuberculate, often shiny, epruinose to slightly pruinose; lacking soredia or isidia; **fertile verrucae:** concolorous with thallus, ampliariate to erect or pertusariate, numerous, *c.* 0.7-2.5 mm in diam.; ostioles 1-6 per verruca, hyaline; **Apothecia:** (1-) 2-4 (-6) per verruca; epithecium: hyaline, yellowish or dark brown to black-brown; hypothecium: hyaline to yellowish; **asci:** cylindrical, 250-450 x 30-70 µm, (2-) 4-spored; **ascospores:** hyaline, ellipsoid, 40-130 x 25-50 µm; spore wall: 2-layered; outer spore wall: *c.* 1-7 µm thick; inner spore wall: 2-12 µm thick; apices: up to 28 µm thick; **Pycnidia:** immersed; **conidia:** bacilliform, 7-10 x 0.5-1.0 µm; **Spot tests:** K- or + weakly yellow, C-, KC-, P+ yellow to orange, UV- or + pale orange-pink; **Secondary metabolites:** 4,5-dichlorolichexanthone and stictic acid (both major), constictic acid (minor).

Substrate and ecology: on bark, including *Abies* and *Quercus*; **World distribution:** pantemperate species in the Northern Hemisphere, in Europe and North America; **Sonoran distribution:** in mountainous areas of southern California at 500-2700 m.

Notes: *Pertusaria leioplaca* is characterized by a light-green thallus, ampliariate or pertusariate verrucae, 4-spored asci, and the presence of 4,5-dichlorolichexanthone and stictic acid. It is hardly confused with any other species in the area, but some poorly developed specimens of *P. texana* or *P. xanthodes* may be morphologically similar. They are readily distinguished by the presence of thiophaninic acid (UV+ orange) and a different number of

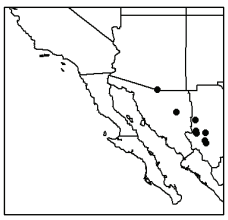
spores per ascus (eight in *P. texana* and two in *P. xanthodes*).

When the starting point for lichens and fungi was unified, this was one of the few lichen names that had to be changed (Santesson 1993).

Pertusaria mariae de Lesd., Lich. du Mexique: 17 (1914).

Illustration: Lumbsch et al. (1999), p. 224.

Thallus: rimose-areolate or continuous to rimose, with thin to moderately thick verrucae; margins: entire, unzoned; **upper surface:** whitish gray to greenish gray, smooth, shiny or dull, epruinose; lacking soredia or isidia; **fertile verrucae:** concolorous with thallus, pertusariate or erect, flat-topped, numerous, often fused, *c.* 0.6-2.0 mm in diam.; ostioles: 1-6 per verruca, slightly sunken, grouped in a central depression, *c.* 0.1-0.5 mm wide, dark brown, whitish gray pruinose; **Apothecia:** 1-4 per verruca, up to 0.7 mm in diam.; epithecium: dark brown, K -; hypothecium: hyaline; **asci:** cylindrical, 320-400 x 52-75 µm, 6-8-spored, uniseriate; **ascospores:** hyaline, broadly ellipsoid to ellipsoid, 75-110 x 36-58µm; spore walls: smooth, *c.* 8-12 µm thick, apices up to 20 µm thick, 2-layered; outer spore wall: *c.* 1-2 µm thick; inner spore wall: 7-11 µm thick; **Pycnidia:** not seen; **Spot tests:** K-, C-, KC-, P-, UV+ yellow; **Secondary metabolites:** lichexanthone and 2-*O*-methylperlatolic acid (both major), planaic acid (minor).



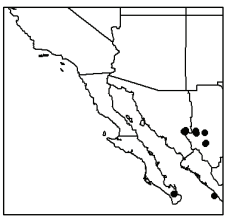
Substrate and ecology: *Pertusaria mariae* grows on siliceous rocks in open situations. A few specimens were also collected on soil; **World distribution:** endemic to North America; **Sonoran distribution:** in mountainous areas of southern Arizona, Sonoran and Chihuahua at 500 -2000 m.

Notes: *Pertusaria mariae* is characterized by the whitish gray, rimose-areolate thallus, the pertusariate to erect verrucae with numerous non-fusing ostioles, the 6-8-spored asci and the presence of lichexanthone (UV + yellow) and 2-*O*-methylperlatolic acid. It is similar to *P. tejocotensis* which can be distinguished chemically by the presence of thiophaninic acid (UV + orange) and confluentic and planaic acids. Morphologically *P. tejocotensis* differs in having a yellowish thallus. Another similar species is *P. wulfenoides* which seldom occurs on rocks, but differs chemically (norstictic and thiophaninic acids) and morphologically (thallus yellowish, ostioles fusing). Another saxicolous species containing lichexanthone is *P. moreliensis*, which can be readily distinguished by the sorediate thallus.

Pertusaria mesotropa Müll. Arg., Flora 19: 350 (1884).

Illustration: Lumbsch et al. (1999), p. 227.

Thallus: variable, verrucose, wrinkled or rimose-plicate to rimose, with thin to thick verrucae; margins: entire, unzoned; **upper surface:** yellowish gray, greenish gray to creamish, smooth to rugose, dull, epruinose; lacking soredia or isidia; **fertile verrucae:** concolorous with thallus, pertusariate, hemispherical to irregular, flat-topped, smooth or deformed, sometimes slightly rimose, numerous, crowded to fused (2-4), rarely scattered, *c.* 0.7-2.0 mm in diam.; ostioles: 1-5 per verruca, hyaline to brown or black, sometimes surrounded by a white border, sunken, grouped in a central depression, rarely papillate, *c.* 0.05-0.14 (-0.24) mm wide; **Apothecia:** 2-5 per verruca, fruit center hyaline to pink; epithecium: hyaline; hypothecium: hyaline; **asci:** cylindrical to subclavate, 285-415 x 40-49 µm, 4-8-spored, uniseriate to biseriate; **ascospores:** hyaline, ellipsoid to fusiform, 55-110 x 22-42 µm; spore walls: smooth, *c.* 5-10 µm thick, thickened at apices, 2-layered; outer spore wall: *c.* 1 µm thick; inner spore wall: 4-9 µm thick; **Pycnidia:** not seen; **Spot tests:** K-, C-, KC-, P-, UV+ gray; **Secondary metabolites:** 2'-*O*-methylperlatolic acid and 4,5-dichlorolichexanthone (both major), 2'-*O*-methylisohyperlatolic and 2'-*O*-methylsuperlatolic acids (both minor).



Substrate and ecology: on bark of *Pinus* and *Quercus*; **World distri-**

bution: described from Sri Lanka and also occurs in western North America; **Sonoran distribution:** mountainous areas of Sonora, Chihuahua and Baja California Sur at 1500-2320 m.

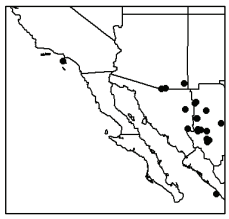
Notes: *Pertusaria mesotropa* is characterized by the 4-8-spored asci, the ellipsoid to fusiform ascospores and the presence of 2'-*O*-methylperlatolic acid and 4,5-dichlorolichexanthone. The species is very similar to the Australian *P. paragibberosa* Archer described recently (Archer 1991) and the distinction of the two species should be reexamined.

Pertusaria moreliensis de Lesd., Lich. du Mexique: 18 (1914).

Synonym: *Pertusaria coccopoda* Vain.; Illustration: Lumbsch et al. (1999), p. 224.

Thallus: rimose-areolate to verrucose, with flat to bullate, moderately thick verrucae; margins: unzoned to seldom zoned; **upper surface:** whitish gray to whitish green, smooth to rugose, dull to slightly glossy, epruinose to slightly grayish pruinose; **soredia:** granulose, 20-25 µm in diam., soredial margins indefinite, occurring in numerous, orbicular soralia, 0.5-1.6 mm in diam., whitish gray; **Apothecia:** no fertile specimens seen; **Pycnidia:** not seen; **Spot tests:** K+ yellow, C-, KC-, P+ yellow, UV+ yellow; **Secondary metabolites:** haemathamnolic acid and lichexanthone (both major), decarboxythamnolic, hypothamnolic and thamnolic acids (all minor).

Substrate and ecology: rather common on siliceous rocks (including conglomerate or rhyolite) in mountainous areas; **World distribution:** endemic to North America from central Mexico to SW U.S.A.; **Sonoran distribution:** coastal California and inland from southern Arizona, Sonora and Chihuahua, primarily at 1200 to 2300 m.



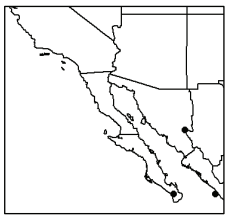
Notes: *Pertusaria moreliensis* is a sorediate species which can be distinguished from other saxicolous sorediate *Pertusaria* species in the area by its whitish gray thallus and the presence of lichexanthone (UV + yellow), while other sorediate taxa (sorediate morphotypes of *P. flavicunda* and *P. tejocotensis*) contain thiophaninic acid (UV + orange) and have a yellowish thallus. Morphologically similar to *P. moreliensis* is *P. excludens* Nyl. which differs in containing a norstictic acid chemosyndrome and having usually smaller soralia. Another saxicolous species with lichexanthone (UV + yellow) in the area is *P. mariae,* which is easily distinguished by the absence of soralia and the presence of norstictic acid.

Pertusaria neolecanina Lumbsch & Nash, Bryologist 102: 229 (1999).

Illustration: Lumbsch et al. (1999), p. 224.

Thallus: verrucose-areolate to rimose-areolate, with thin to moderately thick verrucae; margins: entire, unzoned; **upper surface:** yellowish gray to yellowish white, smooth, dull to shiny, epruinose; lacking soredia or isidia; **fertile verrucae:** concolorous with thallus, pertusariate, flat-topped, numerous, *c.* 0.4-1.0 mm in diam.; ostioles: 1-4 (-6) per verruca, slightly sunken, grouped in a central depression and fusing to form a pseudolecanorate discs, *c.* 0.5 mm wide; **Apothecia:** 1-2 per verruca, up to 0.5 mm in diam.; disc: dark brown to gray brown, epruinose; epithecium: dark brown; hypothecium: hyaline; **asci:** cylindrical, 180-260 x 40-64 µm, 2-spored, uniseriate; **ascospores:** hyaline, ellipsoid, 86-118 x 32-58 µm; spore walls: *c.* 6-10 µm thick; apices: up to 14 µm thick, 2-layered; outer spore wall: *c.* 1-2 µm thick; inner spore wall: 5-9 µm thick; apices: up to 28 µm thick; **Pycnidia:** not seen; **Spot tests:** K+ yellow to red, C+ orange, KC-, P+ yellow to orange, UV+ orange-red*;* **Secondary metabolites:** norstictic and thiophaninic acids (both major), connorstictic acid (minor).

Substrate and ecology: in montane oak-pine forests on *Quercus* bark, associated species include *Lecanora caesiorubella* and *Ochrolechia* spp.; **World distribution:** endemic to North America; **Sonoran distribution:** known



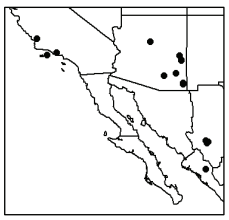
only from a few localities in Baja California Sur, Sinaloa and Sonora at 1600 and 2300 m.

Notes: *Pertusaria neolecanina* is characterized by its verruciform ascomata with blackish ostioles, two-spored asci and the presence of norstictic and thiophaninic acids. Chemically it agrees with *P. lecanina* which also has two-spored asci. This species, however, is readily distinguished by its disciform apothecia and the single-layered ascospores. Another similar species is *P. xanthodes*, that, however, differs in containing stictic acid instead of norstictic acid and not forming pseudolecanorate discs.

Pertusaria ophthalmiza (Nyl.) Nyl., Flora 48: 354 (1865).

Basionym: *Pertusaria velata* ssp. **P. multipuncta* var. *ophthalmiza* Nyl., Lich. Scand.: 180 (1861); Synonyms: see Dibben (1980); Illustrations: Dibben (1980), p. 145; Lumbsch et al. (1999), p. 225; Brodo et al. (2001), p. 530.

Thallus: continuous to fissured or fissured-areolate, with very thin or thin to moderately thick verrucae; margins: entire, often zoned; **upper surface:** ash gray to dark gray, smooth to tuberculate, shiny, epruinose; **soredia:** restricted to verrucae; **fertile verrucae:** sorediate, concolorous with thallus, lecanorate, numerous, sometimes fusing, *c.* 0.4-1.2 mm in diam.; **Apothecia:** 1 (-4) per verruca; disc: blackish brown, level to sunken, whitish pruinose, later totally sorediate; epithecium: dark brown to black, K-; hypothecium: yellowish; **asci:** clavate to cylindrical, 110-240 x 40-80 µm, 1-spored; **ascospores:** hyaline, ellipsoid to cylindrical, 85-190 x 25-65 µm; spore wall: *c.* 2-12 µm thick, 1-layered; **Pycnidia** immersed; **conidia:** bacilliform, 4-7 x 0.5-1.0 µm; **Spot tests:** K-, C-, KC-, P-, UV-; **Secondary metabolites:** no phenolic substances detectable.



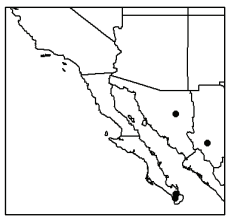
Substrate and ecology: on bark of numerous phorophytes, including *Abies*, *Alnus*, *Juniperus*, *Pinus*, *Pseudotsuga*, and *Quercus*, but also occurs on dead wood; **World distribution:** circumboreal; **Sonoran distribution:** coastal California and mountainous areas of Arizona, Chihuahua and Sinaloa at 2000 to 3000 m.

Notes: *Pertusaria ophthalmiza* is characterized by a gray thallus with lecanorate verrucae with a crenulate margin, a white pruinose disc which soon becomes sorediate, single-spored asci and the absence of phenolic compounds. It is hardly confused with any other *Pertusaria* species in southwestern North America.

Pertusaria pseudocorallina (Lilj.) Arnold, Verh. K. K. Zool.-Bot. Ges. Wien 37: 84 (1887).

Basionym: *Lichen pseudocorallinus* Lilj., Liljeblads Sv. Flora, ed.1: 328 (1792); Synonym: *Pertusaria arsenei* de Lesd., and see Erichsen (1936); Illustrations**:** Lumbsch et al. (1999), p. 225; Riefner (1990), p. 33.

Thallus: areolate to rimose-areolate, with thin to moderately thick verrucae; margins: entire, often zoned; **upper surface:** gray to pale gray, smooth, dull, epruinose; lacking soredia; **isidia:** granular to papillate, 0.12-0.24 mm diam., 0.73-1.2 mm tall, with browned tips, numerous, scattered; **fertile verrucae:** creamish, pertusariate, globose to hemispherical, smooth, sessile, numerous, scattered to crowded, 0.7-1.3 mm diam.; ostioles: 1-8 per verruca, hyaline, rarely dark, 0.02-0.1 (-0.2) mm diam.; **Apothecia:** 1-2 per verruca, fruit center hyaline to pale brown; epithecium: brown; hypothecium: hyaline; **asci:** cylindrical to clavate, *c.* 260 x 50-85 µm, 2-spored; **ascospores:** uniseriate, hyaline, ellipsoid, 90-130 x 42-61 µm, 2-layered; spore wall: 2-layered; outer spore wall: 3.0-7.0 µm thick, smooth; inner spore wall: generally multilayered, 8.5-10.5 µm thick; **Pycnidia:** not seen; **Spot tests:** K+ yellow to red, C-, KC-, P+ yellow to orange, UV-; **Secondary metabolites:** norstictic acid (major), connorstictic and subnorstictic acids (both minor).



Substrate and ecology: siliceous rocks, such as basalt or schist, at 900-2100 m; **World distribution:** western North America and western Europe and the Canary Islands disjunct; common in temperate and Mediterranean Europe, restricted to

the southwestern part in North America; **Sonoran distribution:** mountainous areas of Chihuahua, Sonora, and Baja California Sur.

Notes: *Pertusaria pseudocorallina* is characterized by the presence of verrucose to papillate isidia with darkened tips which leave crater-like hollows on the thallus when broken off. The thallus contains norstictic acid. While most specimens, if not all, in Europe are sterile (cf. Erichsen 1936), the North American material is usually richly fertile. The verrucae are pertusariate and the asci contain two ellipsoid ascospores. No other *Pertusaria* species in the area has isidia and it is therefore easily recognized. Other *Pertusaria* taxa with isidia in North America include species with disciform apothecia, such as *P. bryontha* (Ach.) Nyl. or *P. oculata* (Dicks) Th. Fr., which are hardly confused with *P. pseudocorallina*, since these are more or less arctic-alpine species occurring on soil or mosses. The only other *Pertusaria* species with poriform ascomata and isidia in North America is *P. globularis* (Ach.) Tuck., but this taxon is easily separated by sorediate isidia and the presence of 2'-*O*-methylperlatolic acid and 4,5-dichlorolichexanthone.

Pertusaria pustulata (Ach.) Duby, Bot. Gall. 2 (2): 673 (1830).

Basionym: *Porina pustulata* Ach., Lich. Univ.: 309 (1810); Synonyms: see Dibben (1980), Erichsen (1936) and Oshio (1968); Illustrations: Dibben (1980), p. 147; Wirth (1995), p. 771.

Thallus: continuous to finely fissured or fissured-areolate, with very thin to thin verrucae; margins: entire, unzoned; **upper surface:** yellow-gray to green-gray, smooth to finely tuberculate, shiny, seldom dull, epruinose; lacking soredia or isidia; **fertile verrucae:** concolorous with thallus, ampliariate or erect, numerous, *c.* 0.3-1.4 mm in diam.; ostioles: 1 or 2-8 per verruca, level, sunken or papillate, often fusing in a central depression to form a pseudolecanorate disc; **Apothecia:** 1-5 per verruca; disc: 0.4-0.8 mm wide, blackish brown, epruinose; epithecium: dark brown to black, K; hypothecium: hyaline; **asci:** cylindrical, 160-320 x 35-60 µm, 2-spored (seldom 1- or 3-spored); **ascospores:** hyaline, ellipsoid to cylindrical, 45-160 x 26-48 µm; spore wall: 2-layered; outer spore wall *c.* 1-5 µm thick; inner spore wall: 2-8 µm thick, smooth; apices: up to 20 µm thick; **Pycnidia:** immersed; **conidia:** bacilliform, 9-16 x 1-1.5 µm; **Spot tests:** K+ yellow, C+ orange, KC-, P+ yellow to orange, UV+ orange-red; **Secondary metabolites:** 2-chloro-6-*O*-methylnorlichexanthone and stictic acid (both major), 4-chloro-6-*O*-methylnorlichexanthone, constictic, cryptostictic, hypostictic, menegazziaic, thiophaninic acids (all minor).

Substrate and ecology: A temperate corticolous species; **World distribution:** *Pertusaria pustulata* is a cosmopolitan corticolous lichen; **Sonoran distribution:** only known from southern California.

Notes: This species is characterized by a greenish to yellowish thallus, ascomata with ostiola which may dilate and fuse to form a small pseudolecanorate disc, a K- epithecium, 2-spored asci and the presence of stictic acid and 2-chloro-6-*O*-methylnorlichexanthone. A full discussion of this species is found in Dibben (1980) and Archer and Messuti (1997).

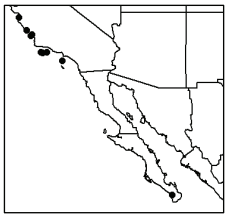
Pertusaria rubefacta Erichsen, Rep. Spec. Nov. 35: 387 (1934).

Synonyms: see Dibben (1980); Illustrations: Lumbsch et al. (1999), p. 225; Dibben (1980), p. 148.

Thallus: continuous to fissured, with thin to moderately thick verrucae; margins: entire, unzoned; **upper surface:** yellow-gray to greenish yellow, smooth, tuberculate to rugose-plicate, shiny or dull, epruinose; lacking soredia or isidia; **fertile verrucae:** concolorous with thallus, pertusariate to frequently falsely lecanorate, numerous and crowded, often fused (2-5) in mutually deformed groups, *c.* 0.4-2.6 mm in diam.; ostioles: 1 or 2-8 per verruca, level to mostly sunken, soon dilating to form a pseudolecanorate disc; **Apothecia:** 1-5 per verruca; disc: black, grayish pruinose or epruinose; epithecium: dark brown to black-brown, K+ strongly violet; hypothecium: hyaline or yellowish; **asci:** clavate, 260-420 x 50-90 µm, (6-) 8-spored; **ascospores:** hyaline, oval to ellipsoid, 55-110 x 30-55 µm; spore wall: 2-layered; outer spore wall: *c.* 2-4 µm thick; inner spore wall: 2-12 µm thick, smooth;

apices: up to 25 µm thick; **Pycnidia:** not seen; **Spot tests:** K+ yellow to red, C+ orange, KC-, P+ yellow to orange, UV+ orange-red; **Secondary metabolites:** norstictic and thiophaninic acids (both major), connorstictic acid, 2-chloro-6-*O*-methylnorlichexanthone, and 4-chloro-6-*O*-methylnorlichexanthone, and gyrophoric acid (all minor).

Substrate and ecology: on bark of deciduous trees, mostly *Quercus*; **World distribution:** only known from the western Hemisphere and shows a disjunct distribution, occurring both in the east and southwest part of North America; **Sonoran distribution:** coastal Califorina at 150-400 m and southern Baja California Sur.

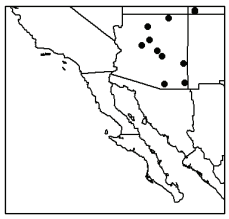


Notes: This species is characterized by a yellowish thallus, ascomata with sunken ostiola which soon dilate and fuse to form a pseudolecanorate disc, a K+ violet epithecium, 8-spored asci and the presence of norstictic and thiophaninic acids. As discussed above, the species is very similar to *P. hymenea* and best distinguished by its different chemistry.

Pertusaria saximontana Wetmore, Publ. Mus. Mich. State Univ. Biol. ser. 3: 369 (1968).

Illustrations: Dibben (1980), p. 148; Lumbsch et al. (1999), p. 225.

Thallus: continuous to fissured or fissured-areolate, with moderately thick verrucae; margins: entire, unzoned; **upper surface:** ash gray to greenish gray, smooth or rugose-plicate, shiny, epruinose; lacking soredia or isidia; **fertile verrucae:** concolorous with thallus, lecanorate, numerous, often fused, c. 0.4-1.2 mm in diam.; **Apothecia:** 1 (-5) per verruca; disc: blackish brown, well sunken, epruinose or grayish pruinose, margins crenulate; epithecium: dark brown, K+; hypothecium: hyaline; **asci:** clavate or cylindrical, 150-250 x 45-70 µm, (1-) 2-spored; **ascospores:** hyaline, oval to ellipsoid, 50-140 x 26-58 µm; spore wall: *c.* 4-14 µm thick, smooth; apices: up to 18 µm thick, 1-layered; **Pycnidia:** not seen; **Spot tests:** K-, C-, KC-, P-, UV-; **Secondary metabolites:** 2-*O*-methylconfluentic acid (major), di-*O*-methylolivetoride, planaic acid and traces of unknowns (all minor).



Substrate and ecology: on conifers (e.g. *Juniperus*) and more common on wood; **World distribution:** endemic to North America, particularly at mid-elevations in the Rocky Mountain region; **Sonoran distribution:** mountainous areas of Arizona at 1700-2100 m.

Notes: *Pertusaria saximontana* is characterized by a shiny gray to gray-brown thallus, numerous disciform apothecia with blackish, epruinose discs, a K+ violet epithecium, 2-spored asci, and the presence of 2-*O*-methylconfluentic acid. It is is a very characteristic species and hardly confused with any other *Pertusaria* species occurring in southwestern North America.

Pertusaria sommerfeltii (Flörke) Fr., Lich. Eur. Ref.: 423 (1831).

Basionym: *Endocarpon sommerfeltii* Flörke ex Sommerf., Suppl. Fl. Lapp.: 134 (1826); Synonyms: see Dibben (1980) and Erichsen (1936); Illustrations: Dibben (1980), p. 149; Lumbsch et al. (1999), p. 226.

Thallus: continuous to weakly fissured, with thin to very thin verrucae; margins: entire, unzoned; **upper surface:** ash gray to greenish or yellowish gray, smooth to finely tuberculate, shiny or dull, epruinose or slightly pruinose; lacking soredia or isidia; **fertile verrucae:** concolorous with thallus, ampliariate or pertusariate, few and well dispersed, *c.* 0.2-1.2 mm in diam.; ostioles: 1-5 per verruca, dark brown; **Apothecia:** 1-3 (-5) per verruca; epithecium: dark brown to yellow-brown, K+ strongly violet; hypothecium: yellowish; **asci:** cylindrical, 140-240 x 18-48 µm, (6-) 8-spored; **ascospores:** hyaline, oval to ellipsoid, 18-46 x 10-32 µm; spore wall: 2-layered; outer spore wall: *c.* 1-3 µm thick; inner spore wall: 1-4 µm thick, smooth; apices: up to 8 µm thick; **Pycnidia:** not seen; **Spot tests:** K- or + yellow, KC+ yellow, C-, P- or yellow to orange, UV- or UV+ weakly yellow; **Secondary metabolites:** 4,5-dichloronorlichexanthone and stictic

acid (both major) constictic acid and traces of unknowns (all minor).

Substrate and ecology: on bark of *Abies lasiocarpa*; **World distribution:** circumboreal in the Northern Hemisphere; **Sonoran distribution:** mountainous areas in eastern Arizona at an elevation of 2600-3200 m altitude.

Notes: This species is easily recognized by a thin, epiphloedal or hypophloedal, grayish thallus, porifom ascomata, a K+ violet reaction of the epithecium, 8-spored asci and the presence of stictic acid and 4,5-dichlorolichexanthone. This species is easily separated from most other *Pertusaria* species, except *P. alpina* Hepp *ex* Ahles or *P. stenhammarii.* The distinction from the latter is discussed below. *Pertusaria alpina* is distinguished from *P. sommerfeltii* in having a K- epithecium and larger ascospores. *Megaspora verrucosa* is superficially similar to *P. sommerfeltii,* which, however, is easily distinguished in lacking secondary metabolites, a K- epithecium, and a different ascus type.

Pertusaria stenhammarii Hellb., Öfvers. Förh. Kongl. Sv. Vet.-Akad. 22: 463 (1866).

Illustrations: Dibben (1980), p. 149; Lumbsch et al. (1999), p. 226.

Thallus: continuous to weakly fissured, with thin to very thin verrucae; margins: entire, unzoned; **upper surface:** ash gray to greenish gray, smooth, shiny, epruinose; lacking soredia or isidia; **fertile verrucae:** darker than thallus, lecanorate, numerous, *c.* 0.2-1.2 mm in diam.; **Apothecia:** 1 (-2) per verruca; disc: black, sunken, grayish pruinose; epithecium: yellowish brown to dark brown, K+ strongly violet; hypothecium: yellowish; **asci:** clavate, 120-250 x 40-70 µm, (-1) 2 (-3)-spored; **ascospores:** hyaline, ellipsoid to fusiform, 60-120 x 30-65 µm, K-; spore wall: *c.* 2-16 µm thick, smooth, apices up to 30 µm thick, 1-layered; **Pycnidia:** not seen; **Spot tests:** K-, C-, KC-, P-, UV-; **Secondary metabolites:** no phenolic substances detectable by HPLC.

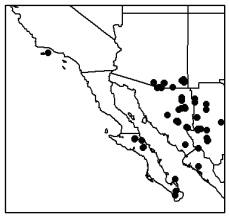
Substrate and ecology: *Pertusaria stenhammarii* grows on bark of high elevation conifers; **World distribution:** circumboreal in the Northern Hemisphere; **Sonoran distribution:** mountainous areas of Arizona.

Notes: This 2-spored species is characterized by a hypophloedal, grayish thallus, disciform apothecia, a K+ violet epithecium, and the lack of lichen substances. It might be confused with *P. sommerfeltii* but this species differs in having poriform ascomata and the presence of stictic acid and 4,5-dichlorolichexanthone.

Pertusaria tejocotensis de Lesd., Lich. Mexique: 18 (1918).

Synonym: *Pertusaria arizonica* Dibben, Millwaukee Publ. Mus., Publ. Biol. Geol. 5: 84 (1980); Illustrations: Dibben (1980), p. 139; Lumbsch et al. (1999), p. 226.

Thallus: fissured to areolate, with thin to moderately thick verrucae; margins: entire, unzoned; **upper surface:** yellow-green to sulfur-yellow, smooth or tuberculate, shiny or dull, epruinose; usually lacking soredia or isidia but some specimens with dispersed soredia; **fertile verrucae:** concolorous with thallus, pertusariate or erect, flat-topped, numerous, *c.* 0.5-1.7 mm in diam.; ostioles: 1-8 per verruca, level to sunken, blackish brown; **Apothecia:** 1-6 per verruca; epithecium: dark brown to black, K-; hypothecium: hyaline to yellowish; **asci:** clavate or cylindrical, 260-400 x 55-84 µm, mostly 4-spored. **Ascospores:** hyaline, oval to ellipsoid, 65-100 x 35-55 µm; spore wall: 2-layered; outer spore wall: *c.* 2-6 µm thick; inner spore wall: 5-15 µm thick, smooth, laminated; apices: up to 25 µm thick; **Pycnidia:** not seen; **Spot tests:** K- or + yellow, C+ yellow, KC+ orange, P-, UV+ orange-red; **Secondary metabolites:** confluentic, planaic, and thiophaninic acids (all major), hyperconfluentic and 2'-*O*-methylmicrophyllinic acids (both minor).



Substrate and ecology: on siliceous rocks, seldom on soil, and up to 3000 m throughout western North America; **World distribution:** endemic to North America from central Mexico to the Southwest; **Sonoran distribution:** widely distributed from coastal Cali-

fornia, but primarily in mountainous areas of Arizona, Chihuahua, Sonora, Sinaloa and Baja California Sur at 700 to 2000 m.

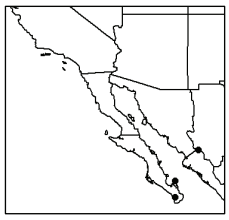
Notes: *Pertusaria tejocotensis* is a characteristic yellowish species with poriform apothecia, white pruinose ostioles that may or not dilate to form a pseudolecanorate disc 4-spored asci and thiophaninic acid and long side chain depsides. It is similar to *P. wulfenoides* which, however, can be distinguished by having larger verrucae and a different chemistry. It usually grows on bark, while *P. tejocotensis* grows seldomly on siliceous rocks. Another similar species is *P. flavicunda* which is easily distinguished by its disciform ascomata and the presence of stictic acid. *Pertusaria tejocotensis* is a uniform species. Some specimens differ in producing soralia instead or in addition to apothecia.

Pertusaria tetrathalamia (Fée) Nyl., Acta Soc. Sci. Fenn. 7: 448 (1863).

Basionym: *Trypethelium tetrahalamium* Fée, Essai Crypt.: 69 (1824); Synonyms: see Dibben (1980); Illustrations: Dibben (1980), p. 151; Lumbsch et al. (1999), p. 227.

Thallus: continuous to fissured, with thin to moderately thick verrucae; margins: entire, zoned or unzoned; **upper surface:** whitish gray to yellowish gray, smooth to tuberculate, shiny, epruinose; lacking soredia or isidia; **fertile verrucae:** concolorous with thallus, ampliariate to erect, few or numerous, *c.* 0.6-3.6 mm in diam.; ostioles 1-7 per verruca, hyaline, level to sunken; **Apothecia:** 1-5 per verruca; epithecium hyaline to black, K-; hypothecium: hyaline; **asci:** cylindrical, 250-460 x 35-60 µm, mostly 4-spored; **ascospores:** hyaline, ellipsoid to fusiform, 75-150 x 30-48 µm; spore wall: 2-layered; outer spore wall: *c.* 1-10 µm thick; inner spore wall: 2-12 µm thick, rough; apices: up to 20 µm thick; **Pycnidia:** not seen; **Spot tests:** K- or + yellow, C-, KC-, P+ yellow to orange, UV- or + weakly orange-pink; **Secondary metabolites:** 4,5-dichlorolichexanthone and stictic acid (both major), constictic, cryptostictic, menegazziaic and norstictic acids (all minor).

Substrate and ecology: on bark of *Quercus*; **World distribution:** North and South America; **Sonoran distribution:** mountainous areas of Baja California Sur and Sinaloa at 800-1900 m.



Notes: This taxon is characterized by a gray to yellowish gray thallus with poriform apothecia, mostly 4-spored asci, ascospores with a rough inner wall, and the presence of 4,5-dichlorolichexanthone and the stictic acid complex. A full discussion of the relationships of *P. tetrathalamia* is given by Dibben (1980). A similar species is *P. leioplaca* which is best distinguished by the smooth inner wall of the ascospores.

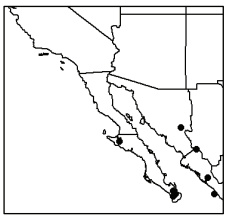
Pertusaria texana Müll. Arg., Flora 67: 399 (1884).

Synonyms: see Dibben (1980); Illustrations: Lumbsch et al. (1999), p. 226; Dibben (1980), p. 152; Brodo et al. (2001), p. 533.

Thallus: continuous to finely fissured, with thin to moderately thick verrucae; margins: entire, unzoned; **upper surface:** green-gray to yellow-gray or yellow-green, dull or shiny, smooth to tuberculate, shiny, epruinose; lacking soredia or isidia; **fertile verrucae:** concolorous with thallus, ampliariate to erect, conical to flat-topped, numerous, *c.* 0.5-2.0 mm in diam.; ostioles: 1-6 per verruca, hyaline to brownish, surrounded by a yellow border, level to papillate; **Apothecia:** 1-5 per verruca; epithecium: hyaline to black, K- or + weakly violet; hypothecium: yellowish to yellow-brown; **asci:** clavate, 210-400 x 32-65 µm, mostly 8-spored; **ascospores:** hyaline, ellipsoid to fusiform, 35-88 x 19-44 µm; spore wall: 2-layered; outer spore wall *c.* 1-5 µm thick; inner spore wall: 2-8 µm thick, smooth; apices; up to 24 µm thick; **Pycnidia:** not seen; **Spot tests:** K+ yellow, C+ orange, KC-, P+ yellow to orange, UV+ orange-red; **Secondary metabolites:** stictic and thiophaninic acids (both major), constictic acid, 2-chloro-6-*O*-methylnorlichexanthone, and 4-chloro-6-*O*-methylnorlichexanthone (all minor).

Substrate and ecology: on bark including *Acacia*, *Jatropha*, and *Quercus*; **World distribution:** North and

Central America; **Sonoran distribution:** coastal and mountainous areas of Baja California Sur, Sonora and Sinaloa at different elevations of 100-1200 m.

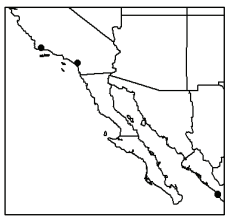


Notes: *Pertusaria texana* is characterized by a yellowish thallus with poriform apothecia, often warted verrucae and small ostioles with yellow papillae at the top, 8-spored asci, ascospores with smooth walls, and the production of thiophaninic and stictic acids. Morphologically it is difficult to separate the species from the largely sympatric *P. xanthodes* which shares the same chemosyndromes, but is distinguished in having hyaline ostioles, 2-spored asci and rough-walled ascospores.

Pertusaria velata (Turner) Nyl., Lich. Scand.: 179 (1861).

Basionym: *Parmelia velata* Turner, Trans. Linn. Soc. London 9: 143 (1808); Synonyms: *Pertusaria santamonicae* Dibben and see Archer and Messuti (1997); Illustrations: Dibben (1980), p. 153; Lumbsch et al. (1999), p. 227.

Thallus: fissured to areolate, with thin to moderately thick verrucae; margins: entire, unzoned; **upper surface:** whitish gray to yellowish gray, rugose-plicate, dull, pruinose; lacking soredia or isidia; **fertile verrucae:** concolorous with thallus, lecanorate, numerous, *c.* 0.2-1.0 mm in diam.; **Apothecia:** 1 (-4) per verruca; disc: pink, sunken, heavily whitish pruinose; epithecium: dark brown to black, K-; hypothecium yellowish; **asci:** clavate, 170-260 x 35-78 µm, 1-spored; **ascospores:** hyaline, fusiform to cylindrical, 130-210 x 28-64 µm; spore wall: *c.* 2-8 µm thick, smooth; apices: up to 30 µm thick, 1-layered; **Pycnidia:** not seen; **Spot tests:** K-, C+ red, KC-, P-, UV-; **Secondary metabolites:** lecanoric acid and lichexanthone (both major) and orsellinic acid (minor).



Substrate and ecology: on bark of *Quercus* species; **World distribution:** cosmopolitan; **Sonoran distribution**: coastal California and inland mountains of Mexico. The Californian material was collected at 200-400 m, while the Sinaloan specimen was collected at 2300 m altitude.

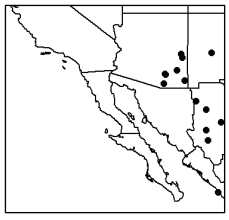
Notes: *Pertusaria velata* is characterized by disciform ascomata with pruinose to sorediate discs, single-spored asci, and the presence of lecanoric acid and lichexanthone (the latter is lacking in some specimens).

Pertusaria wulfenoides de Lesd., Ann. Crypt. Exot. 2: 239 (1929).

Synonyms: see Dibben (1980); Illustrations: Dibben (1980), p. 153; Lumbsch et al. (1999), p. 227.

Thallus: fissured to fissured-areolate, with thin to moderately thick verrucae; margins: entire, unzoned; **upper surface:** yellow-green to sulfur-yellow, smooth to rugose-plicate, dull, slightly pruinose; lacking soredia or isidia; **fertile verrucae:** concolorous with thallus, pertusariate to erect, flat-topped, few or numerous, grouped in a central depression, *c.* 0.6-2.8 mm in diam.; ostioles: 1-7 (-12) per verruca, dark, level to sunken, sometimes dilating and fusing to form a pseudolecanorate disc; **Apothecia:** 1-5 per verruca; epithecium: brown to black, K-; hypothecium: hyaline; **asci:** cylindrical, 280-460 x 50-78 µm, mostly 4-spored; **ascospores:** hyaline, ellipsoid to oval, 68-110 x 38-58 µm; spore wall: 2-layered; outer spore wall: *c.* 2-6 µm thick; inner spore: wall 6-18 µm thick, smooth; apices: up to 32 µm thick; **Pycnidia:** not seen; **Spot tests:** K+ yellow to red, C+ orange, KC-, P+ yellow to orange, UV+ orange-red; **Secondary metabolites:** norstictic and thiophaninic acids (both major), connorstictic acid, 2-chloro-6-*O*-methylnorlichexanthone, and 4-chloro-6-*O*-methylnorlichexanthone (all minor).

Substrate and ecology: on bark, including *Alnus*, *Juniperus*, *Pinus*, *Populus*, *Pseudotsuga*, or *Quercus*, and was also collected on siliceous rocks; **World distribution:** endemic to SW North America; **Sonoran distribution:** widely distributed in mountainous areas at



2000-3100 m.

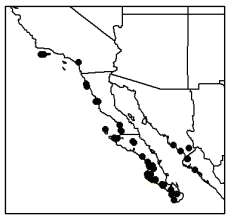
Notes: This taxon is characterized by its yellowish thallus, large verrucae with poriform ascomata with ostioles that dilate and fuse to form pseudolecanorate discs, 4-spored asci, and the presence of the norstictic and thiophaninic acids chemosyndromes. Similar species include *P. azulensis* and *P. tejocotensis* and the differences to these species are discussed above.

Pertusaria xanthodes Müll. Arg., Flora 67: 286 (1884).

Illustrations: Lumbsch et al. (1999), p. 227; Brodo et al. (2001), p. 535; Dibben (1980), p. 153..

Thallus: continuous to fissured or fissured-areolate, with thin to moderately thick; margins: entire, unzoned; **upper surface:** yellow-gray to yellowish green, smooth to tuberculate, shiny or dull, slightly pruinose; lacking soredia or isidia; **fertile verrucae:** concolorous with thallus, ampliariate to pertusariate, numerous, *c.* 0.4-1.6 mm in diam.; ostioles: 1-7 per verruca, hyaline or concolorous with thallus, level to sunken, rarely fusing to form a pseudolecanorate disc; **Apothecia:** 1-6 per verruca; epithecium: hyaline to brown, K-; hypothecium: hyaline; **asci:** cylindrical, 145-300 x 38-68 µm, mostly 2-spored; **ascospores:** hyaline, ellipsoid to cylindrical, 65-150 x 30-52 µm; spore wall: 2-layered; outer spore wall: *c.* 1-6 µm thick; inner spore wall: 2-10 µm thick, rough; apices: up to 28 µm thick; **Pycnidia:** not seen; **Spot tests:** K+ yellow, C+ orange, KC-, P+ yellow to orange, UV+ orange-red; **Secondary metabolites:** stictic and thiophaninic acids (both major), constictic acid, 2-chloro-6-*O*-methylnorlichexanthone, and 4-chloro-6-*O*-methylnorlichexanthone (all minor).

Substrate and ecology: *Pertusaria xanthodes* is a corticolous species occurring on several trees, such as *Beaucarnea*, *Fouquieria*, *Jatropha*, *Pinus*, *Pittosporum*, *Prosopis*, and *Quercus* at the coast or in coastal mountains; **World distribution:** North America and Bermuda; **Sonoran distribution:** coastal California, Baja California, Baja California Sur, Sonora and Sinaloa mainly at 0-400 m.



Notes: *Pertusaria xanthodes* is characterized by a yellowish thallus, poriform apothecia with hyaline ostioles that do not dilate, 2-spored asci, rough inner spore wall, and the production of stictic and thiophaninic acids. It is easily confused with *P. texana* and the differences are discussed above. Another similar species is *P. pustulata* and a full discussion of these two species is listed by Dibben (1980: 120). The most conspicuous characters to distinguish the two species are the ostioles (rarely fused in *P. xanthodes*, often fused in *P. pustulata*), the spore wall (rough in *P. xanthodes*, smooth in *P. pustulata*), and the chemistry (thiophaninic acid in *P. xanthodes*, 2-chloro-6-*O*-methylnorlichexanthone in *P. pustulata*).

PHYSCIA

by R. Moberg

Physcia (Schreb.) Michaux, Flora boreali-americana 2: 326 (1803).

Family: Physciaceae; Type: *Physcia tenella* (Scop.) DC; No. species: *c.* 70 world-wide; Selected lit.: Moberg (1977), Thomson (1963).

Life habit: lichenized; **Thallus:** foliose, often circular in outline, ± loosely adnate, lobate; **lobes:** discrete or overlapping, short to elongate mostly < 3 mm wide, tips with or without cilia; **upper surface:** whitish gray or bluish gray to gray, dull or somewhat shiny, sometimes maculate or white pruinose; with or without soredia or isidia; **upper cortex:** paraplectenchymatous; **medulla:** white; **photobiont:** primary one a trebouxoid alga, secondary photobiont absent; **lower cortex:** proso- or paraplectenchymatous (lumina < 2.5 µm wide or 4-7 µm wide, respectively); **lower surface:** white, pale gray, pale tan or occasionally pinkish, sparsely to densely rhizinate; rhizines simple or furcate; **Ascomata:** apothecial, lecanorine, sessile or shortly stipitate: disc: brown to black, sometimes pruinose; epithecium: pale brown; hymenium and hypothecium colorless; paraphyses: simple or forked above, apices clavate, pale brown with a dark brown cap; **asci:** cylindrical, 8-spored, *Lecanora*-type; **ascospores:** brown, 1-septate, *Physcia* to *Pachysporaria* type, usually 15-25 µm long; **Conidiomata:** pycnidial, immersed, walls colorless except for a dark region around the ostiole; **conidia:** simple, subcylindrical, colorless; **Secondary metabolites:** cortex always with atranorin, medulla with or without atranorin, zeorin or other triterpenes; **Geography:** world-wide, found on all continents, particularly common in temperate regions; **Substrate:** common on bark, wood and rocks; less common on soil and artificial substrates.

Note: Apart from the fact that most Physcias are substantially smaller than Heterodermias, a major difference is that the upper cortex of *Physcia* is always paraplectenchymatous whereas the upper cortex of *Heterodermia* is prosoplectenchymatous. In contrast, *Phaeophyscia* is similar in size to *Physcia*, but it never has atranorin in the upper cortex and hence reacts K-.

Key to species of ***Physcia*** from the Sonoran region:

1. With hairs on the upper surface and/or marginal cilia . 2
1. Without hairs on the upper surface or marginal cilia .. 4

2 Thallus without soralia, usually fertile ... ***P. villosula***
2. Thallus with soralia, mostly sterile 3

3. With hairs on the upper surface, mostly coastal .... ***P. tenellula***
3. Without hairs on the upper surface, mostly upper montane in continental areas ..... ***P. adscendens***

4. Thallus with soralia, often sterile 5
4. Thallus without soralia, usually fertile 19

5. Thallus with pustules often breaking up into granulate soredia that sometimes cover central parts .... ***P. clementei***
5. Thallus with soralia, often sterile 6

6. Lower surface black or very dark brown 7
6. Lower surface white or at most grayish brown 8

7. Soralia laminal, crateriform ..... ***P. erumpens***
7. Soralia marginal ..... ***P. sorediosa***

8. Medulla K–; zeorin absent 9
8. Medulla K+ yellow; zeorin present (note *P. nashii)* 14

9. Lower cortex paraplectenchymatous 10
9. Lower cortex prosoplectenchymatous 11

10. Lobes thin, less than 150 µm, upper surface usually dull, limited to more tropical areas ..... ***P. crispa***
10. Lobes thicker, upper surface usually shiny, cosmopolitan ..... ***P. tribacia***

11. Upper surface usually densely covered with crystals (calcium oxalate) ..... ***P. dimidiata***
11. Upper surface without crystals (but sometimes pruina) 12

12. Lobe tips rounded ..... ***P. dubia***
12. Lobe tips truncate 13

13. Thallus small, less than 1 cm diam., lobes convex, soralia terminal, lower cortex prosoplectenchymatous ..... ***P. nashii***
13. Thallus larger, lobes flat to concave, soralia marginal, granular, lower cortex paraplectenchymatous ..... ***P. neglecta***

14. Upper surface "frosted" ..... ***P. undulata***
14. Upper surface not "frosted" 15

15. Soralia in the lobe sinuses 16
15. Soralia not in lobe sinuses 17

16. Thallus white spotted, lobes long with rounded tips ..... ***P. rolfii***
16. Thallus not white spotted, lobes short with truncate tips ..... ***P. sinuosa***

17. With soralia on small lobules, lobes narrow with crenulate tips ..... ***P. pseudospeciosa***
17. Lobes with rounded tips, soralia usually laminal 18

18. Thallus with crateriform soralia ..... ***P. poncinsii***
18. Thallus with capitate soralia ..... ***P. caesia***

19. Lobes broad (*c.* 2 mm), lobe margin with a white rim . ..... ***P. tretiachii***
19. Lobes narrower (*c.* 1 mm), lobe margin without rim 20

20. Lower cortex paraplectenchymatous 21
20. Lower cortex prosplectenchymatous 23

21. Lower surface black ..... ***P. integrata***
21. Lower surface pale 22

22. Medulla K-, zeorin absent ..... ***P. halei***
22. Medulla K+ yellow, zeorin present ..... ***P. cinerea***

23. Upper surface usually densly covered with crystals (calcium oxalate) ..... ***P. biziana***
23. Upper surface without crystals (but sometimes pruina) 24

24. Medulla K-, zeorin absent 25
24. Medulla K+ yellow, zeorin present 26

25. Lobes sinuose, on rocks ..... ***P. convexella***
25. Lobes not sinuose, on trees ..... ***P. stellaris***

26. Lobes with rounded tips, maculate 27
26. Lobes with truncate tips, not maculate ..... ***P. alba***

27. On trees, lobes usually broader than 1 mm . ***P. aipolia***
27. On rocks, lobes usually less than 1 mm 28

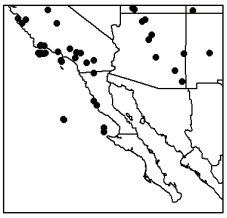
28. Lobes distinctly convex, tips not widening ..... ***P. convexa***
28. Lobes ± flat, tips widening ..... ***P. phaea***

The Species

Physcia adscendens (Fr.) H. Olivier, nom. cons., Flore analytique et dichotomique des lichens de l'Orne I: 79 (1882).

Illustrations: Moberg (1977), p. 50; Thomson (1984), p. 352; Wirth (1995), p. 727; Brodo et al. (2001), p. 550.

Thallus: foliose, up to 2 cm in diam., mostly irregular with confluent thalli; **lobes:** up to 2 mm broad, usually around 1 mm, about the same in length but sometimes much longer, ciliate; cilia: marginal, pale to black, always black in the outer part; **upper surface:** gray to dark gray; lobe tips mostly much darker, sometimes with a white pruina, sorediate; **soredia:** in helmet-shaped soralia, usually abundant, starting as holes just beneth the lobe tips; **upper cortex:** paraplectenchymatous; **medulla:** white; **lower cortex:** prosoplechymatous; **lower surface:** white to grayish; rhizines: white to black; **Apothecia:** not seen in Sonoran material; elsewhere up to 2 mm diam., stipItate; disc: sometimes thinly pruinose; **ascospores:** brown, 1-septate, *Physcia*-type, 10-23 x 7-10 µm; **Pycnidia:** sparse, immersed; **conidia:** subcylindrical, 4-6 x 1 µm; **Spot tests:** upper cortex K+ yellow, C-, KC-, P+ yellow; medulla K–, C-, KC-, P-; **Secondary metabolite:** atranorin in upper cortex.



Substrate and ecology: growing on trees and branches in fairly open situations, probably introduced by man; **World distribution:** widely distributed in temperate and boreal areas in all continents but more common at higher latitude up to 65°N and 60°S; **Sonoran distribu-**

tion: relatively frequent in upper montane forests of Arizona and coastal southern California and Baja California.

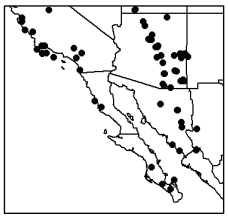
Notes: The species is easy to recognize by the cilia on the lobe margin and the helmet shaped soralia. In the Sonoran Region *P. adscendens* might be difficult to separate from some phenotypes of *Heterodermia erinacea*, and it is then necessary to study the upper cortex, which is prosoplectenchymatous in the latter. *Physcia adscendens* differs from *P. tenellula* in several aspects. The latter is much smaller and has a different type of soralia and hairs on the upper surface.

Physcia aipolia (Humb.) Fürnrohr, Flora Ratisbonensis. Naturhistorische Topographie von Regensburg II: 249 (1839).

Basionym: *Lichen aipolius* Ehrh. *ex* Humb., Fl. Fribergensis: 19 (1793); Synonyms: see Moberg (1977); Illustrations: Moberg. (1977), p. 60; Thomson (1984), p. 353; Wirth (1995), p. 728; Brodo et al. (2001), p. 550.

Thallus: orbicular to irregular, to 5 cm diam.; **lobes:** up to 2 mm broad, flat to convex, eciliate; **upper surface:** whitish gray to dark gray, rarely brownish gray, usually distinctly white-maculate, sometimes weakly white-pruinose; without soredia or isidia; **medulla:** white; **lower cortex:** prosoplectenchymatous with the lowermost part gradually forming rounded, isodiametric cells; **lower surface:** white to dark lead colored; **Apothecia:** usually abundant, up to 2 mm diam.; disc: often white-pruinose; **ascospores:** brown, 1-septate, vary from *Physcia*- to *Pachysporaria*-type, (19-) 21-25 (-28) x 9-11 (-13) µm; **Pycnidia:** common, immersed; **conidia:** subcylindrical, 4-6 x 1 µm **Spot tests:** cortex and medulla K+ yellow, C-, KC-, P+ yellow; **Secondary metabolites:** upper cortex with atranorin; medulla with atranorin, zeorin and rarely other triterpenes.

Substrate and ecology: growing on trees in fairly open situations; **World distribution:** widely distributed within arctic, boreal and temperate areas of North American and Eurasia, also known from South America; **Sonoran distribution:** widely distributed from sea level to upper elevation montane sites from Arizona, southern California, Baja California, Baja California Sur, Chihuahua, Sonora and Sinaloa.



Notes: Some material seen from the Sonoran Region is a somewhat different from ”typical” *P. aipolia*, but the difference is not so obvious that a new species is described. The whole pattern of variation in North America has to be studied further.

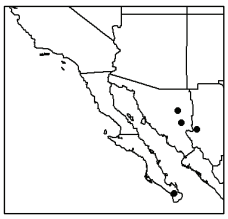
Physcia alba (Fée) Müll. Arg., Rev. Mycol. 9: 136 (1887).

Basionym: *Parmelia alba* Fée, Essai sur les cryptogames des écorces exotiques officinales: 125 (1825); Illustration: Moberg, (1990b), p. 323.

Thallus: orbicular to irregular, sometimes confluent with other thalli, up to 5 cm diam, ± loosely adnate, usually less than 150 µm thick and fragile; **lobes:** radiating, flat to almost concave, truncate and sinuose, up to 1.5 mm wide but usually narrower, distinctly separate or sometimes overlapping, tips often ascending, eciliate; **upper surface:** whitish gray to cream-colored, without pruina, occasionally with a weak maculation; soredia and isidia absent; **upper cortex:** paraplectenchymatous; **medulla:** white; **lower cortex:** prosoplectenchymatous, in lower parts turning ± paraplectenchymatous and thick-walled, usually well delimited from the medulla; **lower surface:** white to pale graphite gray; rhizines: concolorous with the lower surface; **Apothecia:** abundant, variable in size, up to 2 mm diam. but usually around 1 mm; margin: ± thick (*c.* 0.2 mm) and weakly crenulate; disc: brown to black, rarely pruinose; **ascospores:** brown, 1-septate, of *Pachysporaria*-type, (19.5-) 22-27.5 (-32) x (8.5-) 10-13 (-16) µm; **Pycnidia:** sparse to common; **conidia:** subcylindrical, 4-6 x 1 µm; **Spot tests:** cortex and medulla K+ yellow, C-, KC-, P+ yellow; **Secondary metabolites:** upper cortex with atranorin; medulla with atranorin, zeorin, occasionally leucotylin and/or other triterpenes.

Substrate and ecology: mainly corticolous growing in open forests on solitary trees, and also found on rocks in ±

exposed sites; **World distribution:** scattered localities in northern South America and SW North America; **Sonoran distribution:** scattered collections from southern Baja California Sur, Sonora and Chihuahua.



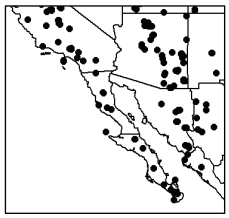
Notes: This species is predominately tropical and is recognized by its narrow ± truncate lobes, the abundant apothecia with thick margins and the pale lower surface. It may be misidentified as *P. stellaris* that is similar in size and also has abundant apothecia. However, they differ in lobe shape, apothecial characters and chemistry.

Physcia biziana (A. Massal.) Zahlbr., Österr. bot. Zeitschr. 51: 348 (1901).

Basionym: *Squamaria biziana* A. Massal., Miscellaniea lichenologica: 5 (1856); Illustrations: Hale (1979), p. 116; Moberg (1986), p. 853; Brodo et al. (2001), p. 552.

Thallus: orbicular to irregular, up to 3 cm diam. with ± imbricate lobes; **lobes:** up to 3 mm wide but usually narrower, distinctly widening and slightly ascending at tips, eciliate; **upper surface:** brownish gray to gray or cream-colored, usually with a dense pruina (crystals); soredia and isidia absent; **upper cortex:** paraplectenchymatous; **medulla:** white; **lower cortex:** prosoplectenchymatous, lowermost part sometimes with rounded cells, ± paraplechtenchymatous; **lower surface:** white to brownish, with white to dark gray, scattered rhizines; **Apothecia:** numerous, up to 2.5 mm across, usually smaller; margin: often with crenulate margin when young; disc: brown to black, mostly covered with a white pruina; **ascospores:** brown, 1-septate, of either *Physcia*-, *Pachysporaria*-type or intermediate, (13-) 15-18.5 (-20.5) x 6.5-8.5 (-11) µm; **Pycnidia:** numerous, immersed; conidia: subcylindrical to cylindrical, 4-6 x 1 µm; **Spot tests:** upper cortex K+ yellow, C-, KC-, P+ yellow; medulla K– (sometimes faintly + yellowish), C-, KC-, P-; **Secondary metabolite:** upper cortex with atranorin.

Substrate and ecology: growing on tree trunks or branches in open situations and on exposed rocks; **World distribution:** known from Africa, North and South America and Europe; **Sonoran distribution:** one of the most common Physcias on bark in the Sonoran region, particularly in montane areas of Arizona, southern California, Baja California, Baja California Sur, Chihuahua, Sonora and Sinaloa.



Notes: *Physcia biziana* is easily recognized by the dense pruina and the K negative medulla. However, fairly often the pruina is sparse and in such cases the rounded lobes with a brownish tinge may be of help in separating the species from *P. stellaris*. The spores from this material are somewhat smaller than reported for South America, but this might be explained by a general tendency for *Physcia* species to have bigger spores in more subtropical areas compared to temperate regions. *P. biziana* is evidently the fertile counterpart of *P. dimidiata*.

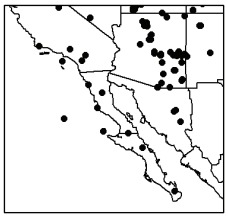
Physcia caesia (Hoffm.) Fürnr., Flora Ratisbonensis. Naturhistorische Topographie von Regensburg II: 250 (1839).

Basionym: *Lichen caesius* Hoffm., Enumeratio Lichenum: 65 (1784); Synonyms: *Physcia wainioi* Räsänen and see Moberg (1977); Illustrations: Thomson (1984), p. 354; Wirth (1995), p. 731; Brodo et al. (2001), p. 553.

Thallus: orbicular to irregular, to 5 cm diam.; **lobes:** up to 3 mm, usually narrower, sometimes overlapping, sometimes distinctly separated, eciliate; **upper surface:** gray to dark gray with white maculae; **soredia:** in marginal to ± laminal, often capitate soralia; **upper cortex:** paraplectenchymatous; **medulla:** white; **lower cortex:** prosoplectenchymatous with the lowermost part gradually forming rounded, isodiametric cells; **lower surface:** white to dark gray with dark, sometimes with black rhizines; **Apothecia:** not seen in the Sonoran Desert material, elsewhere common to rare, sessile, up to 1.5 mm wide, margin: entire or crenulate; disc: brown-black, sometimes pruinose; hymenium: hyaline below, brownish above; hypothecium: hyaline or yellowish; paraphyses: simple or rarely branched, capitate; **ascospores:** brown, 1-septate, *Physcia*-

type, 17-24 x 7-11 µm; **Pycnidia:** not seen in the Sonoran Desert material, elsewhere rare; **conidia:** subcylindrical, 4-6 x 1 µm; **Spot tests:** upper cortex and medulla K+ yellow, C-, KC-, P+ yellow; **Secondary metabolites:** upper cortex with atranorin; medulla with atranorin, zeorin and sometimes unidentified triterpenes.

Substrate and ecology: mainly growing on acid rocks in ± open situations, but it is also known as corticolous (not in the Sonoran Desert); **World distribution:** widely distributed within the arctic, boreal and temperate vegetation zones; **Sonoran distribution:** one of the most common Physcias on rocks at coastal to high elevations in the Sonoran region from Arizona, southern California, Baja California, Baja California Sur and Sonora.



Notes: *Physcia caesia* may sometimes be difficult to distinguish from *P. poncinsii* but the characteristic crateriform soralia and the distinctly convex lobes of the latter make them easy to separate.

Physcia cinerea Moberg, Nord. J. Bot. 10: 325 (1990).

Illustration: Moberg (1990b), p. 325.

Thallus: narrow-lobed, orbicular to irregular, up to 3 cm diam., firmly adnate; **lobes:** up to 1 mm wide but rarely exceeding 0.5 mm, convex and adnate the tips, usually distinctly discrete and deeply divided, eciliate; **upper surface:** gray to very dark gray, not or weakly white spotted; soredia and isidia absent **upper cortex:** paraplectenchymatous; **medulla:** white; **lower cortex:** paraplectechymatous with thick-walled, partly irregular cells, the cortex distinctly delimited from the medulla; **lower surface:** white to brownish with concolorous or darker, ± abundant rhizines; **Apothecia:** usually abundant, up to 1.5 mm diam.; margins crenulate; disc: dark brown to black, without pruina; **ascospores:** brown, 1-septate, *Pachysporaria*-type (15-) 19-24 (-28) x (7.5-) 9.5-12.5 (-14) µm; **Pycnidia:** ± abundant, immersed, rounded, sometimes confluent and forming aggregates; **conidia:** subcylindrical, 4-6 x 1 µm; **Spot tests:** upper cortex and medulla K+ yellow, C-, KC-, P+ yellow; **Secondary metabolites:** upper cortex with atranorin; medulla with atranorin, zeorin and triterpenes.

Substrate and ecology: growing on ± exposed rocks or on mosses on rocks; **World distribution:** northern South America and Mexico; **Sonoran distribution:** known only from two localities, Baja California Sur, Sierra de la Laguna at 1800 m and in Sonora W of Yecora at 1700 m.

Notes: This species is recognized by its narrow, distinctly discrete and deeply incised lobes and the abundant, small, crenulate apothecia. It is similar to *P. alba*, which has ± flat, broader lobes, and mainly grows on bark. The material from Baja California has somewhat smaller spores than the South American material, but this is regarded as being a result of a more northerly site.

Physcia clementei (Sm.) Lynge, in Rabenhorst, Kryptogamen-Flora, ed 2, 9,6,1: 93 (1935).

Basionym: *Lichen clementi* Sm. in Smith & Sowerby, English Botany vol. 25, tab. 1779 (1807); Synonym: *Parmelia clementi* Turner.; Illustration: Fig. 71 below.

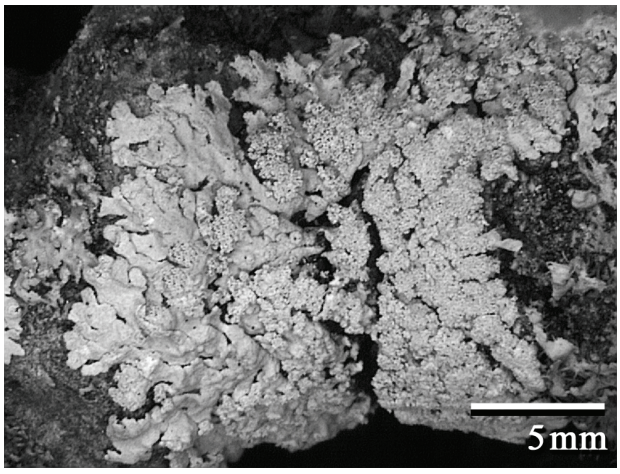


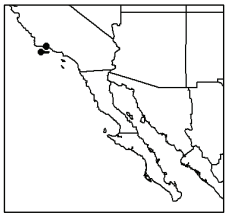
Fig. 71. *Physcia clementei*, photo by R. Moberg.

Type: Tab 1779 in Smith & Sowerby, English Botany vol. 25 (lectotype, here selected). – **Epitype:** France, Fin-

istere, Bretagne, Brest, la gare de la Ligne du Conquet, 12.IV.1931 Gunnar Degelius (UPS).

Thallus: foliose, orbicular to irregular, fragile, up to 2 cm diam, ± firmly adnate, central parts often covered by pustules dissolved into granulate soredia; **lobes:** flat to concave, up to 0.5 mm broad, rarely broader, sparsely divided; tips: truncate or crenulate, occasionally ascending; **upper surface:** whitish, rarely dark gray, usually dull; **pustules** or **isidia:** laminal, often developing into granular soralia or craters that may fuse and cover the whole thallus; **upper cortex:** paraplectenchymatous, **medulla:** white; **lower cortex:** ± prosoplectenchymatous, pale to brownish (inner parts); **lower surface:** white at the tips, darker in inner parts; rhizines: few, concolorous with the underside; **Apothecia:** frequent, up to 2 mm diam., margin often crenulate; **ascospores:** brown, 1-septate, *Pachysporaria* type, (16-) 18.5-22 (-23.5) x (7.5-) 8.5-10 (-11) µm; **Pycnidia:** not seen; **Spot tests:** upper cortex and medulla K+ yellow, C-, KC-, P+ yellow; **Secondary metabolites:** upper cortex with atranorin; medulla with atranorin, lecotylin and traces of other triterpenoids visible in TLC.

Substrate and ecology: growing mainly on trees but also on rocks in open sites; **World distribution:** known from scattered localities in central and southern Europe and from southern California; **Sonoran distribution:** known only from the Channel Islands of southern California and the adjacent mainland.

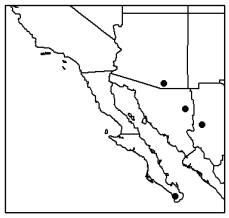


Physcia convexa Müll. Arg., Revue Mycol. 10: 57 (1888).

Illustration: Moberg (1990b), p. 327.

Thallus: orbicular to irregular, firmly adnate, sometimes imbricate, up to 3 cm across; **lobes:** convex to plane, up to 1 mm broad, rarely overlapping, ± truncate, eciliate; **upper surface:** whitish gray to gray, shiny, white maculate, lobe tips often brownish, particularly old herbarium material; **upper cortex:** paraplectenshymatous, **medulla:** white; **lower cortex:** paraplectenchymatous, sometimes indistinctly but the lowermost cells always short and thick-walled; **lower surface:** white to brownish or pinkish yellow, shiny, with few concolorous rhizines; **Apothecia:** ± abundant, up to 2 mm diam.; margin thick; disc: black; ascospores: brown, 1-septate, *Pachysporaria* to *Physcia* type, (15-) 16-19 (-21) x (8-) 9-11 (-14) µm; **Pycnidia:** common, immersed; **conidia:** subcylindrical, 4-6 x 1 µm; **Spot tests:** cortex and medulla K+ yellow, C-, KC-, P+ yellow, Secondary metabolites: cortex with atranorin; medulla with atranorin, zeorin and some unidentified triterpenes.

Substrate and ecology: growing on rocks in exposed habitats, including the seashore and arid habitats; **World distribution:** known from Brazil, Paraguay, Peru and Uruguay; **Sonoran distribution:** intermediate elevations in southern Arizona, Chihuahua, Sonora and Baja California Sur.



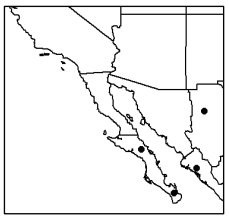
Notes: *Physcia convexa* is easily recognized by the convex, usually well separated lobes with truncate tips, the presence of apothecia and the pale, often pinkish underside. It is similar to *P. phaea* but the latter has less convex lobes with crenulate and widening tips and different lower cortex. Small specimens of *P. convexa* may be mistaken as *P. convexella* but are easily separated by the K- medulla in *P. convexella*. *P. cinerea* is more narrow lobed and has different upper surface and chemistry.

Physcia convexella Moberg, Nord. J. Bot. 10: 327 (1990).

Illustration: Moberg (1990b), p. 327.

Thallus: irregular to orbicular, up to 2 cm diam., often confluent with other thalli forming a larger aggregate; **lobes:** up to 1 mm wide, flat to convex, usually broadest and flattened at the tips, rarely longer than 5 mm, eciliate; **upper surface:** white to grayish, often with a darker zone near lobe tips, weakly maculate and usually shiny, sometimes with a white pruina; soredia and isidia absent; **up-**

per cortex: paraplectenchymatous; **medulla:** white; **lower cortex:** pale, prosoplectenchymatous; **lower surface:** white with a rose tinge; rhizines: concolorous, few and scattered; **Apothecia:** abundant, up to 2 mm; margins: with thick, crenulate; **ascospores:** brown, 1-septate, *Physcia* to *Pachysporaria* type, 15-18 x 7.5-8.5 µm; **Pycnidia:** common, immersed; **conidia:** subcylindrical, 4-6 x 1 µm; **Spot tests:** upper cortex K+ yellow, C-, KC-, P+ yellow; medulla K–, C-, KC-, P-; **Secondary metabolite:** upper cortex with atranorin.



Substrate and ecology: growing on open rocks; **World distribution:** known only from a limited area near Cuzco in southern Peru and SW North America; **Sonoran distribution:** known only from a few montane localities from Baja California Sur, Chihuahua, Sonora and Sinaloa.

Notes: The small size, the ± convex lobes, the presence of apothecia, the lack of soredia and the K– medulla are the main characters of *P. convexella*. It might be the fertile counterpart of *P. nashii.* The corticolous *P. stellaris* is keyed out with *P. convexella* as both have K– medulla. They are, however, in addition to different substrate preference, easily separated by their different lobe shape; truncate in *P. convexella* and rounded in *P. stellaris*.

Physcia crispa Nyl., Syn. Meth. 1 (2): 423 (1860).

Illustration: Moberg (1986), p. 854.

Thallus: irregular to orbicular, thin, rarely exceeding 150 µm thick, up to 3 cm across or larger because of confluent thalli; **lobes:** loosely adnate, up to 1 mm wide, rarely broader, about the same in length; lobe tips ascending and usually crenulate, with small protrusions along the margin becoming isidia-like and eventually forming soredia, eciliate; **upper surface:** gray to cream colored, rarely with a pruina, sorediate; **soredia:** in marginal soralia, well developed in inner parts, particularly at the lobe angles; **upper cortex:** paraplectenchymatous; **medulla:** white; **lower cortex:** paraplectenchymatous; **lower surface:** whitish with a few pale rhizines; **Apothecia:** sometimes present, up to 2 mm diam.; margins: with sorediate; disc: pale brown to brown, not pruinose; **ascospores:** brown, 1-septate, *Pachysporaria*-type, (18-) 20-25 (-27) x (8-) 9-11 (-13) µm; **Pycnidia:** rare; **Spot tests:** upper cortex K+ yellow, C-, KC-, P+ yellow; medulla K–, C-, KC-, P-; **Secondary metabolite:** upper cortex with atranorin.

Substrate and ecology: at the only known locality growing on trees at 500 m; **World distribution:** South America, East Africa and SW North America; **Sonoran distribution:** only one locality in Baja California Sur in the Sierra de La Laguna.

Notes: The thin often undulating thallus, the K- medulla and the paraplectenchymatous lower cortex are the main characters. *Physcia crispa* may have some similarities to *P. undulata* but in the latter species the medulla reacts K+ yellow and the lower cortex is prosoplectenchymatous.

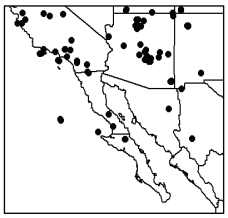
Physcia dimidiata (Arnold) Nyl., Flora 64: 537 (1881).

Basionym: *Parmelia pulverulenta* var. *dimidiata* Arnold, Flora 47: 594 (1864); Illustrations: Moberg (1977), p. 74; Wirth (1995), p. 728.

Thallus: irregular, sometimes orbicular, up to 3 cm diam., with ± imbricate lobes; **lobes:** up to 3 mm wide but usually narrower, crenulate at tips with minute lobules, eciliate; **upper surface:** brownish gray to gray or cream colored, with a ± prominent pruina (crystals), sorediate; **soredia:** granular, in marginal soralia, less frequent on outer lobes; **upper cortex:** paraplectenchymatous; **medulla:** white; **lower cortex:** prosoplectenchymatous; **lower surface:** whitish to brownish, with pale gray to brownish rhizines; **Apothecia:** rare, not seen in Sonoran material, elsewhere up to 2 mm diam.; disc: white-pruinose; **ascospores:** brown, 1-septate, *Physcia*-type, 17-23 x 8-12 µm; **Pycnidia:** rare (not seen); **Spot tests:** upper cortex K+ yellow, C-, KC-, P+ yellow; medulla K–, C-, KC-, P-; **Secondary metabolite:** upper cortex with atranorin.

Substrate and ecology: mainly growing on north exposed rocks; **World distribution:** known from Europe,

East Africa, South America and SW North America; **Sonoran distribution:** a relatively common species from low to intermediate localities in Arizona, southern California, Baja California, Baja California Sur, Chihuahua and Sonora.



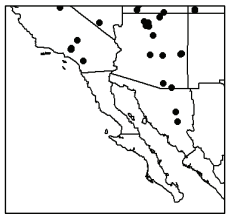
Notes: *Physcia dimidiata* is the sorediate counterpart of *P. biziana* with a similar dull gray upper surface. Like *P. biziana* it has a variable cover of the pruina, but seems to be more often densely pruinose. As the pruina consists of calcium oxalate this may be explained by a greater calcium uptake from a more calcium rich substrate.

Physcia dubia (Hoffm.) Lett., Hedwigia 52: 254 (1912).

Basionym: *Lobaria dubia* Hoffm., Deutschlands Flora: 156 (1796); Illustrations: Moberg (1977), p. 76; Hale (1979), p. 108; Wirth (1995), p. 733; Brodo et al. (2001), p. 554.

Thallus: irregular, rarely orbicular, up to 3 cm diam., gray to gray brown, usually with distinctly darker lobe tips; **lobes:** variable width, but rarely exceeding 1 mm in width, eciliate; **upper surface:** whitish gray to cream-colored, mostly without pruina and maculation, margins of the lobes often paler, sorediate; **soredia:** in marginal soralia that are mostly at the lobe tips and lip-shaped; **upper cortex:** paraplectenchymatous; **medulla:** white; **lower cortex:** prosoplectenchymatous; **lower surface:** pale, with white to black rhizines; **Apothecia:** uncommon, not seen in Sonoran material, elsewhere up to 2 mm diam.; margin: usually sorediate; **ascospores:** brown, 1-septate, *Physcia*-type 16-24 (-28) x 6-10 µm; **Pycnidia:** not seen in material from the area, elsewhere rare; **conidia:** subcylindrical, 4-6 x 1 µm; **Spot tests:** upper cortex K+ yellow, C-, KC-, P+ yellow; medulla K–, C-, KC-, P-; **Secondary metabolite:** upper cortex with atranorin.

Substrate and ecology: growing on acid rocks in open situations; **World distribution:** widely distributed species in boreal and temperate areas of the Northern Hemisphere. It is also known from the southern cold temperate part of South America; **Sonoran distribution:** known from montane to upper montane habitats in Arizona, southern California and Sonora.



Notes: The lip-shaped soralia, the usually nonpruinose thallus with K- medulla and the prosoplectenchymatous lower cortex are the main characters of the species. In the cold temperate areas, where it mainly grows, no other species is known which could be confused with *P. dubia*, but in warm temperate areas it might be confused with *P. tribacia*, which has a shiny upper cortex and paraplectechymatous lower cortex.

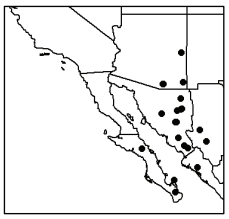
Physcia erumpens Moberg, Nord. J. Bot. 6: 856 (1986).

Illustrations: Moberg (1986), p. 856; Swinscow and Krog (1988), p. 227.

Thallus: orbicular to irregular, up to 3 cm across, usually firmly adnate also at the lobe tips; **lobes:** overlapping to separate, up to 1 mm wide, ± truncate, eciliate; **upper surface:** shining to dull, whitish gray to pale brownish gray, occasionally with a white pruina, sorediate; **soredia:** in laminal, crateriform soralia that sometimes are ± capitate, starting as cracks in the upper cortex; **upper cortex:** paraplectenchymatous; **medulla:** white; **lower cortex:** paraplectenchymatous, the lower part dark brown to black; **lower surface:** black except for the paler tips, with black rhizines; **Apothecia:** not seen in Sonoran material, elsewhere rare, sessile; margin: often sorediate; **ascospores:** brown, 1-septate, *Pachysporaria*-type, 21-27 x 9-12 µm; **Pycnidia** not seen in Sonoran material, elsewhere rare, immersed; **conidia:** subcylindrical, 4-6 x 1 µm; **Spot tests:** upper cortex and medulla K+ yellow, C-, KC-, P+ yellow; **Secondary metabolites:** upper cortex with atranorin; medulla with atranorin and zeorin.

Substrate and ecology: growing on rocks in ± open situations; **World distribution:** SW North America, Mexico, East Africa and South America; **Sonoran distribution:** a species from moist canyons at intermed-

iate elevations at scattered localities SE Arizona south through the Sierra Madre Occidental in Chihuahua, Sonora and Sinaloa and the southern mountains of Baja California Sur.



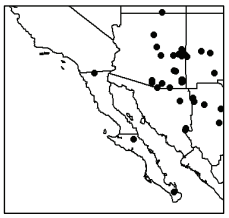
Notes: The black lower surface, the crateriform to capitate soralia and the convex lobes makes *P. erumpens* easily separated from other *Physcia* species in the area. From its close relative, *P. sorediosa*, it is separated by the type of soralia as *P. sorediosa* has marginal, small and delimited soralia.

Physcia halei J. W. Thomson, Beih. Nova Hedwig. 7: 57 (1963).

Illustrations: Hale (1979), p. 112; Brodo et al. (2001), p. 555.

Thallus: orbicular to irregular, up to 3 cm diam., loosely to firmly adnate; **lobes:** up to 1 mm wide, margins mostly crenulate, eciliate; **upper surface:** whitish gray to dark gray or cream-colored, with darker margins, mostly shiny and epruinose; without soredia or isidia; **upper cortex:** paraplectenchymatous with rounded cells; **medulla:** white; **lower cortex:** paraplectenchymatous with rounded cells; **lower surface:** white to brownish gray, often weakly rose colored; **Apothecia:** common, up to 2 mm diam., usually around 1 mm; margins: crenulate; disc: dark brown to black, without pruina; **ascospores:** brown, 1-septate, intermediate between *Physcia*- and *Pachysporaria*-types, (14-) 15-17 (-18.5) x (7.5-) 8-9.5 (-11) µm; **Pycnidia:** usually numerous, immersed; **conidia:** cylindrical, 3-4 x 1 µm; **Spot tests:** upper cortex K+ yellow, C-, KC-, P+ yellow; medulla K–, C-, KC-, P-; **Secondary metabolite:** upper cortex with atranorin.

Substrate and ecology: seeming to prefer ± acid rocks in open situations; **World distribution:** rather limited distribution in southern North America; **Sonoran distribution:** a relatively common species at intermediate elevations in



Arizona, Chihuahua and Sonora and less commonly in Baja California and Baja California Sur.

Notes: *Physcia halei* is evidently the fertile counterpart of *P. tribacia.* It is in some modifications similar to *P. cinerea* but has a different chemistry lacking zeorin and additional triterpenes.

Physcia integrata Nyl., Synopsis methodica lichenum 1: 424 (1860).

Illustrations: Moberg (1986), p. 858; Swinscow and Krog (1988), p. 229.

Thallus: orbicular to irregular, to 5 cm diam., ± closely adnate to the substrate; **lobes:** up to 2 mm wide, mostly *c.* 1 mm, often imbricate, tips rounded, sometimes with the inner parts dissected into small lobes, eciliate; **upper surface:** whitish gray to gray, usually shiny, sometimes with white dots or a pruina; **upper cortex:** paraplectenchymatous; **medulla:** white; **lower cortex:** paraplectenchymatous, thick, brownish to black cell walls; **lower surface:** black except for pale lobe tips, with black, abundant rhizines; **Apothecia:** usually abundant, up to 2 mm across; disc: dark brown to black, sometimes covered with a white pruina; **ascospores:** brown, 1-septate, *Pachysporaria*-type, (18.5-) 21-26 (-32.5) x (8.5-) 9-11.5 (-14) µm; **Pycnidia:** abundant; **Spot tests:** cortex and medulla K+ yellow, C-, KC-, P+ yellow; **Secondary metabolites:** upper cortex with atranorin; medulla with atranorin, zeorin, lecotylin and occasionally some unidentified triterpenes.

Habitat and ecology: growing on tree trunks and rocks in rather open but moist, subtropical situations; **World distribution:** known from a few scattered areas in East Africa, Mexico and South America; **Sonoran distribution:** only known from one locality near Baseseachic Falls in Chihuahua.

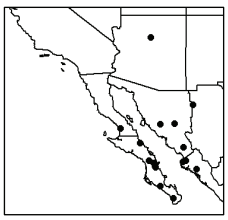
Notes: In its appearance this species is close to *P. aipolia*, but easily separated by its black, distinctly paraplectenchymatous lower cortex and the ± shiny upper surface. In some specimens the thallus is dissected into narrow lobes.

Physcia nashii Moberg, Symb. Bot. Ups. 32: 174 (1997).

Illustration: Moberg (1997), p. 175.

Thallus: orbicular to irregular, up to 1 cm diam., often confluent with other thalli forming a larger aggregate; **lobes:** up to 1 mm wide, convex to flat, usually broadest at the downwardly bent lobe tips, eciliate; **upper surface:** white to grayish, often with a darker zone near lobe tips, weakly maculate, dull to shiny, sometimes with a white pruina, sorediate; **soredia:** in marginal soralia on lobe tips, sometimes big and reflexed or semicapitate; soredia ±granular; **upper cortex:** paraplectenchymatous; **medulla:** white; **lower cortex:** pale, prosoplectenchymatous often labyrinthiform in the lower parts; **lower surface:** white with a rose tinge; rhizines: concolorous or darker than the lower surface, few and scattered; **Apothecia:** rare, up to 2 mm diam.; margins: ± sorediate; **ascospores:** brown, 1-septate, *Pachysporaria*-type (14-) 14.5-18.5 (-20.5) x 7.5-9 (-9.5) µm; **Pycnidia:** ± common, immersed, appearing as black warts; **conidia:** subcylindrical, 4-6 x 1 µm; **Spot tests:** upper cortex K+ yellow, C-, KC-, P+ yellow; medulla K–, C-, KC-, P-; **Secondary metabolites:** upper cortex with atranorin (sometimes extending into algal layer but not below); medulla with some traces of triterpenes but not zeorin.

Substrate and ecology: growing on ± exposed, acid rocks at altitudes from *c.* 50 m to 1200 m; **World** and **Sonoran distribution:** a species of low to intermediate elevations from Arizona, Baja California, Baja California Sur, Chihuahua, Sinaloa and Sonora.



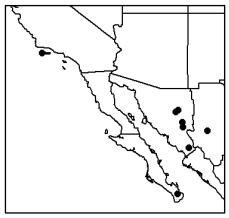
Notes: *Physcia nashii* is recognized by its small size, the convex lobes, the presence of terminal soralia, and the absence of zeorin. In most species of *Physcia* the absence of zeorin in the medulla medulla is connected with a K– medullary reaction, but in the case of *P. nashii* and *P neglecta* a K+ reaction is detected in the medulla even though no zeorin is present. *P. nashii* differ from *P. neglecta* by the type of the soralia and by the narrower lobes. It is also similar to the nonsorediate *P. convexella*, and *P. nashii* could be regarded as the secondary species of *P. convexella*. To some extent *P. nashii* is similar to *P. poncinsii,* but the latter is usually larger, has wider lobes and a different chemistry as it contain zeorin in the medulla.

Physcia neglecta Moberg, Symb. Bot. Ups. 32: 176 (1997).

Illustration: Moberg (1997), p. 176.

Thallus: orbicular to irregular, up to 2 cm diam., usually confluent with other thalli forming bigger patches, ± loosely adnate to the substrate; **lobes**: flat to weakly concave, up to 1.5 mm wide, usually around 1 mm, sparsely branched with ± spreading, truncate lobes, eciliate; **upper surface:** whitish gray to dark gray, ± shiny and without pruina, sorediate; **soredia:** granular (inner parts almost isidiate), in marginal soralia; **upper cortex:** paraplectenhymatous; **medulla:** white, thin; **lower cortex:** paraplectenhymatous; **lower surface:** whitish with few, robust, pale rhizines; **Apothecia:** not common, seen only in the type material, up to 1.5 mm diam.; **ascospores:** brown, 1-septate, sparsely developed, *Pachysporaria* type, 18-22 x 9-11 µm; **Pycnidia:** not common, immersed, appearing as black warts; **conidia:** subcylindrical, 4-6 x 1 µm; **Spot tests:** upper cortex K+ yellow, C-, KC-, P+ yellow; medulla K–, C-, KC-, P-; **Secondary metabolites:** upper cortex with atranorin (sometimes extending into algal layer but not below into the thin medulla).

Substrate and ecology: growing on open rocks, especially sandstone; **World** and **Sonoran distribution:** so far known only from low to intermediate elevations of southern California, Baja California Sur, Chihuahua and Sonora.



Notes: *Physcia neglecta* is a distinctive species recognized by the truncate, loosely adnate, spreading lobes, the granulose, well delimited soralia and the precence of atranorin only. It might be confused with *P. nashii* which is smaller, has convex lobes, soralia on lobe tips, and a prosoplectenchymatous lower cortex. As in *P. nashii* the K

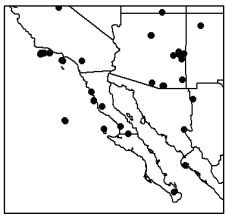
reaction in the medulla is sometimes yellow in spite of absence zeorin.

Physcia phaea (Tuck.) J. W. Thomson, Beih. Nova Hedwigia 7: 54 (1963).

Basionym: *Parmelia phaea* Tuck. in Darlington, Flora Cestrica, 3rd ed.: 440 (1853); Synonym: *Physcia melops* Duf. Ex Nyl.; Illustrations: Moberg (1977), p. 66; Thomson (1984), p. 355; Brodo et al. (2001), p. 557.

Thallus: orbicular to irregular, up to 3 cm in diam. or more when confluent with other thalli, lobes ± imbricate; **lobes:** up to 1.5 mm wide but usually around 1 mm, flat or slightly convex, particularly at tips, eciliate; **upper surface:** gray to dark gray or brownish gray, usually strongly maculate and ± rugose; soredia and isidia lacking; **upper cortex:** paraplectenchymatous; **medulla:** white; **lower cortex:** prosoplectenchymatous; **lower surface:** white to brownish, with white to black, scattered rhizines; **Apothecia:** numerous, up to 1.5 mm across, usually smaller; margin: crenulated when young; disc: brown to black, sometimes covered with a white pruina; **ascospores:** brown, 1-septate, *Physcia*-type, (15-) 16.5-20 (-21.5) x (6.5-) 7-9.5 (-11) µm; **Pycnidia:** numerous, immersed; **conidia:** subcylindrical, 4-6 x 1 µm; **Spot tests:** upper cortex and medulla K+ yellow, C-, KC-, P+ yellow; **Secondary metabolites:** upper cortex with atranorin; medulla with atranorin, zeorin and occasionally some other triterpenes.

Substrate and ecology: growing on rocks in open situations; **World distribution:** known from more northern parts of North America and from Europe; **Sonoran distribution:** a relatively frequent species from coastal regions to upper montane areas in Arizona, southern California, Baja California, Baja California Sur, Chihuahua, Sonora and Sinaloa.



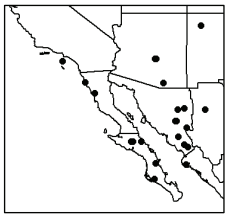
Notes: *Physcia phaea* is easily recognized by the strong maculation and the rugose upper surface, the abundant apothecia and by the chemistry. The K reaction in the medulla is not a good diagnostic character (see *P. nashii* and *P. neglecta*).

Physcia poncinsii Hue, Bull. Soc. Bot. France 63, Mem. 28: 10 (1917).

Illustrations: Moberg (1986), p. 869; Swinscow and Krog (1988), p. 230.

Thallus: orbicular to irregular, very variable in size, up to 5 cm diam., ± closely adnate; **lobes:** very variable in width, up to 2 mm, but in specimens on twigs and rocks not exceeding 1 mm, lobes sometimes imbricate, sometimes distinctly separated, saxicolous material with convex lobes; tips: usually truncate, eciliate; **upper surface:** white to dark gray, sometimes with white dots (*c. P. aipolia*), with or without pruina, some specimens on rocks with shiny upper surface and darker gray margins, sorediate; **soredia:** mainly in laminal, crateriform to almost capitate soralia, usually orbicular, starting as cracks in the upper cortex; in some specimens predominantly marginal soralia which may develop into rounded patches at angles of lobes; **upper cortex:** paraplectenchymatous; **medulla:** white; **lower cortex:** a type between proso- and paraplectenchymatous; **lower surface:** white to pale brownish gray, with white to dark gray rhizines; **Apothecia:** rare, up to 1.5 mm diam.; margins: sometimes with sorediate; **ascospores:** brown, 1-septate, *Pachysporaria*-type, (16-) 19-24.5 (-26) x (7.5-) 8.5-10.5 (-11) µm; **Pycnidia:** rare; **Spot tests:** cortex and medulla K+ yellow, C-, KC-, P+ yellow; **Secondary metabolites:** upper cortex with atranorin; medulla with atranorin, zeorin and sometimes unidentified substances.

Substrate and ecology: growing on rocks in open situations; **World distribution:** known from South America and East Africa, but may also occur in most tropical and subtropical areas; **Sonoran distribution:** scattered localities at coastal to intermediate elevations from Arizona, southern California, Baja California, Baja California Sur, Chihuahua, Sonora and Sinaloa.



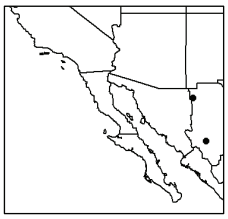
Notes: *Physcia poncinsii* similar to

forms of *P. caesia,* but there are distinct differences in the lobes. *P. poncinsii* has convex lobes with truncate tips but *P. caesia* has flat to convex lobes with rounded tips. *P. poncinsii* also is somewhat similar to *P. nashii* which is, however, smaller, has narrower lobes and different chemistry (no zeorin).

Physcia pseudospeciosa J. W. Thomson, Beih. Nova Hedwig. 7: 91 (1963).

Illustrations: Thomson (1963), Pl. 13; Hale (1979), p. 106.

Thallus: irregular to orbicular, to 3 cm diam. but usually larger when confluent with other thalli, loosly to firmly adnate; **lobes:** up to 1 mm wide, usually narrower (*c.* 0.5 mm), mostly distinctly separate and rarely overlapping, widening at tips and weakly ascending, sparsely lobulate along margin; **upper surface:** gray to whitish gray with a weak maculation, sorediate; **soredia:** granular, in small, delimited, marginal soralia, sometimes sparse; **upper cortex:** paraplectenchymatous; **lower cortex:** paraplectenchymatous; **lower surface:** white to pale brownish, with a few white to blackish rhizines; **Apothecia:** not seen; **Pycnidia:** not seen; **Spot tests:** upper cortex and medulla K+ yellow, C-, KC-, P+ yellow; **Secondary metabolites:** upper cortex with atranorin; medulla with atranorin and zeorin.



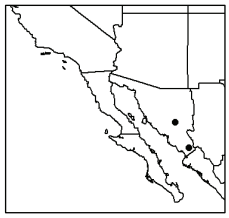
Habitat and ecology: growing on rocks in shade in region with relatively high summer precipitation; **World distribution:** Mexico and SE USA (North Carolina and Georgia); **Sonoran distribution:** Sierra Madre region of Chihuahua.

Note: *Physcia pseudospeciosa* is a very distinct species and easily separated by the spreading lobes and its delimited, small soralia. The species was earlier known only from the type locality but is now found on some additional localities.

Physcia rolfii Moberg, Nord. J. Bot. 10: 337 (1990).

Illustration: Moberg (1990b), p. 337.

Thallus: irregular to orbicular, up to 5 cm diam., ± firmly adnate; **lobes:** mostly narrow, sometimes broader and overlapping, but usually *c.* 1 (-2) mm wide, convex and distinctly discrete, eciliate; **upper surface:** gray to dark gray, usually white maculate and ± pruinose, sorediate; **soredia:** in marginal, well delimited, semicircular to upwardly curved or labriform soralia (sometimes ± helmet-shaped) situated in the lobe sinuses; **upper cortex:** paraplectenchymatous; **medulla:** white; **lower cortex:** proso- to indistinctly paraplectenchymatous; **lower surface:** white to graphite gray or brownish, of the same color or darker than the lower surface, with few rhizines; **Apothecia:** ± abundant, usually to 1 mm diam, rarely larger; margins: sometimes dissolved into soredia; disc: often with a whitish pruina; **ascospores:** brown, 1-septate, *Pachysporaria*-type, (16-) 19.5-24 (-25) x (7.5-) 8.5-11 (-14) µm; **Pycnidia:** not common, immersed; **conidia:** subcylindrical, 4-6 x 1 µm; **Spot tests:** cortex and medulla K+ yellow, C-, KC-, P+ yellow; **Secondary metabolites:** upper cortex with atranorin; medulla with atranorin, zeorin and some unknown triterpenes.



Substrate and ecology: growing on branches of trees in fairly open situation; **World distribution:** scattered localities in South America; **Sonoran distribution:** so far known from only two localities in the Sierra Madre Occidental region of Sonora.

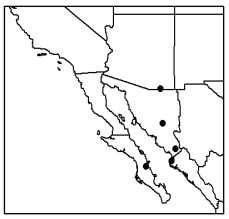
Notes: In its typical appearance *P. rolfii* is easily recognized by the semicircular soralia in the lobe sinuses and the short, widening and white maculate lobes.

Physcia sinuosa Moberg, Nord. J. Bot. 10: 338 (1990).

Illustration: Moberg (1990b), p. 338.

Thallus: orbicular to irregular, up to 2 cm diam. or bigger when confluent with other thalli, ± loosely adnate; **lobes:** radiating, flat to slightly convex, narrow, up to 1 mm but rarely exceeding 0.5 mm, sinuose and truncate, eciliate; **upper surface:** whitish gray to cream-colored, mostly without pruina, sorediate; **soredia:** in prominent, marginal soralia, situated at some distance from the lobe tips, delimited, lip-shaped to semicapitate, sometimes abundant; **upper cortex:** paraplectenchymatous; **medulla:** white; **lower cortex:** proso- to indistinctly paraplectenchymatous with thick walled cells, but thinner thalli are frequently with paraplectenchymatous lower cortex; **lower surface:** white to grayish, rarely brownish, with few pale rhizines; **Apothecia:** ± common, up to 1 mm diam.; margins: usually dissolved into soredia; disc: sometimes pruinose; **ascospores:** brown, 1-septate, *Pachysporaria*-type, 15-19 x 6.5-7.5 µm; **Pycnidia:** not common, immersed; **conidia:** subcylindrical, 4-6 x 1 µm; **Spot tests:** cortex and medulla K+ yellow, C-, KC-, P+ yellow; **Secondary metabolites:** upper cortex with atranorin; medulla with atranorin, zeorin and an unknown triterpene.

Substrate and ecology: growing on rocks in ± open situations; **World distribution:** occurring in a few localities in Brazil and Venezuela; **Sonoran distribution:** only known from widely scattered localities at relatively low elevations from Arizona, Baja California Sur, Sonora and Sinaloa.



Notes: The species is easily recognized by the sinuose and truncate lobes and the well delimited soralia situated in the lobe angles. Superficially it resembles *P. stellaris*, but differs by the presence of soralia and the K+ yellow medulla. *Physcia rolfii* has a similar type of soralia but the lobes are bigger and convex and the the upper surface is maculate. *Physcia sinuosa* is also similar to *P. nashii* but the latter is smaller and lacks zeorin in the medulla.

Physcia sorediosa (Vain.) Lynge, Vid.-Selsk. Skrifter I. Mat.-Naturv. kl., n. 16: 27 (1924).

Basionym: *Physcia integrata* var. *sorediosa* Vain., Acta Soc. Fauna Fl. Fenn. 7: 142 (1890); Illustrations: Moberg (1986), p. 857; Brodo et al. (2001), p. 557.

Thallus: orbicular to irregular, up to 5 cm in diam.; **lobes:** up to 2 mm wide, usually broadest near the tips, usually overlapping, eciliate; **upper surface:** whitish gray to gray, shiny or rarely pruinose, ± distinctly white maculate (*c.* like *P. aipolia*), sorediate; **soredia:** often granular, in marginal, small and delimited soralia that occasionally becomed capitate; **upper cortex:** paraplectenchymatous; **medulla:** white; **lower cortex:** paraplectenchymatous; **lower surface:** black, with dark gray lobe tips; rhizines: black; **Apothecia:** not seen in the Sonoran material, but elsewhere not common, up to 2 mm diam.; margin: crenulated and sometimes disintegrating into soredia; disc: black, with or without pruina; **ascospores:** brown, 1-septate, *Pachysporaria* type, 20-26 x 9-11 µm; **Pycnidia:** not common; **Spot tests:** cortex and medulla K+ yellow, C-, KC-, P+ yellow; **Secondary metabolites:** upper cortex with atranorin; medulla with atranorin and zeorin.

Substrate and ecology: growing both on rocks or on tree trunks in open situation; **World distribution:** known from South America and East Africa and southeastern Asia; **Sonoran distribution:** not known from the Sonoran Desert proper but may be present as it is recorded from Mexico east of the study area.

Notes: The species is closely related and similar to *P. erumpens* as was discussed under that species.

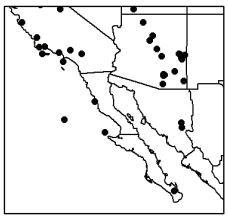
Physcia stellaris (L.) Nyl., Actes Soc. Linn. Bordeaux 21: 307 (1857).

Basionym: *Lichen stellaris* L., Spec. Plant. 1144 (1753); Illustrations: Moberg (1977), p. 72; Wirth (1995), p. 734; Brodo et al. (2001), p. 558.

Thallus: orbicular or irregular, up to 4 cm diam., sometimes confluent with other thalli, loosely adnate; **lobes:** radiating, truncate with open sinuses, up to 1 mm wide

but mostly *c.* 0.5 mm, eciliate; **upper surface:** whitish gray to cream-colored (margin often paler), mostly without pruina and maculation; soredia and isidia absent; **upper cortex:** paraplectenchymatous; **medulla:** white; **lower cortex:** prosoplectenchymatous, cells sometimes short and thick-walled; **lower surface:** white to brownish, with few pale rhizines; **Apothecia:** usually abundant, variable in size, up to 1.5 mm diam., but usually less than 1 mm; margins: thick; disc: often pruinose; **ascospores:** brown, 1-septate, *Physcia*- or *Pachysporaria*-type, (14-) 17.5-22.5 (-28) x (6.5-) 8-10 (-12) µm; **Pycnidia:** ± abundant; **conidia:** subcylindrical, 4-6 x 1 µm **Spot tests:** cortex K+ yellow, C-, KC-, P+ yellow; medulla K–, C-, KC-, P-; **Secondary metabolite**: upper cortex with atranorin.

Substrate and ecology: growing on trees in open situations; **World distribution:** widely distributed species within the arctic, boreal and temperate vegetation zones; **Sonoran distribution:** a relatively frequent species on trees from low to upper montane localities of Arizona, southern California, Baja California, Baja California Sur, and Sonora.



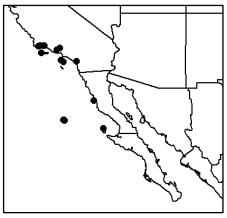
Notes: The abundant apothecia, the K– medulla and corticolous habitat are the main characters of *P. stellaris*. There is a slight difference in morphology and appearance within the range of its distribution (Moberg 1986: 860) and the Sonoran Desert material is closer to the southern type as would be expected. The closely related species *P. convexella* differs in lobe shape and substrate preference.

Physcia tenellula Moberg, Symb. Bot. Upsal. 32: 181 (1997).

Illustration: Moberg (1997), p. 182.

Thallus: irregular, rarely orbicular, small, up to 1 cm diam., ± loosely adnate, rarely confluent with other thalli to form bigger patches; **lobes:** ± ascending, narrow, up to 1 mm, but usually around 0.5 mm, sometimes widening at tips; margins: rarely having gray to black cilia; **upper surface:** gray to dark gray or brownish, without pruina, with white to black hairs, sorediate; **soredia:** in terminal to marginal soralia, which when well developed widen the lobe tips, occasionally covering the whole lower surface of the lobe; **upper cortex:** paraplectenchymatous; **medulla:** white; **lower cortex:** prosoplectenchymatous; **lower surface:** white to brownish, with few white to black rhizines; **Apothecia:** rare; **ascospores:** brown, 1-septate, *Pachysporaria*-type (15-) 16.5-21 (-22.5) x (7.5-) 8-10.5 (-12) µm; **Pycnidia:** not common, immersed, appearing as black warts; **conidia:** subcylindrical, 4-6 x 1 µm; **Spot tests:** cortex K+ yellow, C-, KC-, P+ yellow; medulla K-, C-, KC-, P-; **Secondary metabolite:** upper cortex with atranorin.

Substrate and ecology: growing both on rocks and trees in open situations; **World** and **Sonoran distribution:** presently known from Baja California and southern California.



Notes: *Physcia tenellula* is closely related to *P. tenella* (Scop.) DC and has previously been identified as the latter species. They differ, however, in size and presence of hairs on the upper surface. The restricted distribution to the islands outside the coast also gives evidence for *P. tenellula* being a separate taxon.

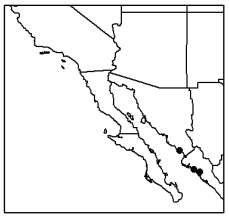
Physcia tretiachii Moberg, Symb. Bot. Upsal. 32: 182 (1997).

Illustration: Moberg (1997), p. 181.

Thallus: orbicular to irregular, loosely attached, up to 5 cm diam.; **lobes:** flat to concave, broad, up to 4 mm wide with rounded tips; margins: often prominent because of the white rim, eciliate; **upper surface:** gray to bluish gray, pruinose, usually with a white ”frosty” rim along the lobe margins; soredia and isidia absent; **upper cortex:** paraplectenchymatous; **medulla:** white; **lower cortex:** prosoplectenchymatous to labyrinthiform with thick walls, usually well delimited; **lower surface:** white to pale brownish, with a few concolorous rhizines; **Apothecia:** usually abundant, shortly stalked, up to 5 mm

diam.; margin: prominent, crenulate; **ascospores:** brown, 1-septate, *Pachysporaria*-type, (17-) 18.5-22 (-22.5) x (8.5-) 9-10.5 (-11) µm; **Pycnidia:** abundant, immersed, appearing as black warts on the surface; **conidia:** subcylindrical, 4-6 x 1 µm; **Spot tests:** cortex K+ yellow, C-, KC-, P+ yellow; medulla only weakly K+ yellow, C-, KC-, P-; **Secondary metabolites:** upper cortex with atranorin; medulla with triterpenes (not zeorin).

Substrate and ecology: growing on branches and twigs of various trees and shrubs in open situations; **World** and **Sonoran distribution:** so far known only from a few scattered coastal localities in Sonora and Sinaloa.



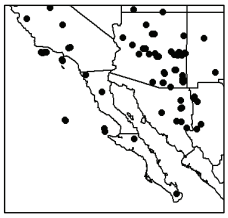
Notes: *Physcia tretiachii* is a very distinct species recognized by the broad lobes with a white marginal rim. No species seems to be very closely related, but it has some similarities to *P. atrostriata* Moberg which, however, has a dark, prosoplectenchymatous lower cortex and a different chemistry (zeorin).

Physcia tribacia (Ach.) Nyl., Flora 57: 307 (1874).

Basionym: *Lecanora tribacia* Ach., Lich. Univ: 415 (1810); Illustration: Moberg (1986), p. 860.

Thallus: foliose, orbicular to irregular, up to 3 cm diam.; **lobes:** up to 1 mm wide, sometimes scale-like; margin: mostly crenulate when soralia not present, eciliate; **upper surface:** whitish gray to dark gray or cream-colored (with darker margins), shiny and epruinose or rarely weakly pruinose, sorediate; **soredia:** in marginal or terminal soralia that develop from the lower surface of the lobe tips, eroding the tip and sometimes also the lower surface; **upper cortex:** paraplectenchymatous with rounded cells; **medulla:** white; **lower cortex** paraplectenchymatous with rounded cells; **lower surface:** white to brownish gray, often weakly rose colored; **Apothecia:** uncommon, up to 2 mm diam.; margins: partly sorediate; disc: dark brown to black, without pruina; **ascospores:** brown, 1-septate, intermediate between *Physcia*- and *Pachysporaria*-types, (16-) 17.5-21.5 (-22.5) x (7.5-) 8.5-10.5 (-12) µm; **Pycnidia:** usually numerous; **conidia:** subcylindrical, 4-6 x 1 µm; **Spot tests:** cortex K+ yellow, C-, KC-, P+ yellow; medulla K–, C-, KC-, P-; **Secondary metabolite:** upper cortex with atranorin.

Substrate and ecology: growing mainly on rocks, often manured by birds in open situations; **World distribution:** widely distributed but not common in northern and southern temperate regions; **Sonoran distribution:** one of the most common Physcias from the northern part of the Sonoran region and in scattered localities farther south, from coastal to upper montane habitats in Arizona, southern California, Baja California, Baja California Sur, Chihuahua and Sonora.



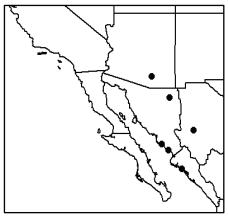
Notes: In its typical appearance *P. tribacia* is easily identified by its narrow lobes, shiny upper surface and paraplectenchymatous lower cortex. However, very small individuals might be difficult to distinguish from *P. subtilis*. In such cases the type of lower cortex separates them. *Physcia halei* is the fertile counterpart and, except for the lack of soralia, differs by having longer lobes. Material from North America determined as *P. callosa* in the sense of Thomson (1963) is included here.

Physcia undulata Moberg, Nord. J. Bot. 6: 861 (1986).

Illustration: Moberg (1986), p. 861.

Thallus: foliose, irregular to orbicular, up to 4 cm diam., usually loosely adnate; **lobes:** thin, usually less than 150 µm thick, loosely adnate to ascending, up to 2 mm wide; tips: rounded, eciliate; **upper surface:** gray to dark gray and "frosted", sorediate; **soredia:** in marginal soralia that give the margins an undulate appearance, usually not reaching the outermost parts of the lobe tips, sometimes eroded; **upper cortex:** paraplectenchymatous; **medulla:** white; **lower cortex:** indistinct proso- to paraplectenchymatous; **lower surface:** whitish gray to brownish, with concolorous or darker rhizines; **Apothecia**: uncommon, not seen in the Sonoran Desert material, elsewhere up to 2

mm wide; margin: sorediate; **ascospores:** brown, 1-septate, intermediate between *Physcia*- and *Pachysporaria*-type, (15-) 18-27 (-33) x (7-) 8-11 (-13) µm; **Pycnidia:** uncommon, not seen in the Sonoran Desert material; **Spot tests:** cortex and medulla K+ yellow, C-, KC-, P+ yellow; **Secondary metabolites:** upper cortex with atranorin; medulla with atranorin, zeorin and additional triterpenes.



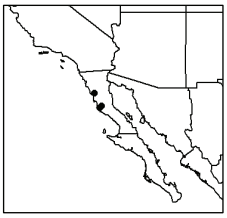
Substrate and ecology: growing on trunks and branches in open situations; **World distribution:** South America and East Africa; **Sonoran distribution:** coastal or montane sites of Sonora, Sinaloa, Chihuahua and southern Arizona.

Notes: The species is extremely variable in lobe size but easily recognized by the "frosted" upper surface, the marginal, ± undulate soralia, and the pale lower surface. These characters separates it from all other *Physcia* species in the area.

Physcia villosula Moberg, Symb. Bot. Ups. 32: 185 (1997).

Illustration: Moberg (1997), p. 185.

Thallus orbicular, small, rarely bigger than 1.5 cm diam., sometimes confluent with other thalli; **lobes:** short (3 mm) and mostly less than 0.5 mm wide, eciliate; **upper surface:** whitish gray to dark gray with darker lobe tips, sometimes pruinose, with short, white to black hairs; soredia and isidia absent; **upper cortex:** paraplectenchymatous; **medulla:** white; **lower cortex:** prosoplectenchymatous; **lower surface:** white to brownish gray, with concolorous or darker rhizines; **Apothecia:** usually abundant and short stalked, very variable in size, up to 2 mm diam., with thick margins; disc: dark brown to black, without pruina. **ascospores:** brown, 1-septate, *Physcia*-type, (14-) 15-18 (-21.5) x (6.5-) 7.5-9.5 (-11) µm; **Pycnidia:** usually abundant, immersed, appearing as black warts; **conidia:** subcylindrical, 4-6 x 1 µm; **Spot tests:** cortex K+ yellow, C-, KC-, P+ yellow; medulla K–, C-, KC-, P-; **Secondary metabolite:** upper cortex with atranorin.



Substrate and ecology: growing on *Idria columnaris* and desert shrubs; **World** and **Sonoran distribution:** so far known only from Baja California where it occurs with the endemic tree *Idria columnaris* and also from two islands off the coast.

Notes: *Physcia villosula* is recognized by the small size, the abundant apothecia and the hairs on the upper surface. These hairs may sometimes be very sparse. The species is similar to *P. stellaris*, but it is much smaller and has hairs on the upper surface. Small specimens of *Heterodermia erinacea* might be similar to *P. villosula* but can easily be separated by the prosoplectenchymatous upper cortex. If soredia are missing on *P. adscendens* it might be difficult to separate it from *P. villosula*. Because even small specimens of the latter have apothecia and hairs on the upper surface, it is usually no problem to separate them.

PHYSCONIA

by T. L. Esslinger

Physconia Poelt, Nova Hedwigia 9: 30 (1965).

Family: Physciaceae; Type: *Physconia distorta* (With.) J. R. Laundon; No. species: *c.* 25 world-wide; Selected lit.: Esslinger (1994), Gunnerbeck and Moberg (1979), Moberg (1977), and Poelt (1966).

Thallus: foliose, small to medium sized, moderately to loosely attached, lobate; **lobes:** linear and discrete to somewhat more rounded, irregular or flabellate; **upper surface:** gray to dark brown or reddish brown, with a white to grayish pruina developed on at least part of the

thallus (lobe ends) and sometimes continuous; one species with coarse cortical hairs near lobe ends; **upper cortex:** paraplectenchymatous or scleroplectenchymatous; **medulla:** white to pale or medium yellow; **lower cortex:** prosoplectenchymatous, often irregularly so (due to the hyphae being curved and zig-zagging, rather than being straight and more strictly parallel to the long axis of the lobes), sometimes missing at the lobe ends and only weakly organized inward; **lower surface:** usually becoming dark brown to black at least in older parts (one species remaining pale, white to tan), often paler at the lobe ends; moderately to densely rhizinate; rhizines: usually blackened and squarrosely branched (mostly simple to furcate in one species); **Apothecia:** with thalline exciple; **asci:** clavate, 8-spored; **ascospores:** *Physconia*-type, brown, 1-septate, 23-38 x 12-21 µm. **Pycnidia:** blackened and immersed; **conidia:** bacilliform to short-cylindrical, 4-6 x ± 1 µm; **Secondary metabolites:** secalonic acid A, variolaric acid, or scabrosin derivatives, but often in variable concentrations or, in many species, lacking altogether; **Geography:** primarily temperate or boreal, North America, Europe, Asia, Africa, South America, Australia; **Substrate:** bark, wood, rock, soil or mosses.

Key to the species of ***Physconia*** occurring in the Sonoran region:

1. Thallus without isidia or soredia, sometimes becoming lobulate; often with apothecia 2
1. Thallus with either isidia or soredia (or isidioid soredia); apothecia present or absent 4

2. Thallus terricolous/muscicolous (very rarely saxicolous), usually divided into irregular lobes and lobules which tend to be concave and ascending, sometimes strongly so and then turf-forming ..... ***P. muscigena***
2. Thallus corticolous (rarely saxicolous), usually ± regular and rosette-forming, the lobes usually prostrate and ± flat 3

3. Lower surface becoming dark brown or black, at least in older parts of thallus, the rhizines concolorous and mostly squarrose; usually with apothecia, thallus not or only irregularly lobulate ..... ***P. americana***
3. Lower surface pale, mostly whitish to pale tan, the rhizines concolorous or darkening, simple to furcate but usually at least some becoming squarrose; apothecia sometimes missing even in large thalli, thalli becoming distinctly lobulate ..... ***P. californica***

4. Thallus with true isidia, the isidia typical and ± cylindrical, with a true cortex like that of the upper surface, located on the surface and often the margins of the lobes, upright to prostrate; lower surface pale, almost white to tan or pale brownish in some old parts; on bark or rock ..... ***P. elegantula***
4. Thallus with soredia or isidioid soredia, no true isidia; lower surface becoming dark brown to black at least in older parts 5

5. Soredia mostly in terminal soralia on the ends of main and/or short lateral lobes, labriform (not always conspicuously terminal in short-lobed specimens); soralia and medulla K-, KC-; lower surface usually very pale or white near the lobe ends and lacking a cortex, the medullary hyphae therefore visible, some of these usually darkening to form very fine brown/black striations a short distance from the lobe ends, a dark but dull lower cortex gradually organizing inward from the periphery; on bark or rock ..... ***P. perisidiosa***
5. Soredia marginal and/or laminal; lower surface dark brown to black centrally, the peripheral lobes often lighter (white to pale brown), but a well-developed cortex occurring on the lower surface essentially right up to the lobe ends 6

6. Thalli often large, the lobes 1.5-4 mm broad, concave and ascending on the ends; soralia irregular on both the upper surface and margins, the soredia granular and becoming isidioid; commonly on mosses over rock, occasionally on bark ..... ***P. isidiomuscigena***
6. Thalli small to moderately sized, the lobes mostly 2 mm broad or less, flat to weakly concave or convex, not ascending on the ends; soralia primarily marginal on lobes, of various shapes, laminal soralia forming only in oldest parts; on bark, wood or rock 7

7. Medulla and soralia K-, KC-, soralia marginal and linear; medulla white or off-white 8
7. Medulla and/or soralia K+ pale yellow to dark yellow and KC+ yellow to orange (containing secalonic acid A); medulla white to pale or medium yellow 9

8. Upper cortex paraplectenchymatous, southern California and Baja California ..... ***P. isidiigera***

8. Upper cortex scleroplectenchymatous, southern Rocky Mountains ..... ***P. detersa***

9. Medulla usually very pale to medium yellow, occasionally white, K+ yellow and KC+ yellow to orange (both reactions can be very pale in specimens with a white medulla, and are correspondingly darker in more yellow medullas); soralia marginal and linear to weakly reflexed, usually K+ and KC+ like the medulla (sometimes weak, however, or obscured by dark pigments); upper cortex paraplectenchymatous ..... ***P. enteroxantha***

9. Medulla white (rarely discolored in infected or necrotic parts, or in old, poorly curated specimens), K- and KC- [or (very rarely) KC+ rose] (take care to not test the medulla too near the lobe edges, where unseen, incipient soralia may have begun to form, causing false positives); soralia K+ yellow and KC+ yellow to orange (to avoid possible masking by dark soredial pigments, test younger soralia or slightly abraded soralia) 10

10. Soralia marginal and sometimes terminal, occurring in a pocket formed by the reflexed cortices, the marginal soralia often in or near lobe axils and becoming distinctly hooded (reminiscent of *Xanthoria fallax* soralia), the terminal soralia appearing ± labriform; upper cortex paraplectenchymatous .... ***P. fallax***

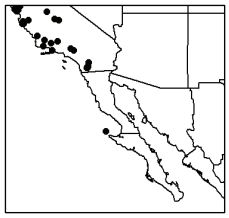
10. Soralia marginal, becoming crisped and reflexed to form ± labriform, apparently separate marginal soralia; upper cortex scleroplectenchymatous .... ***P. leucoleiptes***

The Species

Physconia americana Essl., Mycotaxon 51: 91 (1994).

Illustrations: Esslinger (1994), p. 92; Brodo et al. (2001), p. 562.

Thallus: foliose, up to 10 cm in diam., usually ± orbicular; **lobes:** linear and discrete to somewhat irregularly flabellate and confluent or weakly imbricate, 1-2 (-3) mm broad, ± flat and prostrate; **upper surface:** gray to gray-brown or brown, often with a ± complete pruina or at times the pruina best developed on the lobe ends; without soredia or isidia, but occasionally developing irregular sparse to rather abundant lobules centrally; **upper cortex:** paraplectenchymatous; **medulla:** white; **lower cortex:** irregularly prosoplectenchymatous; **lower surface:** pale tan to pale brown along the peripheral lobes (sometimes up to 4-6 mm from tip), darkening to dark brown or black inwardly, dull to weakly shiny; rhizines: black, mostly squarrosely branched; **Apothecia:** frequent and nearly always present, up to 3 mm in diam., the margin entire or more often developing lobules, pruinose (including discs, margins, and lobules); **ascospores:** brown, 1-septate, 26-36 (-38) x 15-19 µm; **Spot tests:** all negative; **Secondary metabolites:** none detected.



Substrate and ecology: on bark (esp. deciduous trees or shrubs), wood, or occasionally rock; **World distribution:** western North America, southern Europe and northern Africa, Asia; **Sonoran distribution:** southern California and Isla Cedros (Baja California).

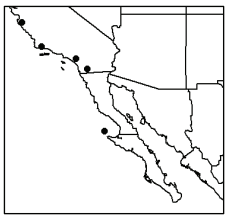
Notes: There are two other *Physconia* species occurring in the Sonoran region which also lack soredia and isidia, and which might be confused with *P. americana. Physconia muscigena* can be distinguished by the concave, upturned peripheral lobes, the frequent development of similarly erect secondary lobules (at times numerous and turf-forming), and the usual substrate (moss or soil, usually over rock). *Physconia californica* is a similar, primarily corticolous species, which differs by having a more uniformly pale, white to tan, lower surface and a regularly lobulate upper surface. *Physconia americana* was long referred to as *P. distorta* or one of its synonyms, but that species is absent from North America.

Physconia californica Essl., Bull. Calif. Lichen Soc. 7: 4 (2000).

Illustration: Esslinger (2000a), p. 3.

Thallus: foliose, up to 7 cm in diam., usually ± regular and orbicular; **lobes:** rather linear and discrete to more irregular-flabellate and contiguous, 1-2 mm broad, ± flat

and prostrate; **upper surface:** gray to gray-brown, completely to rather incompletely (lobe ends only) pruinose; without soredia or isidia, but becoming sparsely to rather abundantly lobulate; lobules: marginal, up to 0.5 mm across; **upper cortex:** paraplectenchymatous; **medulla:** white; **lower cortex:** irregularly prosoplectenchymatous, indistinctly delimited from the medulla in part; **lower surface:** mostly pale, white to very pale tan at the periphery and on most of the lower surface, scattered areas in older parts becoming tawny to very pale brownish, dull; rhizines: pale or darkening in older parts, often largely simple to furcate but with at least some becoming squarrosely branched; **Apothecia:** sometimes frequent but commonly missing from even large thalli, up to 2.5 mm in diam., the margin entire or becoming lobulate; **ascospores:** 28-33 x 14-16 µm; **Spot tests:** all negative; **Secondary metabolites:** none detected.



Substrate and ecology: on bark; **World distribution:** western North America, especially California; **Sonoran distribution:** southern California and Isla Cedros (Baja California).

Notes: This species is similar to some forms of the normally fertile species, *Physconia americana*, from which it is distinguished primarily by the pale lower surface and the more regularly lobulate upper surface. With poorly developed specimens, it can be difficult to distinguish between these two species. When well developed, *P. californica* bears a marked superficial resemblance to two lobulate species known from Japan, *P. lobulifera* Kashiw. and *P. hokkaidensis* Kashiw. Both these taxa have a black lower surface and a scleroplectenchymatous upper cortex.

Physconia detersa (Nyl.) Poelt, Nova Hedwigia 9: 30 (1965).

Basionym: *Parmelia pulverulenta* var. *detersa* Nyl., Synopsis Methodica Lichenum I (2): 420 (1860); Synonym: *Physcia detersa* (Nyl.) Nyl.; Illustrations: Moberg (1977), p. 83; Brodo et al. (2001), p. 563; and Fig. 72 to right.

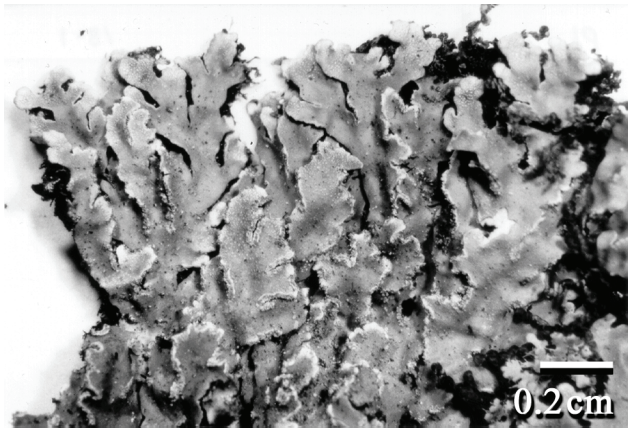
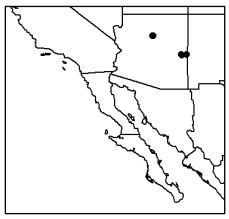


Fig. 72. *Physconia detersa*, photo by T. L. Esslinger.

Thallus: foliose, up to 7 (rarely 8 or 9) cm in diam., irregular to more often orbicular; **lobes:** linear-elongate and discrete to somewhat irregularly rounded and partly imbricate, 1-2 (-3) mm broad, usually ± flat to irregularly concave, prostrate; **upper surface:** gray to mostly gray-brown or brown, with a partial (lobe ends) or occasionally almost completely pruinose, sorediate; **soredia:** in primarily marginal soralia which are elongate (usually becoming ± continuous except on the peripheral lobes), not or only partly reflexed, only rarely appearing weakly labriform, some laminal soralia sometimes also developing, especially in older thallus parts; individual soredia granular to pseudocorticate and isidioid; **upper cortex:** scleroplectenchymatous; **medulla:** white to off-white; **lower cortex:** irregularly prosoplectenchymatous; **lower surface:** peripheral lobes usually dark tan-brown, occasionally paler but almost never white, darkening to dark brown or black inwardly, dull or weakly shiny; rhizines: black and squarrosely branched; **Apothecia:** infrequent, up to 3 mm in diam., sessile, the margin thick and entire, not usually lobulate, soon becoming sorediate; **ascospores:** 26-32 (-35) x 13-18 (-20) µm; **Spot tests:** cortex, medulla and soralia normally with all negative, very rarely the soralia K+ and/or KC+ slight yellow; **Secondary metabolites:** usually none detected, variolaric acid very rarely accessory (apparently in the soralia).

Substrate and ecology: bark, rock, or over mosses on rock (in the study area, known so far only from mosses over rock); **World distribution:** North America, Europe,

Asia; **Sonoran distribution:** central and eastern Arizona in the mountains.



Notes: This species is distinguished by the linear marginal soralia and the usual lack of positive spot tests. A similar species occurring primarily in the western part of the Sonoran Region is *P. isidiigera*, which is distinguished by having a paraplectenchymatous upper cortex. Both these species must also be carefully distinguished from *P. enteroxantha*, which can usually be identified by the positive K and KC (yellowish) spot tests in the medulla (and often also on the soralia).

Physconia elegantula Essl., Mycotaxon 51: 92 (1994).

Illustrations: Esslinger (1994), p. 93; Brodo et al. (2001), p. 563; and Fig. 73 below.

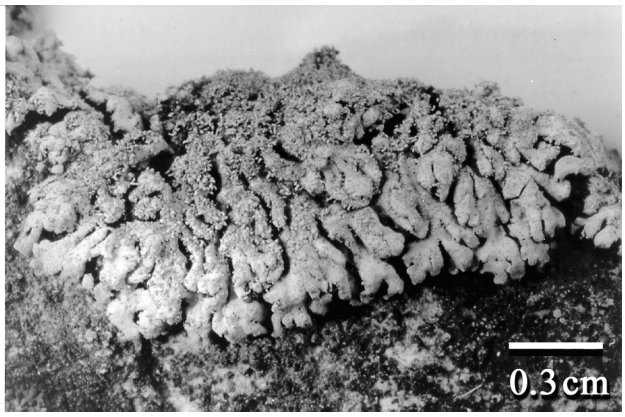
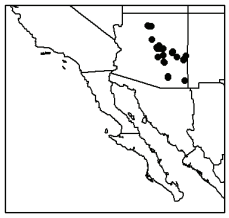


Fig. 73. *Physconia elegantula*, photo by T. L. Esslinger.

Thallus: foliose, up to 6 (-8) cm in diam., orbicular to somewhat irregular; **lobes:** linear and discrete to somewhat irregular-flabellate and confluent to partly imbricate, 0.8-2 mm broad, ± flat to irregularly concave, prostrate; **upper surface:** gray-brown to brown, usually with a ± complete pruina, isidiate; **isidia:** sparse to abundant but often unevenly so, arising as spherical papillae, becoming cylindrical-coralloid and some at times growing into lobules; **upper cortex:** scleroplectenchymatous; **medulla:** white; **lower cortex:** irregularly prosoplectenchymatous; **lower surface:** white to pale tan, darkening only in old necrotic parts of the thallus or not at all, dull to weakly shiny; rhizines: soon blackening, squarrosely branched; **Apothecia:** frequent, up to 3 mm in diam., sessile, the margin becoming crenate and eventually unevenly isidiate-lobulate; **ascospores:** 27-36 x 12-17 µm; **Spot tests:** all negative; **Secondary metabolites:** none detected.

Substrate and ecology: bark (esp. deciduous trees) or rock; **World distribution:** western North America from the Black Hills to Colorado, Utah, New Mexico and Arizona; **Sonoran distribution:** throughout Arizona at higher elevations in the mountains.



Notes: This species is unique in the genus, characterized by the distinctive true isidia and the pale lower surface. Most of the sorediate species of *Physconia* can and do produce strongly isidioid soredia at times, especially in older specimens or older parts of a thallus, but these can be distinguished from the true isidia of *P. elegantula* by their clustering in old soralia patterns and their lack of a true cortex. One specimen exhibited more strongly isidioid propagules, some of which have become dorsiventral, therefore resembling the Asian species *P. grumosa* Kashiw. & Poelt, but the status of that species in North America is still being evaluated.

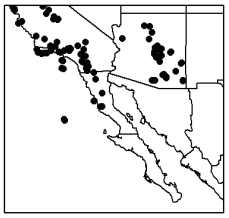
Physconia enteroxantha (Nyl.) Poelt, Nova Hedwigia 12: 125 (1966).

Basionym: *Physcia enteroxantha* Nyl., Flora 56: 196 (1873); Illustrations: Moberg (1977), p. 86; McCune and Geiser (1997), p. 235; Brodo et al. (2001), p. 564.

Thallus: foliose, up to 6 cm in diam., irregular to orbicular; **lobes:** linear and discrete to somewhat irregular-rounded and partly imbricate, 0.5-2 (-3) mm broad, ± flat to irregularly concave; **upper surface:** gray-brown to dark brown, with a partial (lobe ends) to essentially complete pruina, sorediate; **soredia:** in primarily marginal

soralia which are elongate, straight to somewhat curved, the margins weakly reflexed at times so that some marginal soralia may appear weakly labriform, laminal soralia occasionally forming in older thallus parts, the individual soredia granular, coarsely granular to sometimes pseudocorticate and isidioid, often somewhat to distinctly darkened; **upper cortex:** paraplectenchymatous (although often not apparent until at least 1-2 mm from the lobe-tip); **medulla:** usually pale yellowish to yellow in large part, sometimes white to off-white in part (especially but not exclusively in younger thallus parts); **lower cortex:** irregularly prosoplectenchymatous; **lower surface:** peripheral lobes usually pale tan or tan-brown, soon darkening inward to dark brown or black, dull to weakly shiny; rhizines: black and squarrosely branched; **Apothecia:** infrequent, *c.* 2 mm in diam., sessile, the margin thick and entire (non-crenate) but soon becoming sorediate, at least in part; **ascospores:** 28-35 (-38) x 15-18 (-20) µm; **Spot tests:** cortex all negative; medulla K+ yellowish (sometimes very obscure), C-, KC+ yellow to yellow-orange, P-; soralia K+ and KC+ yellowish to yellow orange or K-, KC- (especially when soredia become brown pigmented); **Secondary metabolites:** secalonic acid A in the medulla and soralia (in very variable amounts).

Substrate and ecology: bark, rock, mosses over rock, or on occasion soil (usually over rock); **World distribution:** North America, Europe, North Africa and Asia; **Sonoran distribution:** primarily higher elevations in southern California, Arizona and Baja California.



Notes: The medulla is usually pigmented (pale yellow or darker yellow), and then this sorediate species is difficult to confuse with any other. However, if the concentration of secalonic acid A is very low, resulting in the medulla appearing white, the spot tests can be very obscure also, and requires careful interpretation. Such specimens have usually been misidentified as one of the other sorediate species.

Physconia fallax Essl., Bull. Calif. Lichen Soc. 7: 6 (2000).

Illustrations: Esslinger (2000a), p. 5; and Fig. 74 below.

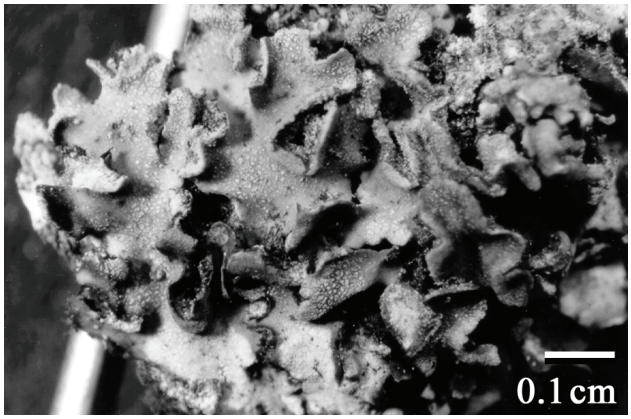
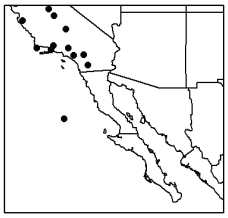


Fig. 74. *Physconia fallax*, photo by T. L. Esslinger.

Thallus: foliose, up to 4.5 cm in diam. but often smaller, ± regular and orbicular; **lobes:** rather elongate and linear, discrete to contiguous or somewhat imbricate, 0.5-1.5 mm broad, ± flat to irregularly concave, prostrate; **upper surface:** gray to gray-brown or dark brown, usually pruinose over much of the upper surface, sorediate; **soredia:** in marginal and terminal soralia on short side branches, the marginal ones often axillary, discontinuous to occasionally almost continuous, forming by separation of the upper and lower cortex and often becoming ear-shaped or hooded (reminiscent of the "nest-shaped" soralia of *Xanthoria fallax*), terminal soralia formed similarly, but often appearing reflexed-labriform; soredia granular, greenish to brownish or sometimes noticeably yellowish; **upper cortex:** paraplectenchymatous; **medulla:** white (areas close to the soralia may be pale yellowish) or occasionally discolored; **lower cortex:** irregularly prosoplectenchymatous, in part poorly delimited from the medulla; **lower surface:** peripheral lobes usually whitish to pale tan for some distance (up to 3 to 4 mm in some cases) from the tip, inward becoming dark brown or black, dull to slightly shiny; rhizines: black and squarrosely branched; **Apothecia:** infrequent, up to 2 mm in diam., the margin thick and becoming lobulate, the lobules eventually developing reflexed soralia on the ends and often becoming quite long (sometimes becoming longer than the breadth of the

apothecium); **ascospores:** 33-38 x 15.5-18 µm; **Spot tests:** cortex all negative; medulla K-, C-, KC- (positive K or KC tests may be obtained if tests are done too close to the soralia or on a lobe edge where unnoticed incipient soralia may occur), P-; soralia K+ faint to dark yellow, C-, KC+ yellow or yellow-orange, P-; **Secondary metabolites:** secalonic acid A (apparently restricted to the soralia).



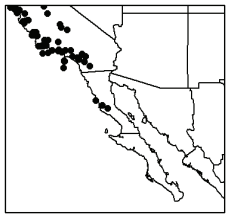
Substrate and ecology: bark or (less often) rock; **World distribution:** western North America: Washington, California and Baja California (Guadalupe Island); **Sonoran distribution:** southern California and Guadalupe Island (Baja California).

Notes: With the marginal, sometimes conspicuously pigmented soralia, this species is most likely to be confused with *P. enteroxantha*, with which it also shares a paraplectenchymatous upper cortex. It can be distinguished from that species, however, by the distinctive shape of the soralia and the K- medulla. The soralia of *Physconia enteroxantha* are usually linear and continuous, and although they may be slightly or at times more strongly reflexed, they are neither hooded nor formed by separating cortices. Another similar species is *P. leucoleiptes*, rare in western North America, which has the same spot tests as *P. fallax* (soralia K+ and KC+ , medulla K-, KC-) but has distinctly labriform soralia which are not at all hooded by the cortices, and has a scleroplectenchymatous upper cortex. *Physconia perisidiosa*, which has terminal labriform or sometimes weakly hooded soralia, has a very different lower surface which is basically ecorticate and pale, darkening only centrally and never with a true cortex.

Physconia isidiigera (Zahlbr. in Herre) Essl., Mycotaxon 51: 94 (1994).

Basionym: *Physcia pulverulenta* subsp. *isidiigera* Zahlbr. in Herre, Proc. Wash. Acad. Sci. 7: 362 (1906); Illustration: Brodo et al. (2001), p. 565.

Thallus: foliose, up to 7 cm in diam., irregular to more often orbicular; **lobes:** linear to somewhat irregular-rounded and partly imbricate, 1-2 (-3) mm broad, ± flat to weakly concave, prostrate; **upper surface:** gray to brown, with a partial (lobe ends) or often almost complete pruina, sorediate; **soredia:** in marginal soralia which are elongate and ± continuous in older parts, laminal soralia sometimes developing in older regions; individual soredia granular to pseudocorticate and isidioid or at times becoming coralloid-stacked and resembling true isidia, pale but darkening with age; **upper cortex:** paraplectenchymatous; **medulla:** white; **lower cortex:** irregularly prosoplectenchymatous; **lower surface:** peripheral lobes pale tan to almost white (sometimes up to 5 mm from tip), inwards becoming dark brown or usually black; rhizines: blackening, squarrosely branched; **Apothecia:** infrequent but not rare, up to 2 mm in diam., the margin thick and entire, becoming sorediate or isidioid but not usually lobulate; **ascospores:** 28-38 x 15.5-18 µm; **Spot tests:** all negative; **Secondary metabolites:** none detected.



Substrate and ecology: bark or wood, less often on rock; **World distribution:** western North America; **Sonoran distribution:** southern California and Baja California.

Notes: In some of its forms, this species is most similar to *P. detersa*, which in western North America appears to be restricted to the southern Rocky Mountains, usually on mosses over rock. That species can also be distinguished from *P. isidiigera* by its scleroplectenchymatous upper cortex. Specimens of *P. enteroxantha* with very low concentrations of secalonic acid A in the medulla and/or soralia are likely to be identified as this species if the medullary spot tests are not very carefully carried out and interpreted.

Physconia isidiomuscigena Essl., Bull. Calif. Lichen Soc. 7: 7 (2000).

Illustrations: Esslinger (2000a), p. 6; and Fig. 75 on next page.

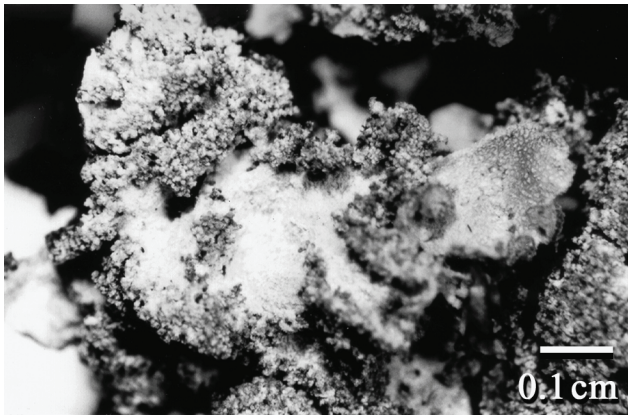
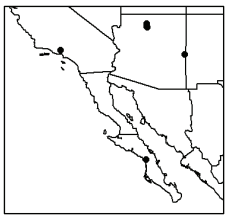


Fig. 75. *Physconia isidiomuscigena*, photo by T. L. Esslinger.

Thallus: foliose, up to 11 cm in diam., somewhat orbicular or often irregular and sometimes entangled with other thalli; **lobes:** irregular-flabellate, contiguous or imbricate, mostly 2-4 mm broad, usually ascending on the ends and therefore distinctly concave; **upper surface:** gray-brown to dark brown, usually whitish pruinose essentially throughout, sorediate-isidiate; **sorediate isidia:** arising first on the lobe margins and under up-turned lobes as very granular soredia, and also later in numerous small patches on the upper surface, propagules becoming rather irregular and strongly isidioid (somewhat similar to blastidia?), often coalescing in central parts of mature thalli; **upper cortex:** paraplectenchymatous; **medulla:** mostly white to off-white but occasionally pale yellowish in patches or where exposed; **lower cortex:** irregularly prosoplectenchymatous; **lower surface:** darkening and becoming black inwardly, the peripheral lobes pale tan to whitish on the ends, dull to weakly shiny; rhizines: black and squarrosely branched; **Apothecia:** not seen (likewise for pycnidia); **Spot tests:** cortex all negative; medulla usually K-, C-, KC-, P-, but sometimes K+ pale yellow and KC+ yellow to orange in scattered areas; soralia (and associated medulla) K-, C-, KC-, P-, or some places K+ and KC+ yellowish; **Secondary metabolites:** variolaric acid, also sometimes small amounts of secalonic acid A.



Substrate and ecology: rock or mosses over rock, rare on bark; **World distribution:** western North America: Utah, Colorado, Arizona and California; **Sonoran distribution:** higher elevations in Arizona, southern California and Baja California Sur.

Notes: Smaller individuals of this species might be confused with either *P. enteroxantha* or *P. isidiigera*, depending on whether or not the sometimes positive medullary/soredial spot tests are observed. Normally, the large size of the thallus and broad peripheral lobes, their tendency to be concave and ascending, and the distinctive laminal soredia which become isidioid, should be enough to distinguish it from those species. The usual presence of variolaric acid also distinguishes *P. isidiomuscigena* from both those species.

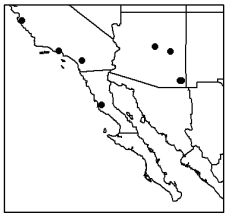
Physconia leucoleiptes (Tuck.) Essl., Mycotaxon 51: 94 (1994).

Basionym: *Physcia pulverulenta f. leucoleiptes* Tuck., Proc. Amer. Acad. Arts and Sciences 1: 224 (1847); Synonyms: *Physcia leucoleiptes* (Tuck.) Lettau, *Physconia kurokawae* Kashiwadani, Ginkgoana 3: 58 (1975): Illustration: Fig. 76 below.

Fig. 76. *Physconia leucoleiptes*, photo by T. L. Esslinger.

Thallus: foliose, up to 6 (-7) cm in diam., irregular to more often orbicular; **lobes:** linear to somewhat irregular-rounded and partly imbricate, 1-2 mm broad, ± flat to weakly and irregularly concave, prostrate; **upper surface:** gray to gray-brown or brown, with a partial (lobe ends) or occasionally almost completely pruinose, sorediate; **so-**

redia: in primarily marginal or terminal soralia, on short lateral branches, discrete and becoming weakly to strongly labriform as the upper cortex reflexes (at times the soralia become occasionally compressed (particularly at nodes along the segments); ± continuous, but the individual labriform portions still apparent), laminal soralia developing rarely; individual soredia granular to pseudocorticate and isidioid, pale or darkening; **upper cortex:** scleroplectenchymatous; **medulla:** white; **lower cortex:** irregularly prosoplectenchymatous; **lower surface:** of peripheral lobes usually distinctly white to off-white for a short distance, inward darkening to dark brown or black; rhizines: black and squarrosely branched; **Apothecia:** infrequent, up to 4 mm in diam., the margin thick and entire, not usually sorediate but becoming lobulate, the lobules often forming labriform soralia at the end; **ascospores:** 28-31 x 16-18 µm; **Spot tests:** cortex all negative; medulla usually K-, C-, and KC- (very rarely C+ rose, KC+ reddish), P-; soralia K+ pale to distinctly yellow, C-, KC+ yellow to yellow-orange, P-; **Secondary metabolites:** secalonic acid A (concentrated in and apparently restricted to the soralia).



Substrate and ecology: bark and rock; **World distribution:** North America and Asia; **Sonoran distribution:** rather rare in Arizona, southern California and Baja California.

Notes: This species is characterized by the marginal, weakly to strongly labriform soralia which contain secalonic acid A and usually react with both K and KC, by the lack of positive spot tests in the medulla, and by the scleroplectenchymatous upper cortex. Specimens with strongly labriform soralia have been commonly misdetermined as *P. perisidiosa*, an easy mistake if the distinctly corticate lower surface and reactive soralia are overlooked. Like essentially all sorediate species in the genus, the soredia of *P. leucoleiptes* sometimes become strongly isidioid and dark pigmented, which can obscure the K and KC spot test reactions. It is therefore essential to select younger and paler soralia for testing. Two other species with reactive soralia, *Physconia enteroxantha* and *P. fallax*, both have differently shaped soralia, as well as a paraplectenchymatous upper cortex.

I have concluded that *P. kurokawae*, which is morphologically identical and differs from *P. leucoleiptes* only by the production of gyrophoric acid in the medulla, does not merit taxonomic recognition, or at least not at the level of species. In eastern North America, where both are very common, there are no discernible differences in their ecology or distributions, and the two very commonly occur in mixed populations (and therefore in mixed collections). Furthermore, according to the intensity of the C and KC spot test reactions as well as the relative size and intensity of chromatogram spots, the concentration of gyrophoric acid in the medulla is extremely variable. The reactions vary from moderately strong to very faint, and in many cases can only be detected in the lower part of the medulla adjacent to the lower cortex. At the present time only one scrappy collection of the C+, KC+ variant has been found from the Sonoran region, that being a collection from the Santa Monica Mountains in California made apparently by Hasse (#161, NY).

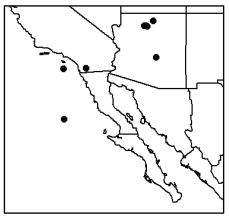
Physconia muscigena (Ach.) Poelt, Nova Hedwigia 9: 30 (1965).

Basionym: *Parmelia muscigena* Ach., Lichenographa Universalis 472 (1810); Synonym: *Physcia muscigena* (Ach.) Nyl.; Illustrations: Moberg, (1977), p. 88; St. Clair (1999), p. 150; McCune and Geiser (1997), p. 236; Brodo et al. (2001), p. 565.

Thallus: foliose, up to 12 cm in diam., usually irregular and often coalescent and entangled with other thalli, only occasionally orbicular; **lobes:** generally linear, discrete to entangled, 1-3 mm broad, usually ascending and noticeably concave, especially near the ends; **upper surface:** gray-brown to dark brown, partly to almost completely pruinose; without soredia or isidia, but sometimes developing smaller lobes or lobules centrally, which may be ascending like the peripheral lobes, sometimes becoming dense and turf-like, without soredia or isidia; **upper cortex:** paraplectenchymatous; **medulla:** usually white, occasionally pale yellow; **lower cortex:** irregularly prosoplectenchymatous; **lower surface:** pale or darker brown on the peripheral lobes, darkening to black inwardly, dull to weakly shiny; rhizines: black, mostly squarrosely branched; **Apothecia:** common but not rarely missing, up to 5

mm in diam., the margin entire or often developing lobules; **ascospores** 24-33 x 12-17 µm; **Spot tests:** usually all negative, the medulla occasionally K+ yellowish, KC+ yellow-orange (when the medulla is pigmented yellowish) [very rarely the upper cortex reacts K+ very faint and KC+ stronger yellowish, apparently due to the presence of variolaric acid]; **Secondary metabolites:** often absent, but sometimes producing secalonic acid A (accessory pigment) and/or variolaric acid (accessory).

Substrate and ecology: on mosses, *Selaginella*, or detritus, usually over soil or rock; **World distribution:** North America, Europe, Africa, Asia, South America; **Sonoran distribution:** southern California, Arizona and Guadalupe Island (Baja California).



Notes: The lack of soredia and isidia, the distinctive growth form with ascending, concave lobes, and the distinctive substrate usually make this a fairly easy to determine species. Moberg (1977) mentioned that extreme forms of this species and *P. distorta* (as *P. pulverulenta*) can be difficult to distinguish, and this is even more true for *P. muscigena* and *P. americana*, since there is no difference in anatomy of the upper cortex to help separate them. Only a few such problematic specimens have been seen, mostly poorly developed material or damaged specimens.

The two specimens from the coastal islands (San Clemente Island, California, and Guadalupe Island, Baja California) are a diminutive form, and bear some resemblance to *P. petraea* (Poelt) Vězda & Poelt, a *P. muscigena* relative so far known only from Europe. These two specimens are rather sparse, however, and one of them is heavily parasitized, and so more adequate material will be needed in order to evaluate the identity of this material.

Physconia perisidiosa (Erichsen) Moberg, Symb. Bot. Upsal. 22: 90 (1977).

Basionym: *Physcia perisidiosa* Erichsen, Verhandl. Bot. Vereins Prav. Brandenburg 72: 57 (1930); Synonym: *Physconia farrea* sensu Poelt (1966) non *Parmelia farrea* Ach.; Illustrations: McCune and Geiser (1997), p. 237; St. Clair (1999), p. 151; Brodo et al. (2001), p. 566; and Fig. 77 below.

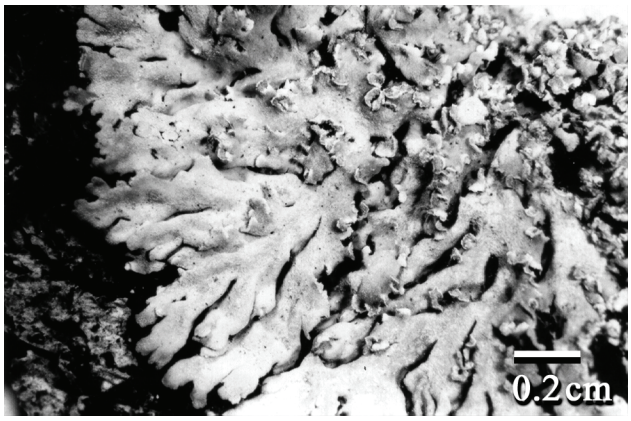
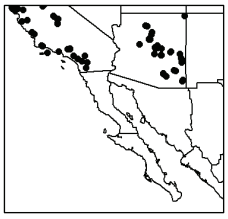


Fig. 77. *Physconia perisidiosa*, photo by T. L. Esslinger.

Thallus*:* foliose, up to 5 cm in diam., irregular and sometimes pulvinate, less often; **lobes:** linear to more often somewhat irregular-rounded and partly imbricate, 1-2 mm broad, mostly flat to weakly concave or convex, ± prostrate, frequently with scattered marginal lobules; **upper surface:** gray to gray-brown or commonly brown to dark reddish brown, orbicular, with a partial (lobe ends) or sometimes almost completely pruinose, sorediate; **soredia:** granular to strongly isidioid in older parts, darkening with age, in labriform soralia, primarily on the upturned lobe ends of lateral lobes or sometimes on main lobes; **upper cortex:** scleroplectenchymatous; **medulla:** white; **lower cortex:** absent or weakly organized and ± prosoplectenchymatous; **lower surface:** pale throughout (small specimens) or darkening centrally (in larger, better developed specimens), the lobe ends distinctly whitish and ecorticate, usually with distinctive blackish striations developing and becoming more numerous inward, these eventually coalescing to form a poorly organized and very dull 'cortex' in many (but not all) specimens; rhizines: black and squarrosely branched; **Apothecia:** rare, up to 1.5 mm in diam., the margin entire, sometimes becoming lobulate (lobules sometimes with labriform soralia); **ascospores:** 26-32 (-34) x 15.5-18 µm; **Spot tests:** all negative; **Secondary metabolites:** none detected.

Substrate and ecology: bark, rock, mosses over rock; **World distribution:** North America, Europe, Asia, Africa and South America; **Sonoran distribution:** southern California and Arizona (primarily upper elevation areas in the mountains).



Notes: The distinctive terminal labriform soralia (occasionally very sparse) and the partly to mostly ecorticate lower surface, usually with blackish striations, distinguish this species from all others in the study area. The lack of positive spot tests in both the medulla and the soralia also serve to separate it from other species with labriform or near labriform soralia (e.g. *P. leucoleiptes*).

PLACIDIOPSIS

by O. Breuss

Placidiopsis Beltr., Lich. Bassan.: 212 (1858).

Family: Verrucariaceae; Type: *Placidiopsis grappae* Beltr. = *P. cinerascens* (Nyl.) Breuss; No. species: 14 worldwide; Selected lit.: Breuss (1996).

Life habit: lichenized, although may appear lichenicolous when superficially growing on algal/lichen crusts; **Thallus:** squamulose, attached by a loose rhizohyphal web, a central bundle of rhizohyphae or rhizines; **upper surface:** continuous, pale to dark brown or greenish gray, dull, smooth or very minutely scabrose, partly with pruina deriving from disintegration of epinecral layer; soredia and isidia absent; **upper cortex:** absent or as in *Catapyrenium*, epinecral layer amorphous, composed of dead collapsed cortical cells; **medulla:** white, filamentous to subparaplectenchymatous; **photobiont:** primary one a chlorococcoid alga, secondary photobiont absent; **lower cortex:** (if present al all) (sub)paraplectenchymatous; **lower surface:** pale to blackish; **Ascomata:** perithecial, laminal, broadly pyriform or subglobose, immersed, without or with a small apical involucrellum in one species; exciple: hyaline, brown or brown-black; interascal filaments: absent or soon disappearing (present in early stages of development); ostiolar filaments: present, simple or distally sparsely furcate; **asci:** clavate, non-amyloid, thin-walled, apically slightly thickened, with a small indentation (ocular chamber), 8-spored; **ascospores:** ellipsoid, ovoid or subfusiform, hyaline, 2-celled; walls: thin, smooth, without halo; **Conidiomata:** not seen; **Secondary metabolites:** none detected; **Geography:** in arid, semi-arid and arctic-alpine regions of the Northern Hemisphere; **Substrate:** on soil, detritus, bryophytes, calciferous or non-calcareous rocks or algal/lichen crusts.

Notes: It is closely related to *Catapyrenium* s. str., from which it is separated by its septate ascospores and the type of ascus apex.

The Species

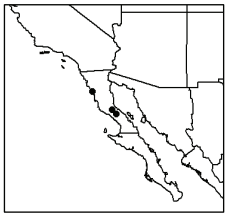
Placidiopsis cinerascens (Nyl.) Breuss, Plant Syst. Evol. 148: 315 (1985).

Basionym: *Endocarpon cinerascens* Nyl., Bot. Not. 1853: 160 (1853); Synonyms: see Breuss (1996); Illustration: Breuss (1996), p. 77.

Thallus: squamulose, 0.3-3 mm diam.; **squamules:** 0.15-0.35 mm diam., 0.15-0.35 mm thick, discrete to contiguous or with margins slightly overlapping, flat or slightly convex, broadly attached to the substrate, roundish or incised-lobed; **upper surface:** greenish gray to brownish, dull, naked or slightly grayish pruinose; **upper cortex:** 15-25 µm, always overlain by an epinecral layer 10-30 µm; **medulla:** white; algal layer: normally filling most of the thallus; algal-free medulla (in thick squamules): with many spherical cells 6-11 µm in diam.; **lower cortex:** indistinct, composed of a few rows of more densely aggregated spherical cells; rhizohyphae: hyaline, 3-4 µm thick; **lower surface:** pale, fastened by a loose rhizohy-

phal weft; **Perithecia:** broadly pyriform to almost globose, up to 0.3 mm broad and ± bulging the lower side of squamules; exciple: colorless to yellowish, black around ostiolum; periphyses: 20-30 x 2.5-3 µm; apical cell: often slightly swollen (-4 µm); **asci:** oblong clavate, 55-65 x 11-16 µm, 8-spored; **ascospores:** ellipsoid or ovoid, 2-celled, often slightly constricted at the septum, *c.* 15-19 x 6-7.5 µm; **Spot tests:** all negative; **Secondary metabolites:** none detected.

Substrate and ecology: on ± calciferous soil on open places; Californian specimens are from serpentine soil; **World distribution:** mediterranean Europe and Morocco, central Asia, SW North America and Mexico in mediterranean climates; **Sonoran distribution:** Baja California.



PLACIDIUM

by O. Breuss

Placidium A. Massal., Symmicta: 75 (1855).

Family: Verrucariaceae; Type: *Placidium michelii* A. Massal.; No. species: 32 world-wide; Selected lit.: Breuss (1990 & 1993).

Life habit: lichenized; **Thallus:** squamulose; **squamules:** almost leafy, appressed or with margins free from the substrate; **upper surface:** various shades of brown, smooth, dull or shiny; **upper cortex:** paraplectenchymatous, 30-130 µm thick, composed of large (6-20 µm), angular, strongly conglutinated cells with the separating hyphal walls ± thickened above, often overlain by an epinecral layer; **medulla:** white, composed of irregularly interwoven filamentous hyphae (prosoplectenchymatous), or with ± numerous globular cells; **photobiont:** primary one a *Myrmecia*, secondary photobiont absent; algal layer: horizontally continuous, sharply delimited from the upper cortex; algal cells: 7-18 µm in diam.; **lower cortex:** paraplectenchymatous or composed of more densely aggregated globular cells or lacking; **lower surface:** pale to black, usually attached by a weft of hyaline or brownish rhizohyphae, with additional true rhizines in a few species; **Ascomata:** perithecial, laminal, immersed, broadly pyriform or subglobose, without involucrellum; exciple: hyaline or yellowish or brown; interascal filaments: absent; hymenial gel: amyloid, I+ reddish or blue, always blue after pretreatment with K; ostiolar filaments: present; **asci:** ± cylindrical, thin-walled (I-), without a tholus, 8-spored; **ascospores:** uniseriate at least when young, ellipsoid to subglobose, obtuse at the poles, aseptate; wall: hyaline, smooth, without thickenings, halo or sculpturing; **Conidiomata:** pycnidial, *Dermatocarpon*-type (Harada 1993), multilocular; **conidia:** oblong-ellipsoid or bacilliform; **Secondary metabolites:** none detected; **Geography:** world-wide, but mainly in temperate regions; **Substrate:** soil, moss, detritus, rock or bark.

Key to the spcies of ***Placidium*** from the Sonoran region:

1. Squamules convex to almost bullate, pedunculate, up to 2 mm wide, forming an areolate appearing thallus 2
1. Squamules flat or variously wavy, not pedunculate, larger 3

2. Spores broadly ellipsoid to subglobose, 13-17 x 8-11 µm; medulla of ± filamentous hyphae .... ***P. acarosporoides***
2. Spores narrower ellipsoid, 15-19 x 5-7 µm; medulla cellular ..... ***P. lesdainii***

3. Cells of lower cortex angular, conglutinated, in distinct vertical columns ..... ***P. lachneum***
3. Cells of lower cortex roundish-angular, irregularly arranged, or lower cortex lacking 4

4. Rhizohyphae entangled in stilt-like fascicles supporting the squamules ..... ***P. tuckermanii***

4. Rhizohyphae intricately interwoven to form a hyphal weft penetrating the substrate, additional rhizines present in some species 5

5. Squamules rhizinate 6
5. Rhizines lacking 7

6. Rhizines thin and inconspicuous; medulla of filamentous hyphae; lower cortex distinct, subparaplectenchymatous ..... ***P. pseudorufescens***
6. Rhizines usually conspicuous; medulla with many spherical cells, lower cortex indistinct or lacking .... ***P. lacinulatum***

7. Perithecial walls black, thin (*c.* 20-25 µm) . ***P. michelii***
7. Perithecial walls pale (colorless or yellowish to pale brown), thicker 8

8. Pycnidia marginal, appearing as ± globular, dark knobs at the edge of the squamules 9
8. Pycnidia laminally immersed, their mouth showing as dark dots on the thallus surface, or unknown 11

9. Ascospores 15-20 x 7.5-9.5 µm; medulla of filamentous hyphae; rhizohyphae 6-7.5 µm in diam. ... ***P. rufescens***
9. Ascospores smaller; medulla with many globular cells; rhizohyphae thinner 10

10. Squamules usually broadly adnate; black-rimmed; lower surface black throughout; ascospores 11-14 x 5-6.5 µm ..... ***P. andicola***
10. Squamules usually with free margins, not black-rimmed; lower surface mostly pale; ascospores 12-17 x 5.5-7.5 µm ..... ***P. pilosellum***

11. Ascospores broadly ellipsoid to subglobose, thick-walled ..... ***P. californicum***
11. Ascospores narrowly ellipsoid, thin-walled 12

12. Medulla of filamentous hyphae; lower cortex well delimited, cells 12-20 µm in diam.; squamules up to 10 mm wide ..... ***P. chilense***
12. Medulla with many globular cells; lower cortex hardly discernible, cells 10-16 µm in diam.; squamules usually smaller 13

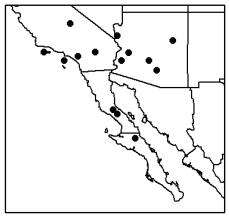
13. Conidia bacilliform, 5-7 x 1 µm; species rare .... ***P. fingens***
13. Conidia oblong-ellipsoid, 2.5-4 x 1.3-2 µm; species common ..... ***P. squamulosum***

The Species

Placidium acarosporoides (Zahlbr.) Breuss, Bull. Calif. Lich. Soc. 7: 39 (2000).

Basionym: *Dermatocarpon acarosporoides* Zahlbr., Beih. Bot. Centralbl. 13: 153 (1903); synonym: *HeteroplacidIum acarosporoides* (Zahlbr.) Breuss; Illustration: Thomson (1987), p. 29 as *Catapyrenium acarosporoides*.

Thallus: squamulose; **squamules:** ± convex to almost bullate, rounded to slightly lobed, each with a central peduncle, up to 2 mm wide and 0.7 mm thick (including the central peduncle), discrete or (mostly) contiguous (thus forming an areolate-appearing thallus); **upper surface:** dark brown to red brown, smooth, matt or glossy; **upper cortex:** 40-60 µm thick; **medulla:** white, nearly prosoplectenchymatous, with a varying number of globose cells (in thick squamules distinctly filamentous); algal layer: *c.* 70-100 µm high; **lower cortex:** indistinctly developed or lacking, composed of ± loosely arranged globular cells (9-12 µm in diam.), brownish below; **lower surface:** brownish; rhizohyphae: hyaline, confined to the central pedunculate area; **Perithecia:** few per squamule, subglobose, up to 0.4 mm wide; exciple: colorless except for the apex; periphyses: short (up to 30 µm); **asci:** primarily cylindrical, later becoming narrowly clavate, 55-60 x 20 µm; **ascospores:** uniseriate at early stages, then subbiseriate, broadly ellipsoid, *c.* 13-17 x 8-11 µm; **Pycnidia:** laminal, immersed; **conidia:** oblong to shortly cylindrical, 3-5 (-6) x 1 µm; **Spot tests:** all negative; **Secondary metabolites:** none detected.



Substrate and ecology: granitic rocks and sandstone on open dry sites; **World distribution:** SW North America, Chile, South Africa; **Sonoran distribution:** fairly common in Arizona, California, Baja California and Baja California Sur.

Notes: This is a characteristic species with ± glossy brown, ± convex squamules and broadly ellipsoid spores. The hyphal construction of the medulla varies somewhat; the medulla of the thickest squamules is distinctly fila-

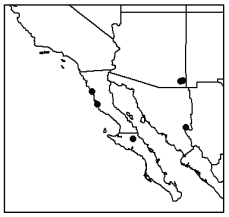
mentous at least partially, especially in the central parts. Globular cells occur in varying numbers and may dominate in thin squamules especially of poorly developed material. The asci tend to be clavate such that the species was included in *Heteroplacidium* by Breuss (1996). However, they are distinctly cylindrical at an early stage. The complex thallus anatomy also is characteristic of *Placidium*. A close relative with narrowly ellipsoid spores is *P. lesdainii*.

Placidium andicola (Breuss) Breuss, Ann. Naturhist. Museum Wien 98 B Suppl.: 38 (1996).

Basionym: *Catapyrenium andicola* Breuss, Pl. Syst. Evol. 185: 20 (1993); Illustration: Breuss (1993), p. 21.

Thallus: squamulose, **squamules:** dispersed or adjacent, broadly adnate but usually the extreme edges slightly ascending, 2-4 mm wide, up to 0.4 mm thick, rounded or lobed, black-rimmed; **upper surface:** brown, dull; **upper cortex:** *c.* 40 µm thick, with or without a thin epinecral layer; **medulla:** with many spherical cells (10-16 µm in diam.; algal layer: *c.* 70-120 µm high; **lower cortex:** indistinct, composed of more densely packed spherical cells; **lower surface:** dark brown to jet black throughout; rhizohyphae: hyaline, becoming slightly brownish, 5-6 µm thick; **Perithecia:** up to 0.5 mm wide, broadly pear-shaped; exciple: pale except for the ostiolum or darkening with age; periphyses: 35-45 µm long; **asci:** cylindrical, 65-80 x 10-14 µm, 8-spored; **ascospores:** uniseriate, ellipsoid, *c.* 11-14 x 5-6.5 µm; **Pycnidia:** marginal, forming knob-like projections; **conidia:** oblong-ellipsoid, 2.5-4 x 1.3-2 µm; **Spot tests:** all negative; **Secondary metabolites:** none detected.

Substrate and ecology: soil, mostly in inland sites at higher, montane elevations, descending to coastal scrubland in Baja California; **World distribution:** South America (Andes), SW North America; **Sonoran distribution:** SE Arizona, Sonora, Baja California and Baja California Sur.

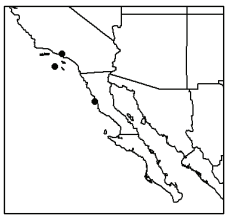


Notes: Anatomically and in pycnidial characters *Placidium andicola* is very similar to *P. pilosellum* that has somewhat larger spores and whose squamules tend to have free margins and usually pale lower surfaces. However, the discrimination may be difficult.

Placidium californicum Breuss, Bull. Calif. Lich. Soc. 7: 39 (2000).

Thallus: squamulose; **squamules:** *c.* 2-4 mm wide and 0.35 mm thick, fully appressed, roundish or slightly lobed, ± dispersed or a few adjacent; **upper surface:** brown, dull; **upper cortex:** *c.* 30-60 µm thick, epinecral layer almost lacking or up to 20 µm thick; **medulla:** white, usually with numerous globose cells (*c.* 9-14 µm in diam.); algal layer: *c.* 70-100 µm high; **lower cortex:** absent or at least lacking distinctive development; **lower surface:** brownish; rhizohyphae: hyaline, rather thin (3.5-4.5 µm); **Perithecia:** broadly pyriform to subglobose, up to 0.45 mm wide, with colorless wall; **asci:** cylindrical, 70-80 x 13-17 µm, 8-spored; **ascospores:** uniseriate, subglobose or broadly ellipsoid, 10-13 (-15) x (7.5-) 8-9 (-10) µm, rather thick-walled; **Pycnidia:** not seen; **Spot tests:** all negative; **Secondary metabolites:** none detected.

Substrate and ecology: soil, in open places, mostly coastal; **World distribution:** endemic to SW North America; **Sonoran distribution:** on coastal sites of southern California and Baja California.



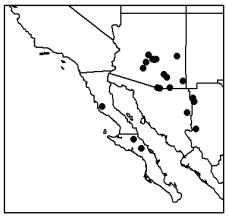
Notes: The species very much resembles *P. squamulosum*, but differs in its almost spherical and thick-walled spores and in having thinner rhizohyphae.

Placidium chilense (Räsänen) Breuss, Ann. Naturhist. Museum Wien 98 B Suppl.: 38 (1996).

Basionym: *Dermatocarpon chilense* Räsänen, Revista Sudam. Bot. 5: 71 (1938); Synonym: *Catapyrenium chilense* (Räsänen) Breuss; Illustration: Breuss (1993), p. 22.

Thallus: squamulose or almost foliose; **squamules:** up to more than 10 mm wide and 0.6 mm thick, loosely adnate with margins free from the substrate or ± wavy and overlapping to imbricate; **upper surface:** light to medium brown, dull to slightly glossy; **upper cortex:** 30-60 µm thick, overlain by an epinecral layer (5-25 µm thick); **medulla:** white, prosoplectenchymatous, up to 300 µm thick, normally with (very) few spherical cells; algal layer: *c.* 80-150 µm high; **lower cortex:** well delimited and 40-90 µm thick, composed of roundish-angular cells (12-20 µm in diam.); **lower surface:** pale along a broad marginal zone, blackening towards the center, rarely dark throughout; marginal zone: bare of rhizohyphae and often slightly scabrous or with short hyphal outgrowths; rhizohyphae: hyaline, *c.* 5-6 µm thick, forming a dense hyphal weft in central parts of the squamules; **Perithecia:** up to 0.5 mm broad, with pale walls; periphyses: 25-35 x 3 µm; **asci:** cylindrical, 60-70 x 7-10 µm, 8-spored; **ascospores:** uniseriate, ellipsoid, *c.* 10-15 x 5-6 (-6.5) µm; **Pycnidia:** laminal, immersed; **conidia:** oblong to shortly cylindrical, 3-4 x 1-1.5 µm; **Spot tests:** all negative; **Secondary metabolites:** none detected.

Substrate and ecology: soil, debris and mossy rocks, rarely directly on rock (sandstone, rhyolite, andesite, limestone) mostly in somewhat protected situations in open woodland or scrubland; **World distribution:** South America and southern North America; **Sonoran distribution:** common in Arizona, California, Baja California and Baja California Sur, Sonora and Chihuahua.



Notes: *Placidium chilense* is an easily discernible species due to its comparatively large, almost leafy, thick squamules with a prosoplectenchymatous medulla, small spores and laminal pycnidia. Specimens with unusually numerous spherical medullary cells may be confused with *P. squamulosum*, but the cells of the lower cortex are smaller in the latter species. *Placidium rufescens* is similar in appearence, but easily distinguished by marginal pycnidia and large spores. Large forms of *P. lacinulatum* may be similar, but differ clearly in the anatomy of medulla and in having rhizines.

Placidium fingens (Breuss) Breuss, Ann. Naturhist. Museum Wien 98 B Suppl.: 38 (1996).

Basionym: *Catapyrenium fingens* Breuss, Stapfia 23: 79 (1990).

Thallus: (description after American material): squamulose; **squamules:** discrete, up to 5 mm wide and 0.25-0.35 mm thick, ± deeply lobate, fully appressed with only the very edges somewhat elevated; **upper surface:** pale to medium brown, dull; **upper cortex:** 40-60 µm thick, with a thin epinecral layer; **medulla:** white, with many spherical cells (10-16 µm in diam.); algal layer: *c.* 50-80 µm high; **lower cortex:** hardly discernible, composed of more densely aggregated spherical cells, the lowermost ones brownish; **lower surface:** pale, brownish, with a rhizohyphal weft over all of the underside and ± projecting outwards; rhizohyphae: hyaline, 5-6 µm in diam.; **Perithecia:** broadly pyriform, up to 0.4 mm wide, with colorless to pale brownish walls; periphyses: 30-35 x 2-3 µm; **asci:** cylindrical, 70-80 x 11-15 µm, 8-spored; **ascospores:** uniseriate, ellipsoid, 11-15 x 5-6.5 µm; **Pycnidia:** laminal, immersed; **conidia:** bacilliform, 5-7 x 1 µm; **Spot tests:** all negative; **Secondary metabolites:** none detected.

Substrate and ecology: soil and bark (*Quercus douglasii* in California) in warm, dry places; **World distribution:** rare in Spain, Canary Islands (Tenerife) and SW North America; **Sonoran distribution:** Arizona and southern California, only a few collections.

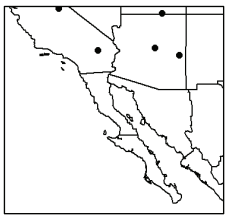
Notes: The corticolous specimens agree in all important respects with terricolous material. All Californian samples were found on bark of oak, growing side by side with *Catapyrenium psoromoides*. *Placidium fingens* comes close to *P. squamulosum*, from which it differs mainly in its longer, bacilliform conidia. Those of the latter species are oblong-ellipsoid and shorter. *Placidium pilosellum* has marginal pycnidia with short, oblong-ellipsoid conidia. The primarily bark-inhabiting *P. tuckermanii* is much different (see under that species).

Placidium lachneum (Ach.) de Lesd., Ann Cryptog. Exot. 5: 100 (1932).

Basionym: *Lichen lachneus* Ach., Lich. Svec. Prodr.: 140 (1798); Synonyms: *Catapyrenium lachneum* (Ach.) R. Sant., *Dermatocarpon lachneum* (Ach.) A. L. Sm.; Illustrations: Breuss (1990), figs. 12-15; Purvis et al. (1992), p. 671.

Thallus: squamulose; **squamules:** scattered to adjacent or slightly overlapping, up to 10 mm wide (but usually smaller), *c.* 0.3-0.6 mm thick, roundish to lobate, appressed throughout or with ascending margins and saucer-shaped or variously wavy, often with somewhat raised edges; **upper surface:** dark brown or red brown, rarely paler, dull, smooth or slightly roughened; **upper cortex:** *c.* 40-60 µm thick; epinecral layer lacking or very thin; **medulla:** white, prosoplectenchymatous, thick (more than 100 µm), composed of irregularly interwoven hyphae with very few globose cells; algal layer: *c.* 100 µm thick; **lower cortex:** abruptly delimited from medulla, composed of conglutinated, perpendicular hyphae (thus cells in distinct vertical columns 40-90 µm high); the lowermost cells: with a conspicuous black pigment; **lower surface:** black throughout, naked where free from the substrate, the remaining part fixed with a dense hyphal weft; rhizohyphae: 6-7.5 µm thick, hyaline or slightly brownish in proximal parts; **Perithecia:** broadly pyriform, normally not bulging the lower side of the squamules, with colorless walls; periphyses: 40-50 x 2.5-3.5 µm; **asci:** cylindrical, 70-90 x 12-15 µm, 8-spored; **ascospores:** uniseriate, ellipsoid, *c.* 14-18 x 6-8 µm; **Pycnidia:** marginal, prominent as black globular knobs; **conidia:** bacilliform, 5-7 x 1-2 µm; **Spot tests:** all negative; **Secondary metabolites:** none detected.

Substrate and ecology: soil, mosses and debris, arctic-alpine; **World distribution:** northern and high-mountainous regions of Europe, Asia, North America, the Venezuelan Andes; **Sonoran distribution:** Arizona and southern California.



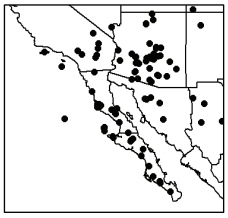
Notes: A very distinctive species that is hardly to be confused with any other *Placidium* species due to its very characteristic lower cortex that is made of conglutinated, angular (not rounded) cells in distinct vertical columns and contrasts sharply from the filamentous medullary tissue. The construction of the lower cortex is similar to that in *Dermatocarpon* but less strongly conglutinated.

Placidium lacinulatum (Ach.) Breuss, Ann. Naturhist. Museum Wien 98 B Suppl.: 39 (1996).

Basionym: *Endocarpon hepaticum* var. *lacinulatum* Ach., Lich. Univ.: 299 (1810); Synonyms: *Catapyrenium lacinulatum* (Ach.) Breuss and *Dermatocarpon hepaticum* var. *pruinosum* de Lesd.; Illustrations: Breuss (1990), fig. 16; Breuss (2000c), p. 706; Brodo et al. (2001), p. 569.

Thallus: squamulose; **squamules:** *c.* 3-8 mm wide, c. 0.3-0.5 mm thick; roundish to deeply lobed, discrete or contiguous, flat and closely adnate to the substrate or loosely adnate with ± raised and wavy margins and then with a crispy appearance, ± overlapping, sometimes forming cushion-like aggregates; **upper surface:** pale to dark brown, dull, epruinose or slightly pruinose; **upper cortex:** 40-80 µm thick; epinecral layer: lacking or very thin; **medulla:** white, with many spherical cells (8-14 µm in diam.); algal layer: *c.* 60-100 µm thick; **lower cortex:** indistinct or lacking, composed of ± densely aggregated, roundish cells; rhizohyphae: colorless, 4-5 µm in diam.; **lower surface:** pale or darkening, rhizinate; rhizines: few to many per squamule, pale or brown, simple or ± branched, partly anastomosing, main strands up to 0.3 mm thick and more than 15 mm long (but often smaller and inconspicuous!); **Perithecia:** broadly pyriform to subglobose, up to 0.6 mm broad and ± bulging on the underside of the squamules; perithecial wall: colorless or brownish, rarely darkening (in overmature specimens and certain varieties): periphyses: 25-35 x 2.5-3.5 µm; **asci:** cylindrical, 65-80 x 12-17 µm, 8-spored; **ascospores:** uniseriate, ellipsoid, *c.* 12-16 x 6-7.5 µm (in the typical form; see below); **Pycnidia:** laminal, immersed; **conidia:** rather variable in shape (ellipsoid-oblong to subcylindrical to shortly cylindrical), 3-5 x 1.3-2 µm; **Spot tests:** all negative; **Secondary metabolites:** none detected.

Substrate and ecology: soil (mostly fine-grained) in open, dry areas from low to high elevations; **World distribution:** Europe, Asia, northern Africa, the Americas in temperate latitudes; **Sonoran distribution:** very common and frequent in Arizona, California, Baja California, Baja California Sur, Chihuahua and Sonora.



Notes: *Placidium lacinulatum* is anatomically very similar to *P. squamulosum* but differs in being rhizinate. The rhizines vary considerably in size and number from few and indistinct to large and conspicuous but are always visible by careful investigation (of wetted specimens as the rhizines easily break off in dry condition). They may originate from most of the underside or centrally crowded. The species is very variable according to thallus form, pigmentation of exciple and underside, and shape and size of ascospores and conidia and may represent several varieties.

Key to varieties of ***Placidium lacinulatum*** in the Sonoran region:

1. Exciple colorless or yellowish brown; rhizines whitish to pale brownish; conidia oblong-ellipsoid to shortly subcylindrical, 3-5 x 1.3-2 µm 2
1. Exciple and rhizines dark brown to blackish; conidia (sub-) cylindrical, 4-6 x 1-1.5 µm ..... var. ***atrans*** in ed.
   2. Underside of squamules ± red ... var. ***erythrostratum***
   2. Underside of squamules pale or darkening (brown, rarely blackish), not reddish 3
3. Ascospores 12-17 x 6-7.5 µm; asci 65-80 x 12-17 µm .. .. var. ***lacinulatum***
3. Ascospores 15-19 x 7.5-9.5 (-10) µm; asci 65-75 x 18-25 µm ..... var. ***latisporum***

Notes: The infraspecific grouping of *Placidium lacinulatum* is not yet fully clear; intermediate types are found due to the high variability of the species. The variety *lacinulatum* and var. *atrans* are widely distributed in North America; var. *erythrostratum* seems to be confined to the southwest; var. *latisporum* is known with certainty only from Baja California.

Placidium lesdainii Breuss, **sp. nov.**

Diagnosis: *Habitu Placidio acarosporoidi congruens a quo differt sporis angustiore ellipsoideis medullaque subparaplectenchymatica.*

Type: MEXICO, Baja California Sur, along Rte 1, 68 km NE of Ciudad Insurgentes, 25°36'N, 111°20'W, in pass through the Sierra de la Giganta, on intrusive volcanic rock, 400 m, 8.1.1989 T. H. Nash 26045 (ASU, holotype).

Illustration: Fig. 78 below.

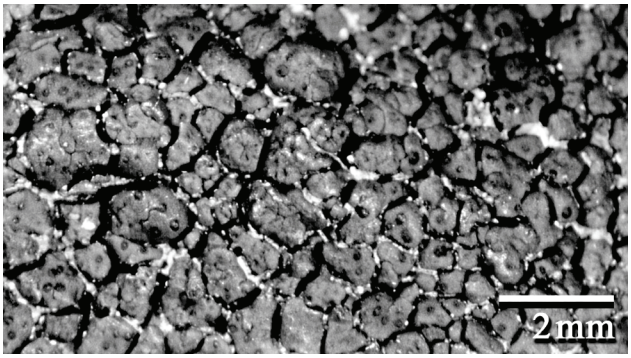
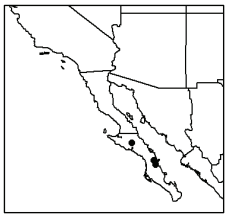


Fig. 78. Holotype of *Placidium lesdainii*, photo by O. Breuss.

Other specimens examined: ibid. H. Sipman 25040, 25043, 25046 (B) & A. Aptroot 24694 (U); Sierra de la Giganta at 70 km post, 25°57'N, 111°30'W, 360-470 m alt., on rocks, 19.2.1993 R. Moberg 10392 (UPS); 3.5 km along road to Punta Abreojos from Hwy 1, hill, 27°15'N, 113°10'W, 150 m, on rocks, 21.2.1993 R. Moberg 10404 (UPS).

Thallus: squamulose; **squamules:** flat to almost bullate, rounded to slightly lobed, pedunculate, up to 1.5 mm wide and 0.6 mm thick, contiguous, secondarily divided by cracks, forming an areolate appearing thallus; **upper surface:** brown, smooth, matt; **upper cortex:** 20-40 µm thick; **medulla:** white, subparaplectenchymatous with globose cells (8-11 µm in diam.); algal layer: *c.* 80-110 µm thick; algal cells: 6-12 µm in diam.; **lower cortex:** not

discernible, composed of more densely packed globose-angular cells (8-11 µm in diam.), the lowermost ones brown; **lower surface:** brownish; rhizohyphae: hyaline, confined to the central peduncle; **Perithecia:** subglobose, up to 0.45 mm wide; exciple: colorless except for the upper third; periphyses: 20-30 µm long; **asci:** subcylindrical to narrowly clavate, 8-spored; **ascospores:** uniseriate at early stages but soon biseriate, narrowly ellipsoid, 15-19 x 5-7 µm; **Pycnidia:** laminal, immersed; **conidia:** cylindrical, 4-6 x 1 µm; **Spot tests:** all negative; **Secondary metabolites:** none detected.



Substrate and ecology: on (volcanic) rocks in dry, open situation. **World and Sonoran distribution:** known only from Baja California Sur.

Notes: *Placidium lesdainii* is morphologically indistinct from *P. acarosporoides*, from which it differs in its cellular medullary tissue and narrow ellipsoid ascospores (15-19 x 5-7 µm versus 13-17 x 8-11 µm). The hyphal texture of the medulla is somewhat variable in *P. acarosporoides* and well developed material necessary to reveal the difference, but the shape of the spores is a constant diagnostic feature. *Placidium lesdainii* was possibly already described by de Lesdain (as one out of several *Endopyrenium* species) but the types were not available, and from the descriptions none of his species could be assigned with certainty to this taxon.

Placidium michelii A. Massal., Sched. Crit. Lich. 5: 100 (1856).

Synonyms: *Catapyrenium michelii* (A. Massal.) R. Sant., *Dermatocarpon michelii* (A. Massal.) Zwackh.

Thallus: squamulose, **squamules:** 1-5 mm in diam., rather thin (up to 0.25 mm thick), dispersed or in groups, appressed to the substrate, roundish or slightly lobed; **upper surface:** pale to dark chestnut brown, dull; **upper cortex:** 20-40 µm thick; epinecral layer: very thin or lacking; **medulla:** white, with many spherical cells (*c.* 9-14 µm in diam.); algal layer: c. 50-80 µm thick; **lower cortex:** composed of 2-3 rows of roundish-angular cells (outermost ones: dark brown); **lower surface:** black, fastened by a dense rhizoidal weft; rhizohyphae: hyaline, 4-6 µm thick; **Perithecia:** pyriform, up to 0.35 mm broad, bulging the lower side of the squamules; wall: dark brown, thinner than in the other *Placidium* species (hardly more than 25 µm wide); periphyses: 30-40 x 2.5 µm; **asci:** cylindrical, *c.* 60-70 x 10-13 µm, 8-spored; **ascospores:** uniseriate, ellipsoid, 11-15 x 5-7 µm; **Pycnidia:** laminal, immersed; **conidia:** ellipsoid-oblong, 2.5-3.5 x 1.5 µm; **Spot tests:** all negative; **Secondary metabolites:** none detected.

Substrate and ecology: soil; **World distribution:** widely distributed but scattered in Europe, Asia and North America, but not known from the Southern Hemisphere; **Sonoran distribution:** rare in Arizona and southern California (San Diego Co.).

Notes: It is very similar to *Placidium squamulosum,* from which it differs primarily in its dark, thin perithecial walls and the thinner periphyses. The squamules tend to be smaller and are always black on the lower side.

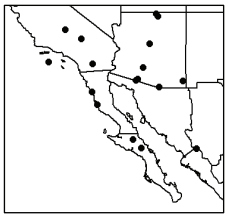
Placidium pilosellum (Breuss) Breuss, Ann. Naturhist. Museum Wien 98 B Suppl.: 39 (1996).

Basionym: *Catapyrenium pilosellum* Breuss, Stapfia 23: 98 (1990); Illustrations: Breuss (1990), fig. 18; Wirth (1995), p. 253.

Thallus: squamulose; **squamules:** *c.* 2-6 mm wide, rather thin (0.25-0.4 mm thick), roundish or lobed, flat and fully attached or ± wavy and with margins free from the substrate (raised or downrolled), adjacent or overlapping; **upper surface:** yellowish brown, tan or dark brown, often with an orangish tinge; **upper cortex:** *c.* 40-60 µm; epinecral layer: 10-40 µm thick; **medulla:** white, with many spherical cells (9-17 µm in diam.); algal layer: *c.* 80-120 µm thick; **lower cortex:** composed of more densely aggregated spherical cells (9-16 µm diam.) if discernible at all; **lower surface:** usually pale, sometimes darkening centrally, rarely black throughout; attached by a rhizohyphal weft; rhizohyphae: hyaline, 4.5-6 µm in diam.; **Perithecia:** broadly pyriform, up to 0.5 mm wide, bulging the lower side of the squamules; exciple: colorless or pale

yellowish brown; periphyses: 30-40 x 2.5-3.5 µm; **asci:** cylindrical, 70-90 x 10-15 µm, 8-spored; **ascospores:** uniseriate, ellipsoid, *c.* 12-17 x 5.5-7.5 µm; **Pycnidia:** marginal, forming knob-like projections; **conidia:** oblong-ellipsoid, 3-4 x *c.* 1.5 µm; **Spot tests:** all negative; **Secondary metabolites:** none detected.

Substrate and ecology: soil, moss, debris, preferably in dry, mild climate; **World distribution:** Europe (excluding the Alps and northernmost parts), North Africa, SW Asia, Australia, temperate North America; **Sonoran distribution:** common in Arizona, southern California, Baja California, Baja California Sur, and Sinaloa.



Notes: The hyphal outgrowths along the lobe margins and even on the upperside of young squamules described from European material are often lacking in extra-European material. Anatomically the species is identical with *Placidium squamulosum*, but easily separable by its marginal pycnidia. The distinction from *P. andicola* may be difficult (see under that species). *Placidium rufescens* also has the same pycnidial characters but thicker squamules with a well developed prosoplectenchymatous medulla, thicker rhizohyphae, and much larger spores.

Placidium pseudorufescens Breuss, **sp. nov.**

Diagnosis: *species habitu Placidio rufescenti similis, sed squamis rhizinis substrato affixis, sporis minoribus, pycnidiis immersis et conidiis cylindricis differt.*

Type: MEXICO, Baja California Sur, 33 mi SW of Loreto, Sierra de la Giganta, 25°43´ N, 111°24´W, on soil over volcanic rock, 28.5.1974, T. H. Nash 8879 (ASU, holotype).

Other specimens examined: Baja California Sur, near Km 68 on road from Ciudad Insurgentes to Loreto (Route 1), pass through the Sierra de la Gigante, 25°36´N, 111° 20´W, *c.* 400 m, rocky mountain slope with thorn forest, on nearly vertical rockface at foot of cliff, H. Sipman 25045 (B); - Baja California Sur, Sierra de La Laguna, along river bottom below Picacho de La Laguna, elev. 500 m, 23°30´N, 110°00´W, C. M. Wetmore 72040 (MIN).

Fig.79. *Placidium pseudorufescens*, photo by O. Breuss.

Thallus: squamulose or subfoliose; **squamules:** rather large (up to 7 mm wide and 0.3 - 0.5 mm thick) and almost leafy, densely aggregated to slightly overlapping, lobate; margins: variously wavy, free from the substrate and upturned or downturned; **upper surface:** medium to dark brown, dull; **upper cortex:** 40-60 µm thick, overlain by a thin epinecral layer; **medulla:** white, thick, composed of intricately interwoven filamentous hyphae; algal layer: about 100-130 µm thick; **lower cortex:** distinct, subparaplectenchymatous, composed of roundish cells (8-13 µm in diam.), up to 50 µm thick; **lower surface:** pale brown, naked where free from the substrate, central parts with a rhizohyphal weft; rhizohyphae: hyaline, *c.* 5 µm in diam., lacking in a broad marginal zone; also rhizinate; rhizines: few, whitish or pale brownish, thin (50-100 µm in diam.), slightly branched; **Perithecia:** broadly pyriform, up to 0.4 mm broad, with colorless exciple; **asci:** subcylindrical to narrowly clavate, 50-65 x 14-18 µm, 8-spored; **ascospores:** primarily uniseriate, soon (sub)biseriate, ellipsoid, 11-14 x 6-7.5 µm; **Pycnidia:** laminal, immersed; **conidia:** bacilliform, 4-5 x 1-1.5 µm; **Spot tests:** all negative; **Secondary metabolites:** none detected.

Substrate and ecology: directly on (volcanic) rock or over cyanophilic lichens thereon or on thin earth cover

over rock; **World** and **Sonoran distribution:** known only from Baja California Sur.

Notes: *Placidium pseudorufescens* is the only rhizinate species of the genus that is found growing directly on rock with rhizines fixed in minute fissures. It is morphologically similar to *P. rufescens*, from which it differs in being rhizinate and having laminally immersed pycnidia with bacilliform conidia, and in having much smaller ascospores. The common *P. lacinulatum* is ecologically different in that it very rarely grows on thin earth covering (crumbling) rock, but usually it occurs on fine-grained soil. Furthermore, it differs in having a medulla rich in spherical cells, and usually thicker, more conspicuous rhizines.

Placidium rufescens (Ach.) A. Massal., Sched. Crit. Lich. 6: 114 (1856).

Basionym: *Endocarpon rufescens* Ach., Lich. Univ.: 304 (1810); Synonyms: *Dermatocarpon rufescens* (Ach.) Th. Fr., *Catapyrenium rufescens* (Ach.) Breuss, and see Breuss (1990 & 1996); Illustration: Wirth (1995), p. 251.

Thallus: squamulose; **squamules:** large (up to 10 mm wide and up to 0.6 mm thick) and leafy, mostly densely aggregated and overlapping, roundish or with broadly rounded lobes, ± wavy with margins free from the substrate; **upper surface:** medium to dark chestnut brown or red-brown, dull or glossy; **upper cortex:** 40-80 µm; epinecral layer: varying from almost lacking to 40 µm thick; **medulla:** white, 100-300 µm thick, composed of intricately interwoven filamentous hyphae, usually without (or with very few) spherical cells; algal layer: *c.* 100 µm thick; **lower cortex:** distinct, paraplectenchymatous, composed of roundish-angular cells (13-20 µm in diam.); **lower surface:** pale to dark brown, blackening centrally; rhizohyphae: hyaline, *c.* 6-7.5 µm thick, lacking in a ± broad marginal zone; **Perithecia:** broadly pyriform, up to 0.5 mm broad, fully immersed in the squamules but without bulging the lower sides; periphyses: 40-60 x 3.5-5 µm; **asci:** cylindrical, 80-100 x 12-19 µm, 8-spored; **ascospores:** uniseriate, ellipsoid, *c.* 15-20 x 7.5-9.5 µm; **Pycnidia:** marginal, knob-like; **conidia:** ellipsoid-oblong, 3-5 x 1.5-2 µm; **Spot tests:** all negative; **Secondary metabolites:** none detected.

Substrate and ecology: on soil, plant debris and moss, also directly on (calcareous) rock; **World distribution:** temperate Northern Hemisphere; Europe, Asia, North Africa, rare in North America; **Sonoran distribution:** rare in upland Arizona.

Notes: Normally *Placidium rufescens* is easily identifiable because of the following combination of characters: large, ± wavy squamules with a thick prosoplectenchymatous medullary tissue, thick rhizohyphae, large ascospores, and marginal pycnidia with ellipsoid-oblong conidia. However, forms with many spherical cells in the medulla do occur, but the large spores and pycnidial characters are distinctive. *Placidium chilense* is anatomically very similar but has smaller spores and laminal pycnidia.

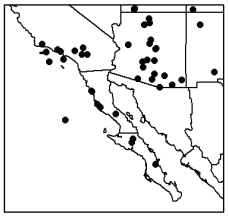
Placidium squamulosum (Ach.) Breuss, Ann. Naturhist. Museum Wien 98 B Suppl.: 39 (1996).

Basionym: *Endocarpon squamulosum* Ach., Method. Lich.: 126 (1803); Synonyms: *Catapyrenium squamulosum* (Ach.) Breuss, *Dermatocarpon hepaticum* auct., *Dermatocarpella squamulosa* (Ach.) Harada; Illustrations: Breuss (1990), fig. 20; Harada (1993), pp. 138 & 140; Wirth (1995), p. 251.

Thallus: squamulose; **squamules:** 2-7 mm wide, *c.* 0.2-0.4 mm thick, discrete to adjacent to slightly overlapping, nearly completely adnate to the substrate, or the margins slightly raised, round to lobed; **upper surface:** pale to dark brown, dull; **upper cortex:** *c.* 30-60 µm thick; epinecral layer: (almost) lacking or up to 50 µm thick; **medulla:** white, usually with numerous spherical cells (*c.* 9-14 µm in diam.); algal layer: about 70-120 µm high; **lower cortex:** hardly discernible or of densely aggregated roundish-angular cells (10-16 µm in diam.); **lower surface:** usually pale, but also blackening, attached with a dense rhizoidal weft; rhizohyphae: hyaline, 4.5-6.5 µm thick; **Perithecia:** broadly pyriform, up to more than 0.5 mm wide and usually bulging the lower side of squamules; exciple: hyaline or yellowish, 25-30 µm thick; periphyses: 30-40 x 3-4 µm; **asci:** cylindrical, 70-90 x 10-15

µm, 8-spored; **ascospores:** uniseriate, ellipsoid, 12-16 x 5.5-7.5 µm; **Pycnidia:** frequent, laminal, immersed; **conidia:** oblong-ellipsoid, 2.5-4 x 1.3-2 µm; **Spot tests:** all negative; **Secondary metabolites:** none detected.

Substrate and ecology: soil, moss, debris, mostly over ± calciferous ground in open situations from low to high elevations: **World distribution:** cosmopolitan, North and South America, Europe, Asia, Africa, Australasia; **Sonoran distribution:** common in Arizona, southern California, Sonora, Baja California, and Baja California Sur.



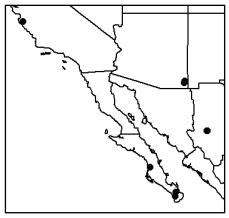
Notes: Together with *Placidium lacinulatum*, *P. squamulosum* is the most common species in the Sonoran region It is very variable species with a broad ecological amplitude. The lack of rhizines easily separates it from *P. lacinulatum*, otherwise these two species are almost identical in habit and anatomy with equally great variability in both species. Unusually large specimens with a thick, almost prosoplectenchymatous medullary tissue may be difficult to separate from *Placidium chilense*, but the latter species has a distinct lower cortex of large cells and narrowly oblong to shortly cylindrical (vs. ellipsoid-oblong) conidia. *Placidium pilosellum* differs further in having marginal pycnidia.

Placidium tuckermanii (Rav. *ex* Mont.) Breuss, Ann. Naturhist. Museum Wien 98 B Suppl.: 39 (1996).

Basionym: *Endocarpon tuckermanii* Rav. *ex.* Mont., Sylloge Gener. Spec. Cryptog.: 359 (1856); Synonyms: *Catapyrenium tuckermanii* (Rav. *ex* Mont.) J. W. Thomson, *Dermatocarpon tuckermanii* (Rav. *ex* Mont.) Zahlbr., and *Dermatocarpon arboreum* (Schweinitz *ex* Mont.) Fink *nom. inval*.; Illustrations: Thomson (1987), p. 30 as *Catapyrenium tuckermanii*; Brodo et al. (2001), p. 570.

Thallus: squamulose; **squamules:** 4-10 mm in diam., comparatively thin, 0.2-0.35 mm (where not swollen by perithecia) thick, lobed, flat or undulate, the edges usually slightly inrolled, loosely appressed, ± overlapping to distinctly imbricate; **upper surface:** pallid alutaceous or tan to grayish brown or darker brown, smooth, dull or subnitid, epruinose or slightly grayish pruinose; **upper cortex:** 25-40 µm thick; **medulla:** white, entirely prosoplectenchymatous, composed of hyphae closely interwoven in various directions; algal layer: about 100 µm thick; **lower cortex:** composed of roundish-angular cells [10-20 (-25) µm in diam.], outwardly becoming gradually dark brown; **lower surface:** pale along margins (rarely dark throughout), minutely scabrid under 10x lens, centrally blackening and ± fasciculate-matted, i.e. with conspicuous, crowded, black (outer ones may be pale) fascicles of rhizohyphae; rhizohyphae: stilt-like, centrally supporting the squamules (marginal zone: bare), hyaline or brownish, 5-6 µm thick, mostly matted together to form brush-like bundles (50-200 µm in diam.); **Perithecia:** broadly pyriform, up to 0.35 mm wide; exciple: pale except for the ostiolum; **asci:** cylindrical, 50-60 x 8-11 µm, 8-spored; **ascospores:** uniseriate, ellipsoid, 9-12 x 4.5-5.5 µm; **Pycnidia:** marginal, appearing as small dark knobs; **conidia:** bacilliform, *c.* 4 x 1 µm; **Spot tests:** all negative; **Secondary metabolites:** none detected.

Substrate and ecology: on bark (mainly oak) in open woodland, rarely on mosses or humus over rock; **World distribution:** North and Central America, especially in the southeast, becoming rarer westward; **Sonoran distribution:** rather rare in SE Arizona, central California, Baja California Sur and Chihuahua.



Notes: It is an easily recognizable species due to its comparatively thin and large squamules that are elevated from the substrate by bundles of rhizohyphae (not true rhizines). The prosoplectenchymatous medulla and small spores are also diagnostic. The species occurs preferably on bark. Specimens on mossy rocks or humus have been misidentified as other species.

PLACOPYRENIUM

by O. Breuss

Placopyrenium Breuss, Stud. Geobot. 7, Suppl. 1: 183 (1987).

Family: Verrucariaceae; Type: *P. bucekii* (Nádv. & Servít) Breuss; No. species: *c.* 15 world-wide; Selected lit.: Breuss (1987).

Life habit: lichenized, in some cases lichenicolous in young developmental stages; **Thallus:** thickly crustose, rimose-areolate, sometimes placodioid, or subsquamulose; **areoles:** flat or convex to almost bullate; **upper surface:** smooth, dull or subnitid, whitish-gray pruinose, or naked and brown; **upper cortex:** paraplectenchymatous, composed of small roundish-angular cells; **medulla:** white, subparaplectenchymatous; **photobiont:** primary one a chlorococcoid alga, secondary photobiont absent; algal layer: continuous; the algal cells: ± in columns; **lower** and **lateral cortices:** where present as in upper cortex; **lower surface:** attached with ± constricted bases or stipes, or rhizine-like structures; rhizohyphae: lacking; **Ascomata:** perithecial, laminal, immersed, subglobose; exciple: colorless or brown to black; involucrellum: lacking (or a very reduced apical lid); interascal filaments: absent; ostiolar filaments: present; **asci:** clavate, wall not amyloid, 8-spored; **ascospores:** biseriate, ellipsoid or oblong-ovoid, hyaline, simple or 1-, rarely 3-septate, non-halonate, smooth; **Conidiomata:** pycnidial, laminal, immersed, *Dermatocarpon*-type; **conidia:** subcylindrical to bacilliform; **Secondary metabolites:** none detected; **Geography:** world-wide, particularly in temperate, semi-arid regions; **Substrate:** calciferous or non-calcareous rock.

Key to the species of ***Placopyrenium*** from the Sonoran region:

1. Thallus brown, epruinose, ± placodioid .... ***P. insuetum***
1. Thallus greenish or bluish gray or ashy, ± pruinose, not placodioid 2
2. Areoles high convex to almost bullate, up to 5 mm broad ..... ***P. caeruleopulvinum***
2. Areoles smaller, not bullate 3
3. Thallus subsquamulose; squamules 2-4 mm broad, adjacent or with overlapping margins, secondarily divided by sparse cracks ..... ***P. heppioides***
3. Thallus chinky-areolate throughout; areoles 0.5-2 mm wide 4
4. Parasitic on *Staurothele areolata*; ascospores 14-18 x 6-9 µm; conidia 5-7 µm long ..... ***P. noxium***
4. Not parasitic; ascospores 17-24 x 6-8 µm; conidia 3-5 µm long ..... ***P. zahlbruckneri***

The Species

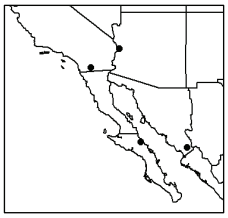
Placopyrenium caeruleopulvinum (J. W. Thomson) Breuss, **comb. nov.**

Basionym: *Catapyrenium caeruleopulvinum* J. W. Thomson, Bryologist 90: 30 (1987); Illustration: Thomson (1987), p 29 as *Catapyrenium caeruleopulvinm*.

Thallus: thickly crustose, areolate; **areoles:** roundish-angular, 1-5 mm broad, convex to almost bullate, up to mm high; marginal areoles: somewhat incised but not effigurate, separated by deep cracks; **upper surface:** strongly gray or bluish gray, pruinose; **upper cortex:** composed of cells *c.* 6-8 µm diam., 15-25 µm thick; **medulla:** thick, composed of densely intricate hyphae with ± many globular cells (7-12 µm diam.); algal layer: *c.* 100 µm high; algal cells: 9-15 µm wide; **lateral** and **lower cortices:** composed of more densely aggregated hyphae, often subparaplectenchymatous; **lateral** and **lower surfaces:** black to dark brown; attached by a central stipe or by several rhizine-like structures (150-350 µm diam. and up to several mm long) originating from the medullary tissue; the outermost hyphae: brown; the central ones: hyaline; **Perithecia:** subglobose, up to 0.4 mm broad; exciple colorless; **asci:** clavate, 60-70 x 14-16 µm;

ascospores: simple, ellipsoid, 13-20 x 5.5-7.5 µm; **Pycnidia:** laminal, with slightly sunken mouth, up to 300 µm wide; **conidia:** bacilliform, *c.* 5 x 1 µm; **Spot tests:** all negative; **Secondary metabolites:** none detected.

Substrate and ecology: on rock and hard stony soil; **World distribution:** SW North America; **Sonoran distribution:** Arizona, CalIfornia, Baja California Sur, Sonora.



Placopyrenium heppioides (Zahlbr.) Breuss, **comb. nov.**

Basionym: *Dermatocarpon heppioides* Zahlbr., Annal. Mycol. 10: 359 (1912); Synonym: *Catapyrenium heppioides* (Zahlbr.) J. W. Thomson; Illustration: Thomson (1987), p. 29 as *Catapyrenium heppioides*.

Thallus: (sub)squamulose; **squamules:** *c.* 2-4 mm broad, 0.4-0.65 mm thick, densely aggregated, adjacent or with overlapping margins, flat or slightly convex or undulate, sparsely divided by cracks; margins: slightly incised or lobate; **upper surface:** greenish to ashy gray; **upper cortex:** very thin (hardly more than 10 µm thick), composed of roundish-angular cells (4-6 µm diam.); **medulla:** up to more than 250 µm thick, composed of intricately interwoven, filamentous hyphae; algal layer: 100-150 µm thick, discontinuous, interrupted by hyphal bundles; algal cells: in vertical rows, 6-10 µm diam.; **lower cortex:** abruptly delimited, paraplectenchymatous, 40-100 µm thick, composed of conglutinated, hyaline, polygonal cells (6-13 µm diam.); lowermost cell layer: blackening; **lower surface:** black throughout, largely free from the substrate, attached by their basal ends or by stipe-like holdfasts; **stipe:** paraplectenchymatous, similar in construction as lower cortex, colorless inside, coated by a black pigment layer; **Perithecia:** broadly pyriform, up to 0.5 mm wide; exciple: pale brown; periphyses: 35-40 µm long and 2-2.5 µm thick; **asci:** no mature ones seen (only immature ones and numerous free, mature ascospores); **ascospores**: simple but partly pseudoseptate, oblong ellipsoid to narrowly ovoid, 16-23 x 7-9 µm; **Pycnidia:** laminal, up to 300 µm wide; **conidia:** bacilliform, 3-4 x 1 µm; **Spot tests:** all negative; **Secondary metabolites:** none detected.

Substrate and ecology: on sandstone; **World** and **Sonoran distribution:** southern California, known only from the type locality in the Santa Monica Mountains.

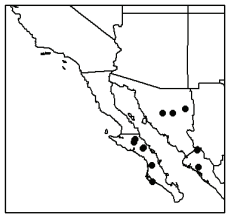
Notes: *Placopyrenium heppioides* has the most distinctly sqaumulous thallus of all species. The squamules are being secondarily divided by few cracks into smaller fragments the margins of which become lobed again.

Placopyrenium insuetum Breuss, Bryologist 103: 705 (2000).

Illustration: Breuss (2000c), p. 708.

Thallus: crustose, chinky-areolate; **areoles:** in the center angular, 1-3 mm broad, flat or ± convex, 0.25-0.55 mm thick; the marginal areoles: effigurate, radiating, up to 4 mm long and 2 mm broad; **upper surface:** brown, smooth, without pruina; **upper cortex:** 20-30 µm thick, of cells *c.* 4-7 µ in diam., overlain by a compact smooth epinecral layer up to 25 µm high; **medulla:** subparaplectenchymatous; cells: *c.* 7-12 µm in diam. in the upper part but somewhat smaller in the lower part and more densely packed; algal layer *c.* 70-100 µm thick, algal cells 5-10 in diam.; **lower cortex:** not clearly delimited, of more densely compacted medullary globose cells 5-8 µm in diam.; **lower surface:** brown, lighter along margins, attached to the substrate by 1 to several stipe-like holdfasts; **stipe:** subparaplectenchymatous with filamentous hyphae in lower parts; **Perithecia:** subglobose, up to 0.4 mm broad; exciple: colorless or slightly brownish; **asci:** clavate, 8-spored; **ascospores:** simple, oblong-ellipsoid, 15-18 x (4-) 5-6 (-7) µm; **Pycnidia:** laminal, immersed, up to 300 µm wide; **conidia:** shortly bacilliform, 4-5 x 1 µm; **Spot tests:** all negative; **Secondary metabolites:** none detected.

Substrate and ecology: on (volcanic) rocks on exposed sites. **World** and **Sonoran distribution:** Baja California Sur, Sinaloa and Sonora.



Notes: *Placopyrenium insuetum* is

the only species of the genus with a brown, epruinose upper surface.

Placopyrenium noxium Breuss, Ann. Naturhist. Mus. Wien 100 B: 675 (1998).

Thallus: crustose, rimose-areolate; **areoles:** 0.5-2 mm wide, flat or slightly convex, grayish, up to 1 mm thick, basally constricted, subangular in the center; the marginal areoles: roundish or somewhat incised or lobed; **upper surface:** grayish; **upper cortex:** 15-20 µm thick, composed of roundish-angular cells (4-6 µm diam., the uppermost ones brown and overlain by a 20-40 µm thick amorphous layer); **lateral** and **lower cortices:** the same type but without amorphous layer; **medulla:** subparaplectenchymatous, composed of densely intricated hyphae which are often divided into spherical cells (6-9 µm diam.); algal layer: *c.* 100-150 µm thick; algal cells: 7-12 µm in diam.; **lower surface:** attached by a stipe; **stipe:** similar in anatomy to the medulla but with more longitudinally arranged hyphae; **Perithecia:** broadly pyriform to subglobose; exciple: 25-30 µm thick, colorless or with the outermost layer darkening; periphyses: 30-40 µm long and 2-3 µm thick; **asci:** clavate, 60-70 x 20-25 µm, 8-spored; **ascospores:** simple, ellipsoid, 14-18 x 6-9 µm; **Pycnidia:** laminal; **conidia:** bacilliform, 5.5-7.5 x 1 µm long; **Spot tests:** all negative; **Secondary metabolites:** none detected.

Substrate and ecology: parasitic on *Staurothele areolata* at least when young, later becoming independent; **World distribution:** North America; **Sonoran distribution:** only known from Baja California Sur.

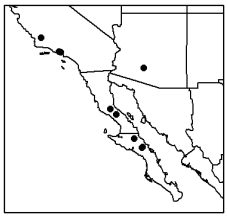
Notes: It is very similar to some *Verrucaria* species, from which it differs in its pycnidial type. *Placopyrenium zahlbruckneri* is similar in habit, but has larger areoles, is not parasitic, and has shorter periphyses and conidia and larger spores.

Placopyrenium zahlbruckneri (Hasse) Breuss, **comb. nov.**

Basionym: *Dermatocarpon zahlbruckneri* Hasse, Bryologist 16: 2 (1913); Synonym: *Catapyrenium zahlbruckneri* (Hasse) J. W. Thomson; Illustration: Thomson (1987), p. 30.

Thallus: chinky areolate; **areoles:** *c.* 1-2 mm broad, up to 0.7 mm high, basally ± constricted, slightly convex, separated by deep cracks, ± angular; marginal areoles: more roundish or slightly incised; **upper surface:** grayish, lateral parts brown to blackish; **upper cortex:** *c.* 15-25 µm thick, continuing laterally, composed of rounded-angular cells (5-9 µm diam.); epinecral layer: thin, causing the pruina; **medulla:** subparaplectenchymatous, composed of cells 6-10 µm diam.; algal layer: 100-150 µm high; algal cells: 8-15 µm in diam.; **lower surface:** brown to black; attached with a central stipe as a holdfast; **stipe:** composed of filamentous hyphae; **Perithecia:** broadly pyriform to subglobose, up to 0.45 mm broad; wall: pale except for the ostiole, browning with age throughout; periphyses: 15-20 x 3-4 µm; **asci:** clavate, 65-75 x 17-25 µm, 8-spored; **ascospores:** simple, ellipsoid, 17-24 x 6-8 µm; **Pycnidia:** immersed; **conidia:** oblong-subcylindrical, 3-4 x 1 µm long; **Spot tests:** all negative; **Secondary metabolites:** none detected.

Substrate and ecology: on rock of different kinds (limestone, granite, sandstone, basalt) from low elevations to 1000 m, often among other crustose lichens, but not truly parasitic; **World distribution:** SW North America in the mediterranean climate, northwards to Oregon; **Sonoran distribution:** Arizona, southern California, Baja California and Baja California Sur.



Notes: Within the genus the species is outstanding in its short and rather thickish periphyses. A specimen from Baja California has larger areoles (-4 mm), slightly broader spores (20-24 x 8-9 µm) often with an end attenuated, and larger conidia and may represent a separate species. *Placopyrenium noxium* has smaller thalli, smaller spores and longer conidia and is a constant parasite on *Staurothele areolata*. *Dermatocarpon lorenzianum* may be morphologically similar and has spores of almost equal size, but is easily separated by its prosoplectenchymatous

medulla and a lower cortex of anticlinally arranged, strongly conglutinated hyphae.

PLACYNTHIUM

by M. Schultz

Placynthium (Ach.) Gray, Natur. Arrang. Brit. Plants: 395 (1821).

Family: Placynthiaceae; Type: *Placynthium nigrum* (Huds.) Gray; No. species: *c.* 25 world-wide; Selected lit.: Henssen (1963d), Purvis et al. (1992), and Wirth (1995).

Life habit: lichenized; **Thallus:** squamulose, sometimes apparently small foliose or crustose, thallus margin often effigurate, stellate to flabellate, sometimes a bluish prothallus present, not gelatinous when wet; **upper surface:** dark olive, brownish or blackish, sometimes grayish pruinose, smooth, uneven, granulose, nodulose or covered by isidia; **lower surface:** usually blackish due to the presence of a hypothallus composed of interwoven bluish-black hyphae, rarely pale and hypothallus lacking; **anatomy:** indistinctly corticate and stratified; **photobionts:** a filamentous cyanobacterium, *Scytonema* or species of Rivulariaceae, secondary photobiont absent; **Ascomata:** apothecial, laminal on thallus, orbicular, half-immersed to sessile or stipitate; margin: distinct to prominent, without thalloid rim or rarely with thalloid margin; exciple: thin or thick, of radiating hyphae; epithecium: dark violaceous to brownish, hymenium: often violaceous; hypothecium: hyaline to brownish; **asci:** lecanoral, apex thickened, with amyloid tube, (4-) 8-spored; **ascospores:** simple when immature, septate when mature, ellipsoid or elongate-fusiform to broadly ellipsoid; 7-53 x 3.5-9 µm; wall: thin, hyaline; **Conidiomata:** pycnidial, laminal, immersed, dark colored; **conidia:** dumbbell-shaped, ellipsoid or bacilliform, *c.* 2.5-5 (-8) x 1 µm; **Secondary metabolites:** none detected; **Geography:** cosmopolitan, usually in wet microhabitats, sometimes in exposed situations; **Substrate:** calcareous or siliceous rock, rarely bark or soil.

Notes: The foliose genera *Koerberia* and *Vestergrenopsis* are superficially similar, but they, of course have a lower surface that is pale. In addition, they have a pale, striate upper surface and lecanorine apothecia. *Parmeliella* is similar in the presence of a blackish hypothallus but has *Nostoc* as photobiont. Well developed thallus margins are essential for proper species determinations. *Placynthium flabellosum* is known from northern California and may eventually be found in the Sonoran region.

Key to the species of ***Placynthium*** from the Sonoran region:

1. Lower surface of the filiform to flattened, elongated lobes pale; blackish hypothallus not present; thallus loosely attached; thallus circular, stellate, greenish brown, central part becoming squamulose or granulose to isidiate and sometimes dying off ..... ***P. stenophyllum*** var. ***isidiatum***
1. Lower surface dark; blackish hypothallus always present; thallus firmly attached; thallus stellate or not 2
2. Thallus squamulose to areolate in the center, thallus margin usually surrounded by a easily seen bluish prothallus, marginal squamules not elongated, effigurate or stellate, central areoles granulose to isidiate; common ..... ***P. nigrum***
2. Thallus with distinctly elongated, filiform marginal lobes or at least with effigurate marginal squamules, up to 0.2 mm wide; usually without bluish prothallus (do not confuse with hypothallus!) 3
3. Thallus forming regular, stellate rosettes; hypothallus inconspicuous ..... ***P. subradiatum***
3. Thallus forming irregular rosettes; hypothallus usually conspicuous ..... ***P. asperellum***

The Species

Placynthium asperellum (Ach.) Trevis., Lichenotheca Veneta No. 98 (1869).

Basionym: *Collema asperellum* Ach., Lichenogr. Univ.: 629 (1810); Synonyms: *Parmelia aspratilis* Ach., *Lichen asperellus* Wahlenb., *Pterygium asperellum* (Ach.) Nyl., *Placynthium vrangianum* Gyeln., *Placynthium aspratile* (Ach.) Henss.; Illustrations: Henssen (1963d), pp. 1711, 1714-6, 1718 & plate III.

Thallus: squamulose to crustose, forming small irregular rosettes up to 2 cm across, lobate; **lobes:** elongated, filiform or canaliculate, irregularly stellate; **center:** with granulose areoles; **upper surface:** dark olive to blackish, sometimes becoming densely isidiate; **lower surface:** dark, resting on a dark, blackish hypothallus; prothallus: absent; **Apothecia:** semi-immersed to sessile, laminal, lecideine, up to 1 mm wide; disc: black, open, at first depressed, later convex; exciple: dark colored; epihymenium: dark; hymenium: up to 100 µm high, amyloid; paraphyses: distinctly septate, sparingly branched, apical cells pointed or thickened; subhymenium: brownish; **asci:** 8-spored, sometimes fewer; **ascospores:** 2- or 4-celled, hyaline, ellipsoid to broadly ellipsoid, (11.5-) 15-18 (-21) x (4.5-) 5.5-7 µm; walls: thin; **Pycnidia:** immersed, marginal, ± globose, up to 0.15 mm wide; **conidia:** cylindrical or party dumbbell-shaped, hyaline, 4.5-8 x 1 µm; **Spot tests:** all negative; **Secondary metabolites:** none detected.

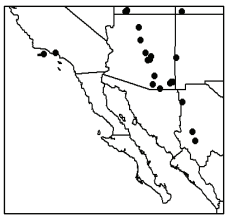
Substrate and ecology: on moist, siliceous rock; **World distribution:** Northern Hemisphere; **Sonoran distribution:** mountains of SE and eastern Arizona and the Sierra Madre Occidental in Chihuahua.

Notes: The species is rather variable in morphology and sometimes hard to separate from *Placynthium nigrum* as both species possess a thick hypothallus and often have a conspicuous blue prothallus. *Placynthium nigrum* is distinguished on account of the marginal squamules that are small and irregular in shape. Although the names *Collema asperellum* Ach. and *Parmelia aspratilis* Ach. both date back to 1810, recent authors (Nimis 1993, Purvis et al. 1992, Santesson 1993, Wirth 1995) give *Placynthium asperellum* (Ach.) Trevis. as the correct name for that species.

Placynthium nigrum (Huds.) Gray, Nat. Arrang. Brit. Plants: 395 (1821).

Basionym: *Lichen niger* Huds., Flora Anglica 2: 524 (1778); Synonyms: *Placynthium corallinoides* (Hoffm.) Jatta, *P. siliceum* Gyeln.; Illustrations: Henssen (1963d), pp. 1711, 1714, 1716-8 & plate I; Wirth (1995), p. 747; Brodo et al. (2001), p. 573.

Thallus: small squamulose, up to several cm across, sometimes appearing areolate; squamules: irregular in shape and with crenate to digitate margins, scattered to confluent; margin: not effigurate nor with elongated, stellate lobules; **upper surface:** dark olive, brownish to black, often isidiate; **lower surface:** dark, thallus resting on a conspicuous hypothallus surrounded by a blue prothallus; **Apothecia:** semi-immersed to sessile, laminal, lecideine, 0.5-1 mm wide; disc: dark brown to black, open, concave, flat to slightly convex; exciple: thick, dark violaceous to greenish, often shiny, becoming flexuose; epihymenium: dark violaceous or dark greenish; hymenium: 70-115 (-175) µm high, amyloid; paraphyses: distinctly septate, sparingly branched, apical cells pointed or thickened; subhymenium: brownish; **asci:** 8-spored, sometimes fewer; **ascospores:** 2 to 4-celled, hyaline, narrowly ellipsoid, (7-) 10-17 (-22) x 3.5-5.5 (-6) µm; walls: thin; **Pycnidia:** dark colored, immersed, laminal, up to 0.1 mm wide; **conidia:** slightly dumbbell shaped, hyaline, 3.5-5 x 1 µm; **Spot tests:** all negative; **Secondary metabolites:** none detected.



Substrate and ecology: on various calcareous rocks, mainly limestone, rarely on limy siliceous rock, soil or bark; **World distribution:** widely distributed in the Northern Hemisphere; **Sonoran distribution:** common in relatively moist habitats in Arizona, southern California and Chihuahua.

Notes: This variable species differs from all other Sonoran *Placynthium* species in the lack of elongated marginal squamules and a non-stellate growth form. A blue prothallus may be also present in *Placynthium asperellum*. Some of the Sonoran samples of *Placynthium nigrum* can

be referred to as either *P. nigrum* var. *tantaleum* or *P. tantaleum* on acount of slightly broader (6-8 µm), (1-) 2-celled spores and a less distinct blue prothallus.

Placynthium stenophyllum var. **isidiatum**

Henss., Can. J. Bot. 41: 1706 (1963d).

Illustrations: Henssen (1963d), pp. 1713-4 & 1716.

Thallus: loosely attached, up to 1.5 cm across, forming small, stellate rosettes that become irregularly squamulose in the center, often dying off and forming arcs, lobate; **lobes:** up to 3 mm long and 0.2 mm wide, **upper surface:** brownish, isidiate; **lower surface:** pale, blackish, hypothallus absent; **Apothecia:** not seen yet in var. *isidiatum*, in var. *stenophyllum* up to 0.4 mm wide; disc: reddish brown, with persisting thalline margin; exciple: thin, reduced to a few rows of cells; epihymenium: brown; hymenium: 70-80 µm high, amyloid; paraphyses: distinctly septate, sparingly branched, apical cells pointed or thickened; subhymenium: hyaline or slightly yellowish-brownish; **asci:** 8-spored; **ascospores:** 2-celled, hyaline, narrowly ellipsoid, sometimes curved, 12-15 (-20) x 3-5 µm; walls: thin; **Pycnidia:** dark colored, immersed, laminal, up to 0.2 mm wide; **conidia:** ellipsoid or bacilliform, sometimes slightly bent, hyaline, 4-6 x 1 µm; **Spot tests:** all negative; **Secondary metabolites:** none detected.

Substrate and ecology: on vertical limestone cliffs and boulders in montane, moist habitats; **World distribution:** North America; **Sonoran distribution:** moist canyons in central Arizona and Chihuahua.

Notes: *Placynthium stenophyllum* var. *isidiatum* differs from all other Sonoran *Placynthium* species in the lack of a black hypothallus and the loosely attached thallus.

Placynthium subradiatum (Nyl.) Arnold, Flora 67: 240 (1884).

Basionym: *Pannaria subradiata* Nyl., Actes Soc. Linn. Bordeaux 1: 314 (1856); Illustrations: Henssen (1963d), pp. 1711, 1714-6 & plate III, and Fig. 80 to right.

Thallus: forming regularly stellate rosettes, up to 1.5 cm across, sometimes forming arcs of up to 2.5 mm, lobate; **lobes:** flat with crenate tips, closely aggregated; **upper surface:** dark olive to brownish, sometimes pruinose; **lower surface:** dark, resting on a thin, inconspicuous, blue-black hypothallus; prothallus: absent; **Apothecia:** semi-immersed to sessile, laminal, lecideine, up to 0.5 mm wide; disc: dark brown to black, open, withou a thalline margin; exciple: thick, dark colored; epihymenium: dark violaceous or dark greenish; hymenium: 50-60 µm high, amyloid; paraphyses: distinctly septate, sparingly branched, apical cells pointed or thickened; subhymenium: light brownish; **asci:** 8-spored, sometimes fewer; **ascospores:** 2-celled, hyaline, ellipsoid, (9-) 11.5-12.5 (-15) x (5-) 6-7 (-8) µm; walls: thin; **Pycnidia:** not seen; **Spot tests:** all negative; **Secondary metabolites:** none detected.

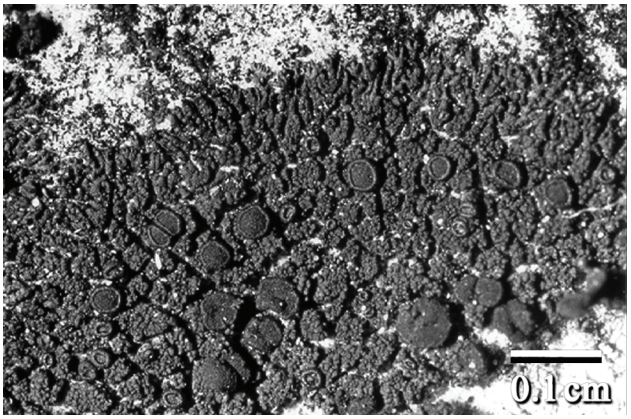


Fig. 80. *Placynthium subradiatum*, photo by M. Schultz.

Substrate and ecology: on limestone in moist, montane habitats; **World distribution:** North America; **Sonoran distribution:** moist canyons in central Arizona and Chihuahua.

Notes: This is a rather distinct species becasue of its small, regular, stellate rosettes resting on a inconspicuous hypothallus. A similar one is *Placynthium asperellum* that forms irregularly stellate rosettes resting on a thick, prominent hypothallus.

PLATISMATIA

by B. D. Ryan

Platismatia W. L. Culb. & C. F. Culb., Contr. U.S. Nat. Herb. 34 (7): 524 (1968).

Family: Parmeliaceae; Type: *Platismatia glauca* (L.) W. L. Culb. & C. F. Culb.; No. species: 10 world-wide; Selected lit.: Culberson and Culberson (1968).

Thallus: foliose, ± rosette-forming or wide-spreading, to subfruticose (suberect), dorsiventral, 5-18 (-23) cm diam.; **lobes:** broad to narrow, (0.1-) 0.3-2.5 cm wide; lobulae: common; margins: often ascending, wavy, sometimes crisped; cilia absent; **upper surface:** ashy white, tan, or greenish-brown, or gray, often rugose; pseudocyphellae: absent or present, punctiform; isidia or soredia: present in some species, marginal or laminal, often inconspicuous; **upper cortex:** well-developed, prosoplectenchymatous, often I+ blue; epicortex non-pored, 15-28 (-32) µm thick; **medulla:** white, (30-) 65-210 (-280) µm thick; cell walls containing *Cetraria*-type lichenan (I+ blue) and isolichenan; **photobiont:** primary one a chlorococcoid alga, secondary photobiont absent; **lower cortex:** well-developed, (10-) 13-28 (-30) µm thick; **lower surface:** pale to ± black, often mottled, punctate in some species; rhizines: usually present but few, scattered, simple; **Ascomata:** apothecial, often absent or rare, marginal or submarginal, roundish; disc: brown, often perforate; thalline exciple: prominent, persistent; usually lacking algae below the hypothecium; exciple: gray or hyaline; hymenium: I+ blue; uppermost part brown or ochraceous-yellowish; paraphyses: not (or scarcely) branched and anastomosing; hypothecium: hyaline, thin, I+ blue, blue-green, lavender, or purple; **asci:** *Lecanora*-type, 8-spored; **ascospores:** subglobose to ellipsoid, obtuse at the poles, simple; walls: hyaline and smooth, without distinct endospore thickening, not amyloid; **Conidiomata:** pycnidial, often absent, marginal, immersed; **conidia:** rare, bacilliform, not swollen at apices, 4-7 x 1 µm; **Secondary metabolites:** cortex with ß-orcinol depsides, medulla with aliphatic acids and a ß-orcinol depsidone in one species; **Geography:** temperate-boreal in the Northern Hemisphere; **Substrate:** mostly on bark or wood, rarely on mossy rocks.

Notes: The related genus *Cetrelia* differs especially in having perforate apothecia with thick, I- hypothecium, with thick zone of algae usually present immediately below it, larger and always ellipsoid spores, and frequent pycnidia with bifusiform conidia. *Platismatia* differs from *Parmotrema* in lacking cilia, usually having pseudocyphellae, having having marginal to submarginal apothecia and pycnidia, smaller ascospores, lacking depsides and depsidones in the medulla, and having a non-pored (rather than pored) epicortex.

The Species

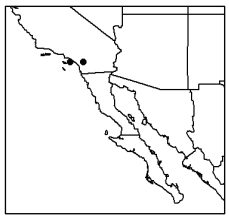
Platismatia glauca (L.) W. L. Culb. & C. F. Culb., Contr. U.S. Nat. Herb. 34: 530 (1968).

Basionym: *Lichen glaucus* L., Sp. Pl.: 1148 (1753); Synonyms: *Cetraria glauca* (L.) Ach.and see Culberson and Culberson (1968); Illustrations: Culberson and Culberson (1968), figs. 70-71; Wirth (1995), p. 750; McCune and Geiser (1997), p. 242; Brodo et al. (2001), p. 575.

Thallus: foliose to subfruticose, up to *c.* 3 cm across [up to 8-15 cm elsewhere], thin (< 1 mm thick), papery; **lobes:** few to numerous, upcurved, up to 2-5 (-20) mm wide; margins "ragged" [elsewhere sometimes branched and divided into fruticose lobes]; **upper surface:** whitish, whitish green, pale blue-greenish gray, to pale greenish tan (turning green to olive or greenish gray or tan when wet), or occasionally tinged with yellow or reddish, often with darkened areas, shiny to matt, smooth or becoming incompletely and inconspicuously wrinkled to strongly reticulately wrinkled, without distinct pseudocyphellae but ± maculate in places; **upper cortex:** *c.* 15-25 µm thick; **soredia:** initially white and granular, sometimes becoming brown and isidioid (simple to coralloid), often in lam-

inal, rounded to irregular soralia or marginal, crescent-shaped soralia; **medulla:** white, *c.* 60-200 µm thick, I+ lavender; **lower cortex:** 16-25 µm thick; rhizines: absent to few (to many), brown or black, simple or branched; **lower surface:** jet black towards center, or irregularly mottled or spotted brown or white towards the margins; shiny, smooth or reticulately wrinkled and coarsely and sometimes foveolate; **Apothecia:** very rare, 0.5-1 cm broad, marginal, perforate or not; without algae below; hymenium: 34-56 µm; "subhymenium" 16-52 µm, I+ lavender to bright purple; **asci:** clavate, I+ blue or blue-green, 8-spored; **ascospores:** hyaline, simple, ellipsoid to ovoid, 3.5-8.5 x 3-5 µm; **Pycnidia:** not seen; **Spot tests:** cortex K+ yellow, C-, KC-, P+ yellow; medulla K-, C-, KC-, P-, UV-; **Secondary metabolites:** cortex with atranorin and chloroatranorin; medulla with caperatic acid.

Substrate and ecology: on trees (usually conifers) or shrubs, or wood, occasionally on rocks and rarely soil; in open woods; **World distribution:** circumpolar and circumboreal in the Northern Hemisphere, Macaronesia; southern South America and E Africa; **Sonoran distribution:** southern California, coastal mountains in chaparral and on *Pseudotsuga macrocarpa*.



Notes: It is characterized by its loosely attached, suberect, greenish gray, smooth to ± wrinkled thallus with broad, dissected, rounded lobes with marginal soredia (often mixed with isidia) and a mottled brown and white lower surface, nearly without rhizines. It is extremely variable over its full range. Some forms might be confused with *Esslingeriana idahoensis* [non-Sonoran; with a black lower side and often black rimmed upper side], *Cetrelia* species, which have more distinct pseudocyphellae on the upper surface, or *Parmotrema* species, which usually have marginal cilia and a different chemistry. The two specimens seen from the Sonoran region are rather small and poorly developed.

POLYCHIDIUM

by B. D. Ryan and M. Schultz

Polychidium (Ach.) S. Gray, Nat. Arr. Brit.. Pl. 1: 402 (1821).

Family: Placynthiaceae?; Type: *Polychidium muscicola* (Sw.) Gray; No. species: two world-wide; Selected lit.: Purvis et al. (1992).

Life habit: lichenized; **Thallus:** minutely shrubby, ± dichotomously branched, often hemispherical, heteromerous; **branches:** filamentous, dendroid and often complex, ± terete, with thicker secondary branches towards base and thinner, anastomosing branches at apices; **surface** dark, greenish blue to brownish, often shiny towards lobe tips; **cortex:** well developed, cellular, 1-several cells thick, surrounding a central medullary strand of hyphae; **photobiont:** primary one a *Nostoc* or *Scytonema*, secondary photobiont absent; **medulla:** loosely interwoven, often paraplectenchymatous towards the base; **Ascomata:** apothecial, mostly lateral, orange, red-brown or brown, with a sunken disc; exciple: often with pitted, thick-walled cells; paraphyses: unbranched, septate; apices capitate; **asci** broadly cylindrical; apices thickened, I+ blue, 8-spored; **ascospores:** colorless, polymorphic, ellipsoid to spindle-shaped, simple to 1- or 2-septate, thin- or thick-walled; **Conidiomata** pycnidial, brown, lateral; conidiogenous cells generally short; **conidia** bacilliform; **Secondary metabolites:** none detected; **Geography:** North and South America, high altitude areas in tropical E Africa, the Pacific region and Europe; **Substrate:** on bark or moss.

Notes: The genus is rather distinctive because of its small fruticose growth form with dichotomously branched, terete, corticate lobes. Dwarf fruticose species of *Leptogium* also have corticate lobes, but these are often wrinkled. Fruticose species of *Lichinella* lack any cortex and the hymenium is covered by single-celled cyanobacteria and the asci are polyspored and thin-walled. The fruticose

species of *Peccania* possess single-celled cyanobacteria, the lobes lack any cortex, the upper parts of the hymenium is conspicuously reddish-brown colored, the conidia are large and filiform and the asci are thin-walled. In *Ephebe* and *Zahlbrucknerella* the fruticose-filamentous thallus lobes are usually adpressed and ecorticate. However, in *Zahlbrucknerella* there are hyphal strands surrounding the photobiont trichomes. Both, *Ephebe* and *Zahlbrucknerella* have thin-walled, often polysporous asci. *Thermutis velutina* grows on rock and its lobes are smaller and more slender, and its asci are thin-walled. In *Spilonema revertens* and *S. paradoxum* the lobes are ecorticate, more irregularly branched and fastened to the substrate by a bluish-black hypothallus.

The Species

Polychidium muscicola (Sw.) Gray, Nat. Arr. Brit.. Pl. 1: 402 (1821).

Basionym: *Lichen muscicola* Sw., Nov. Act. Acad. Upsal. 4: 248 (1784).

Thallus minutely fruticose, forming small, loosely interwoven, decumbent to cushion-like masses and strands; **branches:** dichotomous or palmate, not coralloid; lateral axes of similar size or with a main axis and smaller side branches, up to 4 mm tall; **lobes:** 60-125 (-200) µm thick, progressively narrowed toward apices; tips: terete, often nodulose; short cilia present, toward the base these becoming rhizines; **surface:** chestnut brown, dark brown, or blackish (sometimes grayish in shade), sparsely to richly and divergently branched; tips shiny; **cortex:** 1-2 (-3) cells thick, cells rounded or ± angular, 4-7 µm diam., the wall somewhat thickened, colorless or ± brown; **photobiont:** *Nostoc*, with bluegreen or green cells, not in obvious chains; **medulla:** interior hyphae loosely interwoven, more or less parallel to the surface, toward the base forming a paraplectenchyma; **Apothecia:** often common, up to 2 mm in diam., lateral; disc: red-brown, brighter when wet; margin: paler, concolorous with thallus; hymenium: 90-100 µm; paraphyses: septate, unbranched, 1-2 um thick, with a swollen apical cell to 4.5 µm wide; subhymenium: 70-100 µm; **asci:** clavate, 45-62 x 4.5-6.5 µm, 8-spored; **ascospores:** fusiform, hyaline, sometimes becoming pale red-brown, 1-septate, 19-25 (-29) x (4-) 4.5-6.5 (-7) µm; **Pycnidia:** sometimes present; **conidia:** bacilliform, 1.5-3.5 x 1 µm; **Spot tests:** K-, C-. KC-, P-; **Secondary metabolites:** none detected.

Substrate and ecology: on moss (or soil), usuaully in moist situations and over acidic rocks, often in and near streams, sometimes also at the bases of mossy trees; **World distribution:** North America, Europe, tropical East Africa and the Canary Islands; **Sonoran distribution:** southern California.

PORINA

by A. Aptroot

Porina Müll. Arg., Flora 66: 320 (1883).

Family: Trichotheliaceae; Type: *Porina nucula* Ach.; No. species: *c.* 320 world-wide; Selected lit.: Harris (1995), and Purvis et al. (1992), McCarthy (2000), and McCarthy and Malcolm (1997).

Life habit: lichenized; **Thallus:** crustose, superficial or immersed, often surrounded by a prothallus, often inconspicuous; **upper surface:** various shades and combinations of white, gray, green, orange to pink, or brown; occasionally with isidia or schizidia; **photobiont:** a trentepohlioid alga or *Phycopeltis*; **Ascomata:** perithecial, often partly immersed in the thallus, occasionally with hairs or bristles; **involucrellum:** always present but sometimes inconspicuous; true **exciple:** colored or not; yellowish to brownish, orange, reddish or black, often continuous below the hamathecium; **hamathecium:** composed of unbranched or sparingly branched paraphyses; paraphyses: not anastomosing, non-amyloid; periphyses: present in a

few species; **asci:** cylindrical or sometimes elongate-ellipsoid or narrowly obclavate, functionally unitunicate, without conspicuous tholus, uniformly thin-walled, often with a tiny refractive apical ring, non-amyloid, 8-spored; **ascospores:** 2-3 seriate, hyaline, fusiform to filiform, ellipsoid, bifusiform, or oblong, transversely 3-35 septate to muriform with eusepta, 13-120 x 2-20 µm; walls: not ornamented, with or without a gelatinous sheath; **Conidiomata:** pycnidial, immersed to ± sessile; **conidia:** bacilliform, rarely with macroconidia; **Secondary metabolites:** absent or not characterized; **Geography:** cosmopolitan, but most diverse in the tropics; **Substrate:** mostly on bark, but also on living leaves, bryophytes, soil and on calcareous or siliceous rock.

Notes: The new (different) systems of generic segregates within *Porina* as proposed by Harris (1995) and Hafellner and Kalb (1995) are not followed here, because several taxa are known that transcend the proposed borders (McCartney and Malcolm 1997). The genus is characterized by a combination of trentepohlioid photobiont (or *Phycopeltis* in many foliicolous species), perithecial ascomata with a hamathecium of usually simple paraphyses, uniformly thin-walled, functionally unitunicate asci, and colorless, euseptate and multiseptate to muriform ascospores.

Key to the species of ***Porina*** from the Sonoran region:

1. Ascospores 3-septate 2
1. Ascospores (5-) 7-9 (-11)-septate 3

2. Thallus a shade of gray or brown, not glossy; on bark ..... ***P. aenea***
2. Thallus a shade of green, glossy; on rocks (Sonoran region) ..... ***P. chlorotica***

3 Ascomatal wall continuous below the hamathecium; perithecia 0.38-0.63 mm diam.; hamathecium inspersed; thallus thick, areolate, on rocks ..... ***P. "peregrina"***

3 Ascomatal wall absent below the hamathecium; perithecia 0.2-0.35 mm diam., hamathecium not inspersed; thallus thin, continuous, on bark ..... ***P. cestrensis***

The Species

Porina aenea (Wallr.) Zahlbr., Cat. lich. univ. 1: 363 (1922).

Basionym: *Verrucaria aenea* Wallr., Fl. Crypt. Germ. 3: 299 (1831); Synonyms: *Pseudosagedia aenea* (Wallr.) Hafellner & Kalb, *Trichothelium aeneum* (Wallr.) R. C. Harris; Illustration: Swinscow (1962), p. 25 as *P. chlorotica* var. *carpinea*.

Thallus: continuous, superficial to semi-immersed in the substrate, forming small ± delimited patches; prothallus: absent; **upper surface:** dark gray (elsewhere deep red-brown or dark brown and becoming olivaceous in shade), smooth; **photobiont:** a trentepohlioid alga; **Perithecia:** hemispherical, black, semi-immersed in the thallus, usually scattered, 0.1-0.5 mm diam.; **involucrellum:** black, exposed, shiny; true **exciple:** semi-opaque, ± colorless with brown inclusions; **ascomatal wall:** black, absent below the hamathecium; **hamathecium:** composed of nearly unbranched pseudoparaphyses, not anastomosing; filaments: *c.* 0.5-1 µm wide, not inspersed with oil droplets; **asci:** cylindrical, *c.* 70-100 x 10-15 µm, with 8, irregularly arranged ascospores; **ascospores:** hyaline, fusiform, 3-septate (starting with a median euseptum), 19-22 x 4.5-5.5 µm; walls: not ornamented, without a gelatinous sheath; **Pycnidia:** immersed; **conidia:** macroconidia: 1-septate, 12-16 x 4.5 µm; microconidia: ellipsoid, 2 x 0.5 µm; **Spot tests:** all negative, UV negative; **Secondary metabolites:** none detected.

Substrate and ecology: on bark of *Quercus*; **World distribution:** temperate in the Northern Hemisphere; **Sonoran distribution:** only collected on the Channel Islands (California).

Porina cestrensis (Tuck. *ex* Michener) Müll. Arg., Flora 64: 338 (1883).

Basionym: *Verrucaria cestrensis* Tuck. *ex* Michener, in Darlington, Fl. cestr., ed. 3: 452 (1853); Synonym: *Trichothelium cestrense* (Tuck. *ex* Michener) R. C. Harris.

Thallus: continuous, dull, superficial on the substrate, brownish; **photobiont:** a trentepohlioid alga; **Perithecia:** hemispherical, black, semi-immersed in the thallus, 0.2-0.5 mm diam.; **involucrellum:** black, absent below the hamathecium; true **exciple:** colorless to violet-black; **hamathecium:** composed of nearly unbranched pseudoparaphyses, not anastomosing; filaments: *c.* 0.5-1 µm wide, not inspersed with oil droplets; **asci:** cylindrical, *c.* 70-100 x 6-10 µm, with 8, irregularly arranged ascospores; **ascospores:** hyaline, long-fusiform, 7 (-11)-septate with eusepta, (35-) 45-50 (-70) x (3-) 3.5-4.5 (-6) µm; walls: not ornamented, without a gelatinous sheath; **Spot tests:** all negative, UV negative; **Secondary metabolites:** none detected.

Substrate and ecology: on bark of e.g. *Quercus*; **World distribution:** pantemperate or possibly nearly cosmopolitan; **Sonoran distribution:**.only found on the Channel Islands (California), where it seems to be rather common, according to the numerous collections.

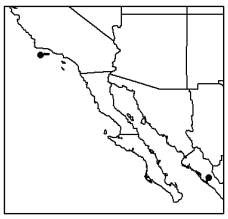
Notes: This species has been incorrectly reported as *Porina hibernica* P. James and Swinscow (syn. *Zamenhofia hibernica* (P. James and Swinscow) Clauz. and Roux), which, according to Harris (1995) is not known from America.

Porina chlorotica (Ach.) Müll. Arg., Rev. Mycol. (Toulouse) 6: 20 (1884).

Basionym: *Verrucaria chlorotica* Ach., Lichenogr. univ.: 283 (1810); Synonyms: *Pseudosagedia chlorotica* (Ach.) Hafellner & Kalb, *Trichothelium chloroticum* (Wallr.) R. C. Harris; Illustration: Swinscow (1962), p. 22.

Thallus: continuous, usually superficial on the substrate and well defined but sometimes disappearing; **upper surface:** greenish brown, gray, brown or blackish, smooth or cracked; **photobiont:** a trentepohlioid alga or absent; **Perithecia:** hemispherical, black, semi-immersed in the thallus or sessile, *c.* 0.2-0.35 mm diam.; **incolucrellum:** shiny, black, extending ± halfway down exciple, not continuous below the exciple; true **exciple:** outer layers brown-black, inner layers ± colorless; **ascomatal wall:** black, absent below the hamathecium; **hamathecium:** composed of nearly unbranched pseudoparaphyses, not anastomosing; filaments: *c.* 0.5-1 µm wide, not inspersed with oil droplets; **asci:** cylindrical, *c.* 75-100 x 10-15 µm, with 8, irregularly arranged ascospores; **ascospores:** hyaline, fusiform, 3-septate (starting with a median eusептum), 16-25 x 4-6 µm; walls: not ornamented, without a gelatinous sheath; **Spot tests:** all negative, UV negative; **Secondary metabolites:** none detected.

Substrate and ecology: on various rock types; **World distribution:** cosmopolitan but primarily temperate; **Sonoran distribution:** so far collected on the Channel Islands (Califonia) and in Sinaloa.



Porina "peregrina" Tretiach & McCarthy, in prep.

Illustrations: Figs. 81 and 82 below.

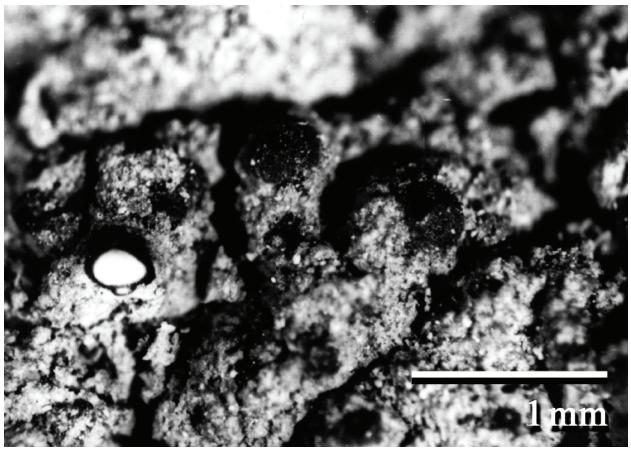


Fig. 81. *Porina* "*peregrina*", photo by M. Tretiach.

Thallus: epilithic, determinate, verrucose-areolate, *c.* 0.7-0.8 mm thick, impregnated with rock fragments and crystals, **upper surface:** pale brown with an olive-green tinge, dull, ecorticate, K-, prothallus not apparent, basal layer absent; algae: *Trentepohlia*; cells (12-) 14.6-17.1-19.6 (-23) x (11-) 12.6-14.3-16.0 (-19) µm [*n* = 42]; **Perithecia:** very numerous, hemispherical to subglobose, not attenuate at the base, half-immersed in the thallus, solitary or more rarely crowded in small groups of 2-3 (Fig. 81),

0.38-0,45-0.52 (-0.63) mm in diam. [*n*=30]; apex: rounded or slightly flattened; ostiole: often slightly concave and quite large, with periphyses up to 15 µm long; **involucrellum:** contiguous with the exciple and extending to excipular basal level, often continuous, opaque, in section dull brown to blackish, K-, the upper parts H_2SO_4 golden brown, then red after some minutes, up to 60 µm near the apex, covered by a thin hyaline layer up to *c.* 7-12 µm thick, better seen after treatment with H_2SO_4; exciple: colorless, up to 30-40 µm near the ostiole, and up to 60 µm near the base; hymenium: inspersed with minute granules; subhymenium: 25-30 µm thick;

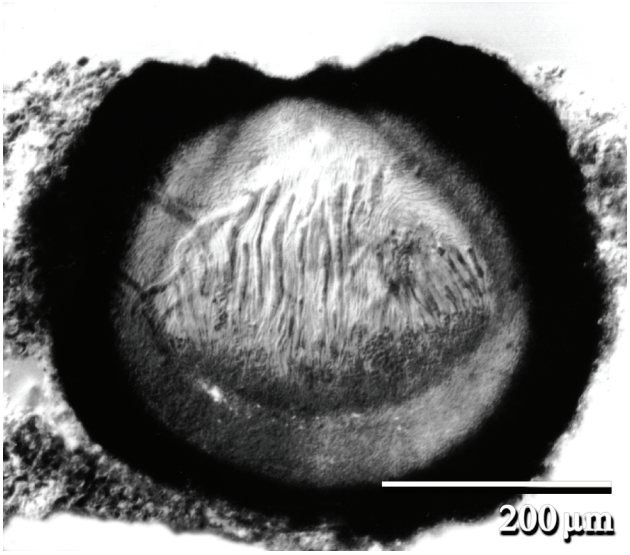


Fig. 82. *Porina* "*peregrina*", photo by M. Tretiach.

hamathecium: composed of simple, filiform paraphyses, less than 1 µm in thickness, not constricted at septa, obscurely branched at the tips; **asci:** 135-160 x 10-13 µm, with a rounded apex and an indistinct apical chitinoid ring in congo red, I-, cytoplasm I+ yellow, 8-spored; **ascospores:** colorless, 7 (-9) -septate, narrowly fusiform or elongate-fusiform, straight, with acute ends, (31-) 40-46-52 (-62) x (3.5-) 4-6 µm, length/width ratio (6.5-) 8.1-9.8-11.5 (-15.5) [*n* = 99, 10 perithecia examined]; walls: some immature spores with a thin, gelatinous perispore; **Pycnidia:** rare, immersed or semi-immersed, blackish; **conidia:** 2-4 x *c*. 0.7 µm; **Spot tests:** all negative, UV negative; **Secondary metabolites:** none detected.

Substrate and ecology: on a seepage track of north-facing**,** exposed conglomerate rocks effervescent in HCl, not overgrowing the largest siliceous pebbles present on the surface of the substratum (see Fig. x); **World** and **Sonoran distribution:** southern California, currently only collected at a single locality on Santa Rosa in the Channel Islands.

Notes: The epithet *peregrina* means pilgrim, and was selected because the type material, collected in California, was sent from Italy to several fellow lichenologists all around the world. This very distinctive lichen is characterized by a thick thallus, moderately large 7 (-9)-septate ascospores, the presence of periphyses, and the size of conidia. The reaction of the involucrellum to K and H_2SO_4 distinguishes it from species of sect. *Limosagedia*, although in *P. peregrina* some portions of the involucrellum near the ostiole may occasionally react K+ blue. In the keys to the saxicolous taxa of *Porina* of McCarthy (2000) the new species would key out close to *P. riparia* P. M. McCarthy and *P. curnowii* A.L. Sm. However, *P. riparia* has a thinner, smoother thallus, smaller perithecia, discontinuously smaller asci and 4-10 x 1.5 2.2 µm conidia, while *P. curnowii* has a very thin thallus, perithecia lacking periphyses and shorter, narrower and persistently 7-septate ascospores.

POROCYPHUS

by M. Schultz

Porocyphus Körb., Syst. Lich. Germ.: 425 (1855).

Family: Lichinaceae; Type species: *Porocyphus coccodes* Flot. *ex* Körb.; No. species: *c.* 10 world-wide; Selected lit.: Henssen (1963a).

Life habit: lichenized; **Thallus:** crustose, placodioid, subfruticose, gelatinous when wet; **surface:** blackish, smooth or uneven, sometimes granulose; **anatomy:** ecorticate, homoiomerous, fan-shaped or paraplectenchymatous hyphal arrangement; **photobionts:** primary one a filamentous (Rivulariaceae) or chroococcoid cyanobacterium, secondary photobiont absent; **Ascomata:** apothecial, laminal on thallus or terminal, orbicular, immersed to sessile, margin indistinct to prominent, with thin thalloid rim, sometimes evanescent; **ontogeny:** hemiangiocarpous, forming pycnoascocarps from ascogonia beneath pycnidia; **anatomy:** exciple: hyaline, faintly yellowish-brown to brownish; epithecium: brownish yellow; hypothecium hyaline to faintly yellowish-brown; **asci:** prototunicate, wall thin, nonamyloid, 8-spored; **ascospores:** simple, ellipsoid to broadly ellipsoid; 8-24 x 5-13 µm; walls: thin, hyaline; **Conidiomata:** pycnidial, laminal, immersed; **conidia:** ellipsoid, *c.* 3 x 1 µm; **Secondary metabolites:** not detected; **Geography:** world wide in arid to humid regions; **Substrate:** calcareous and siliceous rocks.

Notes: The filamentous nature of the cyanobiont is often hard to observe, and it seems likely that single celled cyanobacteria may also occur. *Psorotichia* and *Lemmopsis* are very similar in external appearance, but they differ in the type of ascoma ontogeny and possess more robust paraphyses.

The Species

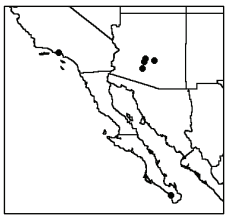
Porocyphus coccodes (Flot.) Körb., Syst. Lich. Germ.: 426 (1855).

Basionym: *Collema coccodes* Flot. "ad int.", Linnaea 23: 152 (1850); Synonyms: see Henssen (1963a & 1974); Illustration: Fig. 83 below.

Fig. 83. *Porocyphus coccodes*, photo by M. Schultz.

Thallus: crustose, effuse, areolate; **areoles:** irregular in outline, 0.25-1.5 (-2) mm wide, 0.2-0.5 (-1) mm thick, **surface:** black, warty to granulose, uneven, rarely smooth; **lower surface:** attached to the substrate by rhizohyphae; **Apothecia:** semi-immersed to sessile, zeorine, 1-3 per areole, up to 0.4 mm wide; disc: at first punctiform and depressed, later open and ± flat, reddish brown, with persisting, thin thalline margin; exciple: 25-50 (-75) µm wide, thick only in mature apothecia, hyaline or yellowish brown in apical parts, often visible as a light ring when mature apothecia are moistened, in juvenile apothecia remnants of conidiophores often present between hymenium and exciple (former pycnidial wall); epihymenium: faintly reddish brown; hymenium 125-200 µm high, hyaline, amyloid; paraphyses: very thin, indistinctly septate, sparingly branched and anastomosing; api-

cal cells: slightly thickened (-3 µm); **asci:** 8-spored; **ascospores:** simple, hyaline, broadly ellipsoid to globose, (7.5-) 10-12.5 (-15) x (5-) 7.5-10 µm; walls: thin; **Pycnidia:** immersed, globose to broadly pyriform, 0.075-0.125 mm long, 0.075-0.1 mm in diam.; **conidia:** cylindrical, 3 x 1 µm; **Spot tests:** all negative; **Secondary metabolites:** none detected.



Substrate and ecology: on siliceous (granite or volcanic) or calcareous rocks, sometimes mixed with mosses over weathered rocks, inclined or horizontal surfaces in shaded or sheltered rock faces of boulders; mainly montane; **World distribution:** North America, Europe, North Africa; **Sonoran distribution:** central and southern Arizona, southern California; Baja California Sur.

Notes: Very similar are species of *Psorotichia*, which have a thinner (<15 µm) proper exciple, that may even lack and a subhymenium that usually extends as a stipe deeper into the thallus. Also similar is *Lemmopsis arnoldiana* whis apparently is confined to limestone or caliche and which shows a characteristic yellowish-golden coloration in the entire exciple. Unlike *Porocyphus*, in *Psorotichia* and *Lemmopsis* the ascomata arise from a tangle of generative hyphae and the paraphyses are more robust.

PROTOPANNARIA

by P. M. Jørgensen

Protopannaria (Gyeln.) P. M. Jørg. & S. Ekman, Bryol. 103: 699 (2000).

Family: Pannariaceae; Type: *Protopannaria pezizoides* (Weber) P. M. Jørg. & S. Ekman; No. species: five worldwide; Selected Lit.: Jørgensen (1994 & 2000a).

Life habit: lichenized; **Thallus**: small-squamulose to granular, often forming crustose mats over the substrate; hypothallus: poorly developed and inconspicuous; **upper surface:** usually olivaceous to blackish, sometimes gray to dark brown, dull; **upper cortex:** paraplectenchymatous; **medulla:** composed of intricately interwoven, lax plectenchyma; **photobiont:** primary one a *Nostoc*, secondary photobiont absent; **Ascomata:** apothecial, common, with strong thalline margin; disc: bright orange-brown to olivaceous or dark brown; hymenium: I+ dark blue; **asci:** clavate to subcylindrical, without internal apical amyloid structures but with an I+ deep blue external cap, 8-spored; **ascospores:** simple, colorless, ellipsoid, with prominent rugulose to warted epispore; **Conidiomata:** pycnidial, pale brown; **conidia:** simple, bacilliform, colorless; **Secondary metabolites:** none detected; **Geography:** widespread in cool to cold temperate to polar habitats, primarily in the Southern Hemisphere; **Substrate:** on soil.

Notes: The genus is a small, bipolar genus. It was recently erected as a segregate from *Pannaria* (Jørgensen 2000a), and is similar to *Psoroma* in many respects except for the apical apparatus of the asci. Molecular data (unpublished) do not support its retention within *Pannaria*.

The Species

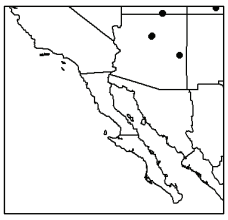
Protopannaria pezizoides (Weber) P. M. Jørg. & S. Ekman, Bryol.103: 699 (2000).

Basionym: *Lichen pezizoides* Weber, Spicil. Fl. Goett.: 200-201 (1778); Synonym: *Pannaria pezizoides* (Weber) Trevis., *Pannaria brunnea* (Swartz) A. Massal.; Illustrations: Goward et al. (1994), p. 90; McCune and Geiser (1997), p. 181; Jørgensen (1978), p. 52; Jørgensen (1994), p. 201; Jørgensen (2000a), p. 699; Wirth (1995), p. 635; all as *Pannaria pezizoides*.

Thallus: small-squamulose, forming compact mats over the substrate; hypothallus: poorly developed and inconspicuous;

squamules: small, up to 1 mm wide and up to 200 µm thick, often imbricate; **upper surface:** gray, bluish gray to dark brown (when wet), sometimes with a reddish tinge; **upper cortex:** paraplectenchymatous, 40-50 µm thick; **medulla:** composed of intricately interwoven, lax plectenchyma, 20-40 µm thick and merging into the hypothallus below; **photobiont:** a cyanobacterium (*Nostoc*, forming clumps); **Apothecia:** common, often aggregated, up to 2 mm in diam., flat to convex, with a strong crenulate thalline margin; disc: bright orange-brown to dark brown; exciple: subparaplectenchymatous, up to 40 µm thick; hymenium: I+ dark blue, up to 150 µm high; paraphyses: simple, septate, slightly clavate at apices; **asci:** clavate to subcylindrical, 8-spored.; **ascospores:** simple, colorless, ellipsoid, 25-30 x 9-12 µm (including the distinct, warted epispore; otherwise 19-25 x 8-10 µm); **Conidiomata:** pycnidial; **Spot tests:** all reactions negative; **Secondary metabolites:** none detected.

Substrate and ecology: on damp mosses or soil, mainly in montane regions; **World distribution:** widespread in the cool, temperate regions of the Southern and Northern Hemispheres, mountains of East Africa; **Sonoran distribution:** high elevations in Douglas fir and spruce-fir zones above 2500 m in the mountains of central and eastern Arizona.



Notes: It is characterized by the numerous, conspicuous brightly colored apothecia with a pertsistant granular thalline margin, and the often brownish, nearly crustose thallus, though often confused with *Psoroma hypnorum*, a species found in similar habitats, which is easily distinguish on its greenish squamulose thallus and large, convex apothecia with squamulose thalline margin. *Protopannaria pezizoides* contains a cyanobacterium and hence is very dark bluish brown when wet; whereas *P. hypnorum* is bright green when wet due to its chlorococcoid alga.

PROTOTHELENELLA

by H. Mayrhofer

Protothelenella Räsänen, Ann. Bot. Soc. Zool.-Bot. Fenn. "Vanamo" 18: 102 (1943).

Family: Protothelenellaceae; Type: *Protothelenella reducta* (Th. Fr.) Räsänen [= *Protothelenella sphinctrinoidella* (Nyl.) H. Mayrhofer & Poelt]; No. species: nine worldwide; Selected lit.: Mayrhofer and Poelt (1985) and Mayrhofer (1987b).

Life habit: lichenized, saprophytic or lichenicolous; **Thallus:** indistinct to crustose, superficial, attached by the whole lower surface; **upper surface:** membrane-like, evanescent, granular to cracked-areolate; soredia and isidia absent; **photobiont:** primary one a chlorococcoid alga (*Elliptochloris bilobata*), secondary photobiont absent; **Ascomata:** perithecial, sessile to immersed, globose to pear-shaped, pale brown to blackish; exciple: mostly pale brown to pale green towards the base, brown to greenish blue in upper part, of strongly anastomosing, conglutinate hyphae with narrow lumina; involucrellum: absent; hamathecium: composed of perisistent paraphysoids, strongly branched and anastomosed, amyloid; periphysoids absent; **asci:** bitunicate, fissitunicate dehiscence, thick-walled, with an I+ blue ± layered tholus, 6 (-8)-spored; **ascospores:** four-celled, submuriform to strongly muriform, ellipsoid to narrowly ellipsoid or fusiform, the outer wall distinctly thicker than the septa, colorless; **Conidiomata:** not seen; **Secondary metabolites:** none detected; **Geography:** Northern Hemisphere; **Substrate:** on acid substrata including rocks, soil, mosses, plant detritus and on rotten wood or lichenicolous on *Solorina*, *Peltigera* and *Cladonia* squamules.

Notes: The genus is characterized by bitunicate asci with an amyloid tholus.

The Species

Protothelenella sphinctrinoidella (Nyl.) H. Mayrhofer & Poelt, Herzogia 7: 47 (1985).

Basionym: *Verrucaria sphinctrinoidella* Nyl., Flora 47: 355 (1864); Synonyms: *Microglaena sphinctrinoidella* (Nyl.) Arnold, *Microglaena reducta* (Th. Fr.) Hellbom, *Microglena geoctona* Hellbom, *Thelenella coenosa* Vain.; Illustrations: Mayrhofer and Poelt (1985), pp. 24 & 51.

Thallus: indistinct, thin; **upper surface:** membrane-like, evanescent, pale gray, greenish when wet; **prothallus:** absent; **Perithecia:** 0.1-0.3 mm diam., sessile to slightly immersed, black, rounded to pyriform, discrete, very rarely 2-4 contiguous; exciple: dull greenish above (K+ violaceous), paler below, 15-20 µm thick; **asci:** cylindrical, 8-spored; **ascospores:** colorless, submuriform, elongate or narrowly ellipsoid, 22-33 x 7-10 µm; **Pycnidia:** not seen; **Spot tests:** all negative; **Secondary metabolites:** none detected.

Substrate and ecology: encrusting dead mosses and dead lichen thalli, rarely on acid soil and plant detritus in upper montane to alpine habitats; **World distribution:** mountains of central Europe, northern Europe, North America; **Sonoran distribution:** only known from one locality in Apache National Forest in Arizona at 3000 m.

Notes: This species is characterized by an indistinct thallus, small sessile black perithecia with a dull greenish exciple and elongate submuriform ascospores. Another species known from North America is *Protothelenella sphinctrinoides* (Nyl.) H. Mayrhofer & Poelt, which is distinguished by larger partly immersed perithecia and larger muriform ascospores.

PSEUDEPHEBE

by B. D. Ryan

Pseudephebe M. Choisy, Icon. Lich. Univ. ser. 2, fasc. 1, unpaged (1930).

Family: Parmeliaceae; Type: *Pseudephebe pubescens* (L.) M. Choisy; No. species: two world-wide; Selected lit.: Brodo and Hawksworth (1977), Kärnefelt and Thell (1992), and Common and Brodo (1995).

Life habit: lichenized; **Thallus:** fruticose-filamentous to subfruticose or caespitose, prostrate, closely appressed (under 1 cm tall), sometimes becoming compacted and subcrustose centrally, loosely or ± tightly attached to the substrate by scattered, expanded, disc-like holdfasts (hapters) at unspecialized attachment points along the length of the branches and not merely at the base, base sometimes dying such that the thalli often form rosettes; **branches:** up to 4-10 (-15) mm long, mostly narrow, up to 0.1-0.5 mm wide (to 1-2 mm wide near base), pliant or brittle, solid, in section rounded to flattened (dorsiventrally compressed) parallel to the substrate; **branching:** ± thickly isotomic-dichotomous (often strictly so, but sometimes anisotomic); **surface:** brown to deep black-brown, dull to slightly shiny, usually concolorous except where attached to substrate, even or uneven; lacking pseudocyphellae, true lateral spinules, and vegetative propagules; **cortex:** 2-layered; outer layer: almost paraplectenchymatous, with cells rectangular to irregular and knobby at the surface, inner layer: prosoplectenchymatous, composed of periclinal, longitudinal hyphae, 75-85 µm thick; **medulla:** white, hyphae not granular encrusted nor ornamented; cell walls: with *Cetraria*-type and intermediate-type lichenan, and possibly traces of isolichenan; **photobiont:** primary one a chlorococcoid alga, secondary photobiont absent; **Ascomata:** apothecial, sometimes frequent, lateral, roundish, sessile; thalloid margin: concolorous with thallus, slightly prominent to prominent, persistent to pressed back, not incurved, sometimes “ciliate” (with elongated, spine-like projections); disc: dark brown to almost black; exciple: ± distinct, slightly gelatinized, hyaline; hymenium: hyaline below, olive-brown above, turning grayish greenish yellow in K, 75-85 µm tall; paraphyses: branched and anastomosing, the tips not capitate or pig-

mented; **asci:** clavate, 20-45 x 6.7-9.0 µm, thick-walled, *Lecanora*-type, I+ blue, with robust tholus, 8-spored; **ascospores:** simple, ellipsoid or broadly ellipsoid, hyaline at maturity, smooth, without perispore or a distinct endospore thickening, I-, *c.* 7-12 x 6-8 µm; **Conidiomata:** pycnidial, very common, laminal, immersed, with wide ostioles; **conidia:** bifusiform, simple, colorless; **Secondary metabolites:** none detected; **Geography:** circumbipolar and alpine in temperate regions; **Substrate:** on acidic rock, rarely on old wood or baked soil.

Notes: It is distinguished from rock or soil species of *Bryoria* by its 2-layered cortex, that has rectangular to irregular and knobby cells at the surface, its low, prostrate habit and its attachment by hapters, lack of isidia, soredia and pseudocyphellae, its frequent pycnidia, and its absence of secondary lichen products (see also Common and Brodo 1995).

Key to species of ***Pseudephebe*** in the Sonoran region:

1. Thallus loosely adnate and prostrate to subpendulous, often semi-erect towards thallus center, usually interwoven and forming loose to dense, rather thin (1-2 mm) mats; basal branches usually terete (to slightly compressed); branches fine and ± evenly thin (*c.* 0.2 mm); tips not attached; internodes elongate, (0.6-) 1-3 (-5) mm, giving a loose hairy appearance to the thallus; apothecia very rare ..... ***P. pubescens***
1. Thallus closely attached to appressed, nearly crustose toward thallus center; basal branches becoming ± flattened, ± terete towards tips; basal branches coarse, unevenly thickened, to *c.* 1 mm broad, irregularly isotomic dichotomous with numerous short lateral branchlets; tips becoming adnate; internodes short, 0.2-0.5-(-1 mm), giving the thallus a rather dense appearance; apothecia often present ..... ***P. minuscula***

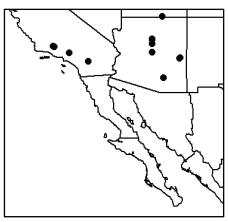
The Species

Pseudephebe minuscula (Nyl. *ex* Arnold) Brodo & D. Hawksw., Opera Bot. 42: 140 (1977).

Basionym: *Imbricaria lanata* var. *minuscula* Nyl. *ex* Arnold, *Ver. Zool.-Bot. Ges. Wien* 28: 293 (1878); Synonyms: *Alectoria minuscula* (Nyl. *ex* Arnold) Degel. and see Brodo and Hawksworth (1977); Illustrations: Brodo and Hawksworth (1977), p. 18; Thomson (1984), p. 373; Goward (1999), p. 204; Wirth (1995), p. 185; Brodo et al. (2001), p. 588.

Thallus: prostrate and decumbent, in extreme forms becoming almost subfoliose or even virtually crustose, generally forming ± circular adpressed thalli 2-6 cm in diam., closely attached, adnate at the tips; **branches:** becoming ± flattened, especially towards the base, unevenly thickened, up to *c.* 1 mm broad, tapering irregularly to 0.2-0.5 mm on main stems and 0.1 mm at tips, where the branches are very uneven and ± terete; **branching:** irregularly isotomic-dichotomous with numerous short lateral branchlets giving thallus a "ciliate" appearance; internodal distance: short, usually *c.* 0.2-0.5 (-1.0) mm, giving the thallus a rather dense appearance; **upper surface:** dark brown to black, shiny (to dull), sometimes pale brown at the base; true lateral spinules: absent, but simple or branched isidioid adventitious branches not uncommon in one morphotype; soralia and pseudocyphellae: absent; **lower surface:** dark brown; **Apothecia:** often present, lateral; disc: 1-3 mm broad, dark red-brown to black, plane; thalline exciple: persistent, smooth or verrucose; **asci:** clavate, 8-spored; **ascospores:** broadly ellipsoid to subglobose, 6.7-9.0 x 7.7-8.0 µm; **Pycnidia:** very abundant, embedded in thallus, ostioles: broad; **conidia:** bifusiform, 4.7-8 x 0.9-1.1 µm; **Spot tests:** K-, C-, KC-, P-, UV-; **Secondary metabolites:** none detected.

Substrate and ecology: on acidic or occasionally base-rich rock faces, boulders, and windswept gravels. In exposed sites, in drier inland areas, in temperate areas mostly in alpine sites; **World distribution:** circumpolar in both the Northern and Southern Hemispheres; **Sonoran distribution:** moderately frequent at high alpine (3000-3650 m) in north-central to eastern Arizona, occasionally lower, also known from three montane localities in southern California.



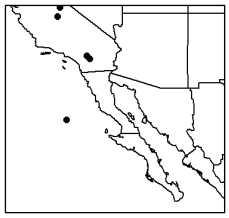
Notes: It is highly variable and sometimes rather similar to *P. pubescens*, but usually separated from that species by the partly broader, more flattened and knobby branches (especially towards the base) and the short internodes. Specimens (including some from Arizona) with especially broadened lobes have occasionally been confused with *Cornicularia normoerica*, which has an ± erect and sparingly branched thallus and terminal apothecia with dentate or fibrillate margins, or with species of *Melanelia* or *Neofuscelia*, both of which have more flattened lobes usually with rhizines on the underside.

Pseudephebe pubescens (L.) M. Choisy, Icon. Lich. Univ., ser. 2, 1: without pages (1930).

Basionym: *Lichen pubescens* L., *Sp. Pl.* 2: 1155 (1753); Synonyms: *Alectoria pubescens* (L.) R. Howe; *Alectoria pacifica* Stizenb.; *Parmelia lanata* (L.) Wallr.; Illustrations: Thomson (1984), p. 374; McCune and Geiser (1997), p. 249; Hansen (1995), p. 58; Wirth (1995), pp. 185 & 781; Goward (1999), p. 204; Brodo et al. (2001), p. 588.

Thallus: decumbent (prostrate) to ascendent and shrubby, 1-7 cm in diam., loosely adnate, not attached at the apices, usually forming loose to dense, rather thin (1-2 mm) mats; **branches:** up to 1 cm long, usually ± terete throughout (to slightly compressed towards base), ± evenly thin (0.1-0.2 mm near base, 0.05-0.1 mm near tips); internodal distance generally long, (0.5-) 1-3 (-5) mm, giving a loose hairy appearance to the thallus; **branching:** frequent, divergent, regularly isotomic-dichotomous, often interwoven; **surface:** dark brown to black, shiny to satiny, sometimes paler at base; **Apothecia:** usually very rare, up to 5.5 mm diam.; disc: gray-black or brown; **ascospores:** broadly ellipsoid, *c.* 7-12 x 6-8 µm; **Pycnidia:** on tubercles, abundant and conspicuous, especially near the axils, up to 0.5 mm diam., black; **conidia:** bifusiform, 5-7 x 1 µm; **Spot tests:** K-, C-, KC-, P-, UV-; **Secondary metabolites:** none detected.

Substrate and ecology: on acidic rock faces and boulders (especially igneous rocks, sometimes shale), rarely on wood; usually on exposed rocky ridges or boulders in wind-swept sites, usually in regions with a continental climate, but in somewhat moister areas than *P. minuscula*; also reported from dry, sandy, or stony ground; **World distribution:** circumpolar in both the Southern and Northern Hemispheres; low to high Arctic and temperate regions in subalpine to alpine sites; **Sonoran distribution:** southern California and from Baja California (Guadalupe Island) as the type collection of *Alectoria pacifica* (Brodo and Hawksworth 1977).



Notes: It is not likely to be confused with other lichens, other than slender morphs of *P. minuscula*. The description based on the North American literature on the species in general. It has apparently not been collected in the Sonoran region since the late 19th century.

PSEUDEVERNIA

by T. H. Nash III and J.A. Elix

Pseudevernia Zopf, Beih. Bot. Centralbl. 14: 124 (1903).

Family: Parmeliaceae; Type: *Pseudevernia furfuracea* (L.) Zopf; No. species: six world-wide; Selected lit.: Hale (1968).

Life habit: lichenized; **Thallus:** foliose to subfruticose or caespitose, separate, loosely imbricate, lobate, **lobes:** linear, frequently subdichotomously branched; apices: usually subtruncate, eciliate; **upper surface:** light gray to gray, smooth, plane to rugulose, shiny or dull, maculate or not, usually epruinose; with or without isidia or soredia; pseudocyphellae absent; **upper cortex:** with a pored epicortex, palisade paraplectenchymatous; **medulla:** white,

loosely packed, cell walls containing *Cetraria*-type lichenan; **photobiont:** primary one a *Trebouxia*, secondary photobiont absent; **lower surface:** tan to black, sometimes mottled white, naked, channeled revealing part of the medulla between inrolled cortices on either side, erhizinate, attached by basal holdfasts; cyphellae, pseudocyphellae and tomentum absent; **Ascomata:** apothecial, laminal, orbicular, cup-shaped, subpedicellate or pedicellate; margin: prominent, with thalloid rim; disc: imperforate, brown to dark brown; exciple: gray or hyaline; epithecium: brown or brownish yellow; hypothecium: hyaline; **asci:** lecanoral, wall layers apex thickened, apex I+ blue, with wide, axial body divergent towards apex, *c.* 8-spored; **ascospores:** simple, ellipsoid; 7-10 x 4-6 µm; walls: thin, hyaline, I-; **Conidiomata:** pycnidial, laminal or marginal, immersed or emergent to sessile; **conidia:** bifusiform, 5.5-7 x *c.* 1 µm; **Secondary metabolites:** upper cortex with atranorin and chloroatranorin; medulla with some combination of orcinol depsides, depsidones, or ß-orcinol depsidones; **Geography:** temperate Europe to north Africa and Pakistan, NE and SW North America extending to Central America; **Substrate:** mostly bark, particularly common on conifers.

Notes: Although the name implies a relationship to the common fruticose genus *Evernia*, the similarity is not very great. In general habit they are perhaps closest. But *Evernia* is only weakly dorsiventral, has a lax medulla and has a different cortical and medullary chemistry. In the southern part of the Sonoran region, it is more likely to be confused with *Everniastrum*, that has a similar subfruticose to caespitose growth form. However, the latter genus differs in having marginal cilia (and occasionally short rhizines), a paraplectenchymatous upper cortex, has substantially larger spores and isolichenan in the medullary cell walls.

Key to the species of ***Pseudevernia*** from the Sonoran region:

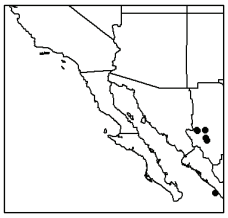
1. Thallus isidiate, narrow lobed (1-2 mm wide) .... ***P. consocians***
1. Thallus not isidiate, becoming broader lobed (up to 4 mm wide) ..... ***P. intensa***

The Species

Pseudevernia consocians (Vain.) Hale & W. L. Culb., Bryol. 69: 165 (1966).

Basionym: *Parmelia consocians* Vain., Dansk Bot. Ark. 4: 6 (1926); lllustrations: Hale (1979), p. 88; Brodo et al. (2001), p. 590.

Thallus: foliose to subfruticose to caespitose, 4-10 cm across, separate, lobate; **lobes:** linear, 0.5-1.5 mm wide, subdichotomously branched, loosely imbricate; apices: usually subtruncate, eciliate; **upper surface:** light gray to gray, smooth, plane to rugulose, shiny or dull, weakly maculate, usually epruinose; **isidia:** abundant, cylindrical; tips: darker than the thallus, sometimes abrading, but not sorediate; soredia absent; **medulla:** white, loosely packed; **lower surface:** tan to black, sometimes mottled white, naked, channeled, erhizinate, attached by basal holdfasts; **Apothecia:** not seen; **Pycnidia:** laminal or marginal, immersed or emergent to sessile; **conidia:** not seen; **Spot tests:** upper cortex K+ yellow, C-, KC-, P+ yellow; medulla K-, C+ red, KC+ red, P-; **Secondary metabolites:** upper cortex with atranorin and chloroatranorin; medulla with lecanoric acid (major).



Substrate and ecology: usually on conifers (especially pines) in open pine-oak forests; **World distribution:** neotropics from northern Mexico to Central America; **Sonoran distribution:** in the Sierra Madre Occidental, Chihuahua and Sinaloa, at 1500-2300 m.

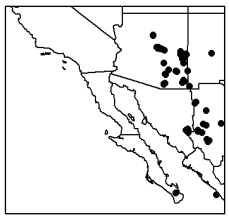
Notes: In comparison with the European *P. furfuracea*, which can also be isidiate, *P. consocians* is a less robust species with narrower lobes. Although both may have a C+ medulla, in *P. furfuracea* it is due to olivetoric acid; in *P. consocians*, due to lecanoric acid.

Pseudevernia intensa (Nyl.) Hale & W. L. Culb., Bryol. 69: 165 (1966).

Basionym: *Evernia intensa* Nyl., Bull. Linn. Soc. Normandie, ser. 2, 6: 269 (1873); Synonym: *Parmelia intensa* (Nyl.) Vain.; Illustrations: Hale (1979), p. 97; Brodo et al. (2001), p. 591.

Thallus: foliose to subfruticose to caespitose, 5-20 cm across, lobate; **lobes:** linear, 1-3 (-5) mm wide, separate, subdichotomously branched, loosely imbricate; apices: subtruncate, eciliate; **upper surface:** light gray to gray, smooth, plane to rugulose, shiny or dull, maculate or not, usually epruinose; soredia and isidia absent; **medulla:** white, loosely packed; **lower surface:** tan to black, sometimes mottled white, naked, channeled, erhizinate, attached by basal holdfasts; **Apothecia:** usually present, laminal on thallus, orbicular, cup-shaped, subpedicellate or pedicellate, 2-10 mm in diam.; margin: prominent, with a thalloid rim; disc: dark brown; **asci:** lecanoral, *c.* 8-spored; **ascospores:** simple, ellipsoid, 7-10 x 4-6 µm; walls: thin, hyaline, not amyloid; **Pycnidia:** laminal or marginal, immersed or emergent and sessile; **conidia:** not seen; **Spot tests:** upper cortex K+ yellow, C-, KC-, P+ yellow; medulla K-, C+ red, KC+ red, P-; **Secondary metabolites:** upper cortex with atranorin and chloroatranorin; medulla with lecanoric acid (major).

Substrate and ecology: usually on confers (especially *Pseudotsuga* and *Abies*) in mixed conifer forests; **World distribution:** neotropics from Central America through Mexico to southwestern U.S.A.; **Sonoran distribution:** eastern and especially SE Arizona south through the Sierra Madre Occidental of Chihuahua, Sonora and Sinaloa.



Notes: *Pseudevernia intensa* is one the most common montane lichens on confers from eastern Arizona southwards and exhibits considerable morphological plasticity from narrow to wide lobed individuals and from clearly foliose to robustly subfruticose.

PSEUDOCYPHELLARIA

by B. D. Ryan & D. J. Galloway

Pseudocyphellaria Vain., Acta Soc. Fauna Flora fenn. 7: 182 (1890).

Family: Lobariaceae; Type: *Pseudocyphellaria aurata* (Ach.) Vain.; No. species: 112 known world-wide; Selected lit.: Galloway (1985, 1988, 1992a & 1994), Galloway and Arvidsson (1990), Hale and Cole (1988), and McCune and Geiser (1997).

Life habit: lichenized; **Thallus:** foliose, dorsiventral, lobed, often very large, spreading, orbicular and ± rosette-forming and radiate, or irregularly laciniate, or ± dichotomously or irregularly branched, or polyphyllous, rarely ± monophyllous, loosely to tightly adnate; **lobes** narrow and strap-shaped or broad, ± dichotomously branching with distinctly bifurcate apices which may be rounded, pointed or truncate, often imbricate; margins: entire or variously incised or folded, often free and ascending; **upper surface:** blackish, brown, olive, green, blue-green, gray, ochraceous, yellow, or white, continuous, smooth or wrinkled, sometimes ± scabrid or hairy, sometimes shallowly foveolate, with faint or marked reticulum of interconnecting ridges, shiny or matt, often conspicuously maculate, with or without pseudocyphellae, isidia, phyllidia or soredia; cephalodia present or absent; goniocysts absent; margins often with conspicuous, elongate or verruciform pseudocyphellae; **upper cortex:** paraplectenchymatous, anticlinally arranged, ± isodiametric, thick-walled cells; **medulla:** loose, white or yellow; **photobiont:** primary photobiont a cyanobacterium (*Nostoc*), or chlorococcoid alga (*Dictyochloropsis* or *Chlorella*-like); accessory photobiont (*Nostoc*) present in some green algal species; **lower cortex:** paraplectenchymatous, anticlinally arranged, ± isodiametric, thick-walled cells; **lower sur-**

face: glabrous or usually ± tomentose, the tomentum pale to dark, thick and felted to indistinctly pubescent, always pseudocyphellate; pseudocyphellae: white or yellow, sparse to frequent, ± immersed in tomentum to raised-conical, round to irregular, the margins distinct or indistinct; attached to substrate by rhizoids which often form a mat; **Ascomata:** apothecial, often absent but abundant in a few species, roundish, emergent, becoming sessile to substipitate, marginal or laminal, hemiangiocarpic; disc: brown or red-brown, dull or shining, sometimes white-pruinose, round, usually concave; thalline exciple: well developed, prominent or slightly prominent, entire or crenate-striate, phyllidiate, isidiate or sorediate in some species, smooth to verrucose or areolate-scabrid, hairy or maculate; true exciple: hyaline to yellow-brown; hymenium: hyaline and brown or olivaceous above; hypothecium: pale or dark, hyaline to ochraceous, brown or violet; paraphyses: unbranched, not anastomosing; **asci:** clavate, *Peltigera*-type, unitunicate, with amyloid (I+ blue) cap in tholus, 8-spored; **ascospores:** oblong-fusiform, fusiform, fusiform-ellipsoid, obtuse or apiculate at the poles, simple then polarbilocular to transversely 1-3 (-5)-septate, wall hyaline becoming pale to dark brownish, grayish, or blackish, smooth, 20-38 (-43) x 6-11 µm; **Conidiomata:** pycnidial, laminal-lateral, immersed, *Lobaria*-type, globose or ovoid, 0.2-0.6 mm diam., walls dark brown at ostiole, paler below; **conidia:** straight, cylindrical, bacilliform, or bifusiform, 3-5 x 0.7-1 µm; **Secondary metabolites:** orcinol depsides, ß-orcinol depsides (including atranorin) or depsidones, terphenylquinones, pulvinic acid derivatives, usnic acids; triterpenoids (hopanes, stictanes, lupanes, and fernenes); **Geography:** temperate (primarily Southern Hemisphere) to tropical; **Substrate:** on bark, wood, soil, detritus, or non-calciferous, siliceous rock, in humid, sheltered, oceanic woodlands.

Notes: It is characterized by the presence of pseudocyphellae on lower (and sometimes upper) surface, emergent apothecia with colorless or brown, 1-3 septate or polarbilocular spores, and a diverse chemistry.

Key to species of ***Pseudocyphellaria*** in the Sonoran region:

1. With abundant soredia; upper surface plane or if somewhat ridged, then interspaces not deeply pitted; apothecia rare ..... ***P. anomala***
1. Soredia absent; upper surface strongly ridged, the interspaces deeply pitted; apothecia common ***P. anthraspis***

The Species

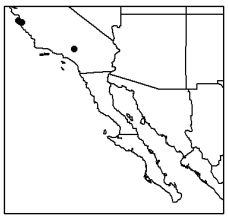
Pseudocyphellaria anomala Brodo & Ahti, Mycotaxon 28: 95 (1987).

Synonyms: *Sticta limbata* var. *anomala* G. K. Merrill, nom. nud., *Pseudocyphellaria anomala* G. K. Merrill *ex* H. Magn., nom. inval. (see Notes); Illustrations: Vitt et al. (1988), p. 236; Hale and Cole (1988), pl. 8d; Goward et al. (1994), p. 119; McCune and Geiser (1997), p. 251; Brodo et al. (2001), p. 592.

Thallus: foliose, loosely adnate, free at edges, up to 6-20 (-40) cm wide; **lobes** mostly 6-14 (-30) mm broad, little branched, lobules absent; **upper surface:** pale or dark brown or gray-brown (sometimes with conspicuous roundish black areas caused by a parasite), plane or with a network of ± strong ridges but with the interspaces not deeply pitted; **soredia:** white, gray or blue-gray to gray-black, in roundish to irregular, verruciform soralia that are mainly on ridges and along the margins; **medulla:** white; **photobiont:** cyanobacterial; **lower surface:** wrinkled to smooth, pale brown, with short tomentum; pseudocyphellae: numerous, scattered, white, irregular in outline, often elongated, scarcely verruciform; **Apothecia:** rare, 1.5-2 mm diam.; disc: dark brown; **Pycnidia:** unknown; **Spot tests:** cortex K-, C-, KC-, P-; medulla K+ yellow, C-, KC-, P+ orange, UV-; **Secondary metabolites:** stictic and constictic acids and unidentified terpenes in California material (Hale and Cole 1988); earlier reports, from more northern areas, listed norstictic, stictic, and salazinic acids as accessory substances in addition to the unknown mentioned by Krog (1968).

Substrate and ecology: on bark and wood, most often branches and trunks of deciduous trees and shrubs, oc-

casional on conifers and logs, rarely on rock; *c.* 150-1350 m in California; **World distribution:** western North America in the Pacific region; **Sonoran distribution:** very rare in southern California, the southernmost collection being a Bratt specimen from Santa Barbara Co.



Notes: The specimen cited above was not seen by the authors. The species was reported under the cited names in numerous articles before the name *P. anomala* was validly published in the paper by Ahti et al. (1987). See below under *P. anthraspis* for differences between the two species.

Pseudocyphellaria anthraspis (Ach.) H. Magn., Meddel. Göteb. Bot. Trädg. 13: 248 (1939).

Basionym: *Sticta anthraspis* Ach., Meth. Lich.: 280 (1803); Synonym: *Stictina anthraspis* (Ach.) Nyl.; Illustrations: Hale (1979), p. 55; Goward et al. (1994), p. 119; Hale and Cole (1988), fig. 44; Brodo et al. (2001), p. 593; McCune and Geiser (1997), p. 252.

Thallus: foliose, up to 5 cm diam. in the specimen seen (up to 40 cm diam. in the Pacific Northwest), leathery, loosely attached, free at the edges; **lobes** rounded, sometimes elongated and spatulate, somewhat imbricate, (5-) 15-25 (-30) mm across; margins: crenate; **upper surface:** pale to dark brown or pale green-brown, turning somewhat yellowish olive in herbarium, smooth, shiny to matt; often strongly reticulately ridged (with broad foveoles between), soredia and isidia absent; **medulla:** white; **photobiont:** cyanobacterial; **lower surface:** pale brownish, yellowish brown near margin, darker and more grayish toward center, with short spongy tomentum (patchily distributed, with the hairs longer and more clustered in some places); pseudocyphellae: whitish, interspersed among the tomentum and along the margins, 0.1-0.3 (-1.0) mm diam.; **Apothecia:** common, 1.5-3 (-4) mm diam., scattered, laminal along the ridges, emergent then sessile to narrowly short-stipitate; disc: concave and shiny then flat to convex and dull, red-brown to blackish; thalline margin: pale yellow-brown, initially pubescent, thin, subsequently usually disappearing; hymenium: hyaline below and yellowish above, 75-100 µm high; paraphyses simple, coherent at tips; hypothecium: fulvous; **asci:** clavate, 8-spored; **ascospores:** fusiform, 1-septate to eventually 3-septate, straight to curved, 23-32 x 6-8 (-10) µm; **Pycnidia:** immersed, especially on the ridges, ostiole black; **conidia:** bifusiform, 5-7 x 1 µm; **Spot tests:** K- or K+ yellow, C+ reddish or C-, KC+ red or C-, P+ orange or P-; **Secondary metabolites:** two hopanes, with variable amounts of tenuiorin, methyl gyrophorate, and gyrophoric acid with the constant addition of the stictic acid aggregate (Kondratyuk and Galloway 1995).

Substrate and ecology: on coniferous and hardwood trees, and shrubs, or over moss, rarely on rock; in moist forests, especially riparian areas, often near the coast in partially open habitats; *c.* 1350 m in California; **World distribution:** western North America in the Pacific region; **Sonoran distribution:** mountains of southern California, now apparently extinct except for Santa Barbara County.

Notes: Galloway (1995) typified this taxon and discussed the original material. This species is characterized by the abundant apothecia, white medulla and pseudocyphellae. Some early records of *P. anthraspsis*, at least from more northerly parts of California, were based on *P. anomala*, which is sorediate, but sometimes has apothecia-like galls (blackish and lacking a thalline margin) caused by a parasitic fungus; according to Goward et al. (1994), at least in British Columbia a rare form of *P. anomala* has sparse soralia, but can be distinguished from *P. anthraspis* by the more even upper surface and frequent occurrence of apothecia. Although Ohlsson (1973) regarded *P. anomala* as simply the sorediate counterpart of *P. anthraspis*, with the same two chemical strains, the two species also differ in other aspects of morphology (Krog 1968, Ahti et al. 1987), and according to McCune and Geiser (1997) in the Pacific Northwest they also differ somewhat in ecology and distribution, with *P. anthraspis* less common and occurring mainly in riparian areas.

PSEUDOPELTULA

by M. Schultz

Pseudopeltula Henssen, Lichenologist 27: 279 (1995).

Family: Gloeoheppiaceae; Type: *Pseudopeltula myriocarpa* Henssen; No. species: three world-wide; Selected lit.: Henssen (1995a).

Life habit: lichenized; **Thallus:** umbilicate, squamulose, placodioid, subgelatinous when wet; **surface:** olive or sometimes grayish pruinose, smooth or rimose; **anatomy:** ecorticate, homoiomerous, densely reticulate; **photobionts:** primary one a chroococcoid cyanobacterium, secondary photobiont *Stigonema* or absent; **Ascomata:** absent or present, apothecial, laminal on thallus, orbicular, sometimes irregular, immersed to semi-immersed, margin indistinct to distinct, with thalloid rim; **anatomy:** exciple: hyaline; epithecium: brownish yellow; hypothecium: hyaline; **asci:** prototunicate, wall thin, non-amyloid, 8-spored; **ascospores:** simple, rarely one-septate, ellipsoid; 9.5-14 µm x 6-8.5 µm; walls: thin, hyaline, rarely pale brownish; **Conidiomata:** pycnidial, laminal, immersed; **conidia:** bacilliform, *c.* 3 x 1 µm; **Secondary metabolites:** none detected; **Geography:** arid, semi-arid regions in SW North America and Central America; **Substrate:** soil crusts over calcareous and volcanic rock.

Notes: The presence of multiply divided hymenia is considered diagnostic of *Pseudopeltula*. In other characteristics it is similar to *Gloeoheppia*.

The Species

Pseudopeltula heppioides Henssen, Lichenologist 27: 283 (1995).

Illustrations: Henssen (1995a), p. 278 (figs. 9d-f), due to an editorial error, fig 9c is incorrectly labelled as the species (Henssen, personal communication), and Fig. 84 to right.

Thallus: squamulose-umbilicate, 1.5-5 mm wide, **margin:** slightly incised, sometimes downcurved, sometimes distinctly placodioid; **surface:** brownish olive, basal parts sometimes lighter, smooth, sometimes slightly pruinose, especially around the apothecia, **lower surface:** attached to the substrate by rhizohyphae; **Apothecia:** immersed to semi-immersed, zeorine, up to 10 per squamule, 0.25-0.75 mm wide; disc: slightly depressed to flat, brownish, smooth to rigid, open, with persisting thalline margin; exciple: distinct, up to 20 µm wide, hyaline, composed of strongly gelatinized hyphae; epihymenium: yellowish-brown; hymenium: hyaline, amyloid, divided by bands of sterile hyphae, 95-140 µm high; paraphyses: distinctly septate, sparingly branched and anastomosing, straight, apical cells thickened, 2.5-5 µm wide; **asci:** 8-spored; **ascospores:** simple, hyaline, ellipsoid, rarely well developed, 10-14 µm x 4-8 µm; walls: thin; **Pycnidia:** immersed, globose to broadly pyriform, 0.1 mm wide; pycnidial wall: convoluted with age; **conidia:** cylindrical, 2.5 x 1 µm; **Spot tests:** all negative; **Secondary metabolites:** none detected.

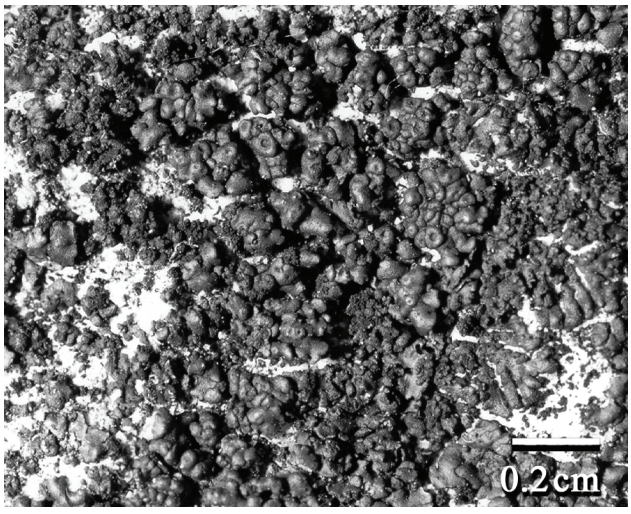
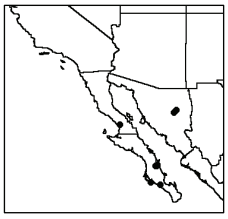


Fig. 84. *Pseudopeltula heppioides*, photo by M. Schultz.

Substrate and ecology: on thin soil crusts over calcareous, rarely volcanic rocks on rocky slopes; coastal to montane; **World distribution:** SW North America; **Sonoran distribution:** Baja California Sur, Baja California and Sonora.



Notes: In some respects the species resembles *Gloeoheppia turgida*, a species distinguished from *P. heppioides* by its inflated thallus with large internal air-spaces.

PSEUDOPYRENULA

by A. Aptroot

Pseudopyrenula Müll. Arg., Flora 66: 247 (1883).

Family: Trypetheliaceae; Type: *Pseudopyrenula diluta* (Fée) Müll. Arg.; No. species: six world-wide; Selected lit: Harris (1998).

Life habit: lichenized or non-lichenized and saprophytic; **Thallus:** crustose, mostly immersed in the substrate; **photobiont:** a trentepohlioid alga or absent; **Ascomata:** perithecial, semi-immersed; **Involucrellum:** pseudostromatic, blackened, sometimes forming a clypeus; **ascomatal wall:** black, continuous below the hamathecium; true **exciple:** black; **hamathecium:** composed of branched pseudoparaphyses, anastomosing between and above the asci, non-amyloid, but often yellowish colored (with anthraquinones); **asci:** bitunicate, cylindrical, with tholus, non-amyloid, 8-spored; **ascospores:** hyaline, ellipsoid to fusiform, 3-septate with distosepta and occasionally also eusepta, 18-55 x 5.5-17 µm; walls: not ornamented. **Conidiomata:** pycnidial; **conidia:** filiform; **Secondary metabolites:** lichexanthone in the thallus and/or anthraquinones in the ascomata or absent; **Geography:** mostly tropical; **Substrate:** only on bark.

Notes: The genus is characterized by its hyaline, 3-septate ascospores with diamond-shaped lumina due to its irregular distoseptum thickening and its anastomosing hamathecium filaments, in combination with uniloculate ascomata and an immersed to absent thallus.

The Species

Pseudopyrenula subnudata Müll. Arg., Flora 66: 272 (1883).

Synonyms: *Pseudopyrenula diluta* var. *degenerans* Vain., *Pseudopyrenula subgregaria* Müll. Arg.; Illustration: Harris (1975a), p. 263 as *Pseudopyrenula subgregaria*.

Thallus: continuous, superficial or semi-immersed in the substrate; **upper surface:** white, smooth; **photobiont:** a trentepohlioid alga; **Perithecia:** spherical, black, semi-immersed in the thallus, 0.3-0.7 mm diam.; **ascomatal wall:** black, continuous (but thinner) below the hamathecium; **hamathecium:** composed of branched pseudoparaphyses, anastomosing above and between the asci; filaments: *c.* 2 µm wide, heavily inspersed with yellowish oil droplets in gel; **asci:** cylindrical, *c.* 90-110 x 12-17 µm, with 8, irregularly arranged ascospores; **ascospores:** hyaline, fusiform to long-ellipsoid, 3-septate with distosepta leaving angular, diamond-shaped lumina, 21-24 x 6-8 µm; walls: not ornamented, without a gelatinous sheath; **Spot tests:** all negative, UV+ yellow; **Secondary metabolite**: lichexanthone.

Substrate and ecology: on bark of unidentified woody plants; **World distribution:** pantropical and extending somewhat northwards; **Sonoran distribution:** only collected once on the Channel Islands (California).

PSORA

by E. Timdal

Psora Hoffm., Deutschl. Fl. 2: 161 (1796), nom. cons.

Family: Psoraceae; Type: *Psora decipiens* (Hedwig) Hoffm.; No. species: *c.* 30 world wide; Selected lit.: Schneider (1979) and Timdal (1984a & 1986).

Life Habit: lichenized, not lichenicolous; **Thallus**: squamulose, attached by the whole lower surface or basal end of squamule; **squamules**: dispersed, adjacent, imbricate, or ascending, 2-10 mm wide, rounded to elongate, with entire, crenulate or lobed margin, without vegetative dispersal units; **upper surface**: from grayish or greenish to dark brown, sometimes red or yellow, dull or shiny, epruinose to densely white pruinose, smooth to deeply fissured; **upper cortex**: varying from 35 to 200 µm thick, containing remnants of algae (chlor-zinc-iodine!), consisting of an upper epinecral layer and a lower stainable layer, the latter composed of thick- to rather thin-walled, anticlinally oriented hyphae with shortly thread-like, angular, or round lumina, often containing lichen substances and/or calcium oxalate; **algal layer**: 40-80 µm thick, horizontally continuous; **photobiont**: primary one a chlorococcoid alga, secondary photobiont absent; algal cells: 10-15 µm diam.; **medulla**: white, of intricately interwoven hyphae, I-, often containing lichen substances and/ or calcium oxalate; **lower cortex**: poorly to well developed, composed of periclinally or anticlinally oriented hyphae, sometimes containing calcium oxalate or anthraquinones; **lower surface**: white to brown; **Ascomata**: apothecial, laminal or marginal, sessile, with a constricted base, simple or rarely somewhat conglomerate, usually convex and immarginate but often plane and indistinctly marginate when young, up to 2 mm diam., brown to black, dull to shiny, epruinose or with yellow or white pruina; exciple: annular, continuous with upper cortex, colorless to pale brown, composed of thick-walled, strongly conglutinated, radiating hyphae; hypothecium: colorless to pale brown, composed of intricately interwoven hyphae densely inspersed by crystals of calcium oxalate and sometimes lichen substances, I-; epithecium: brown, containing brown cell wall pigments and orange crystals of anthraquinones (mainly parietin [polarized light!]), K+ red; hymenium: hyaline, I+ blue, 60-100 µm high; paraphyses: straight, sparingly branched and anastomosing, strongly conglutinated, apical cell slightly swollen; **asci**: clavate, with a well developed, amyloid tholus containing a deeper amyloid tube and lacking an ocular chamber (*Porpidia*-type), 8-spored; **ascospores**: colorless, simple, ellipsoid, smooth, without halo; **Conidiomata**: pycnidial, laminal, immersed, with colorless or pale brown ostiole, with short, sparingly branched conidiophores; **conidia**: acrogenous, bacilliform; **Secondary metabolites**: anthraquinones, depsides, depsidones, aliphatic acids, pulvinic acids, triterpenes, and usnic acids; **Geography**: arctic to subtropical regions of the world, highest diversity in arid zones; **Substrate**: soil and rock, often calciferous.

Notes: The circumscription of the genus is based mainly on the following features: squamulose thallus, anthraquinones in the epithecium, calcium oxalate in the hypothecium, *Porpidia*-type ascus, immersed, laminal pycnidia and acrogenous, bacilliform conidia (Timdal 1984a). Color reactions caused by compounds located in a brown upper cortex or in a medulla filled with calcium oxalate are difficult to observe, and examination by TLC is crucial for the identification of some species. The five brown species lacking secondary metabolites (*P. globifera*, *P. himalayana*, *P. luridella*, *P. pseudorussellii*, and *P. tuckermanii*) form a complex in which some specimens are difficult to identify.

Key to the species of ***Psora*** in the Sonoran region:

1. Squamules orange to red, rounded; apothecia marginal, black 2

1. Squamules gray, yellow, or brown, rounded to elongate; apothecia marginal or laminal, brown to black 3

2. Squamules up to 10 mm wide, usually with a central depression; margin usually down-turned, more or less entire; thallus containing norstictic acid ... ***P. crenata***
2. Squamules up to 6 mm wide, without a central depression; margin (especially in young specimens) usually slightly up-turned and weakly crenulate; thallus not containing secondary metabolites or traces of norstictic acid ..... ***P. decipiens***

3. Squamules yellowish brown to bright yellow (rhizocarpic acid) ..... ***P. icterica***
3. Squamules gray to brown 4

4. Squamules gray to olivaceous brown, sometimes entirely white pruinose, rounded, containing atranorin; apothecia marginal, black ..... ***P. cerebriformis***
4. Squamules medium brown to dark brown, epruinose or partly pruinose, rounded to elongate, not containing atranorin; apothecia marginal to laminal, brown to black 5

5. Squamules up to 10 mm wide, ascending, containing gyrophoric acid; margin usually white; lower cortex well developed, composed of anticlinally oriented hyphae covered by calcium oxalate ..... ***P. nipponica***
5. Squamules up to 6 mm wide, adnate or ascending, with various chemistries; margin white or brown; lower cortex composed of periclinally oriented hyphae or poorly developed, lacking calcium oxalate 6

6. Squamules densely pruinose except along the slightly raised margin, containing pannarin ..... ***P. pruinosa***
6. Squamules epruinose or pruinose mainly along the margin, lacking pannarin; margin not raised 7

7. Squamules containing norstictic acid (medulla K+ red)8
7. Squamules not containing norstictic acid (medulla K-) 9

8. Squamules rounded, often with a central depression; apothecia brown, often with yellow pruina ..... ***P. russellii***
8. Squamules elongate, plane to weakly convex; apothecia black, epruinose ..... ***P. peninsularis***

9. Squamules containing gyrophoric acid (TLC!) 10
9. Squamules not containing gyrophoric acid 13

10. Lower cortex K+ red (anthraquinones) ..... ***P. hyporubescens***
10. Lower cortex K- 11

11. Apothecia marginal, black; squamules rounded, often with a central depression; gyrophoric acid located in medulla (C+ red) ..... ***P. nitida***
11. Apothecia laminal, brown to black; squamules elongate, without central depression; gyrophoric acid located in upper cortex (polarized light!) 12

12. Squamules up to 6 mm wide, adnate to imbricate, shiny, epruinose, containing bourgeanic acid; apothecia dark brown to black ..... ***P. californica***
12. Squamules up to 3 mm wide, imbricate to ascending, dull or somewhat shiny, often partly pruinose, not containing bourgeanic acid; apothecia medium brown to reddish brown ..... ***P. pacifica***

13. Squamules containing two unknown compounds ..... ***P. brunneocarpa***
13. Squamules not containing lichen substances 14

14. Apothecia medium brown to reddish brown 15
14. Apothecia dark brown to black 16

15. Species saxicolous on calciferous rock; apothecia reddish brown, plane and marginate when young; squamules up to 4 mm diam. ..... ***P. pseudorussellii***
15. Species terricolous or saxicolous, on calciferous and non-calciferous substrates; apothecia medium brown, convex and immarginate when young; squamules up to 6 mm diam. ..... ***P. tuckermanii***

16. Squamules distinctly white pruinose along the margin; lower side white near the margin; calcium oxalate present in the medulla and/or lower cortex ..... ***P. himalayana***
16. Squamules not, or only faintly, pruinose along the margin (but sometimes pruinose on the upper side, especially near the margin); lower side pale to medium brown; calcium oxalate absent from medulla and lower cortex 17

17. Squamules adnate to ascending, often imbricate; upper side sparingly to strongly fissured; upper cortex com-

posed of thick-walled hyphae with more or less angular lumina, 10-15 cell layers thick .... ***P. globifera***

17. Squamules mostly adnate, sometimes ascending near the margin, rarely imbricate; upper side smooth to sparingly fissured; upper cortex composed of rather thin-walled hyphae with round or somewhat angular lumina, 15-25 cell layers thick ..... ***P. luridella***

The Species

Psora brunneocarpa Timdal, **sp. nov.**

Diagnosis: *Squamae ad* 3 *mm latae, adnatae vel partim adscendentes, olivaceae vel brunneae, epruinosae. Apothecia ad* 1.5 *mm lata, laminalia, immarginata, brunnea, epruinosa. Thallus duo acida ignota continens.*

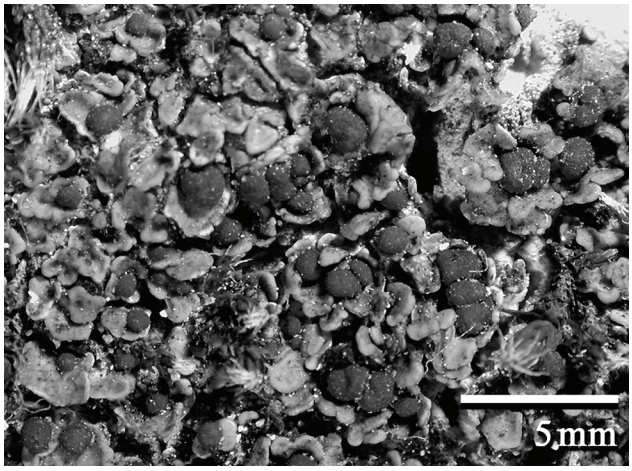


Fig. 85. *Psora brunneocarpa*, photo E. Timdal.

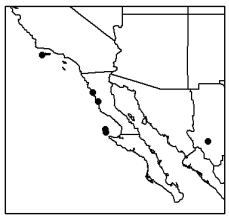
Type: MEXICO, Chihuahua, small ridge within Barranca del Cobre above Basihuare with numerous rhyolite outcrops, oaks, manzanita (*Arctostaphylos* spp.) and dispersed pines, 27°27.0'N, 107°29.3'W, 2000 m, 1994, Timdal SON 69/4 (O, holotype).

Additional specimens examined: U.S.A, California, Santa Barbara Co., Santa Rosa Island, South Point, 33°54'N, 120°07'W, 270 m, S-facing slope, chaparral area with frequent boulders, Nash 33008 (ASU); - MEXICO, Baja California, 5 miles E of San Quintín, foothills above coastal plain, 30°28'N, 115°49'W, 60 m, on soil, 1974, Nash 8743 (ASU); - along Route 1, 2 km S of Colonet, 31°04'N, 116°13'W, 50 m, coastal scrub community back shore with *Agave shawii, Ambrosia chenopodifolia, Machaerocereus gummosus*, 1988, Wetmore 63522 (MIN); - Isla Cedros, north-facing slope on NE ridge top with pines at north end of the island, 28°22'N, 115°15'W, *c.* 400 m, on soil, 1994, Nash 34312 (ASU, mixed with *Psora nitida*) and mountain slope W of the town of Cedros, 28° 08'N, 115°12'45"W, 510 m, on soil, Nash 34552 (ASU); - Chihuahua, collection data as for the holotype, Nash 37208 (ASU) and Barranca del Cobre, small, broad secondary valley within the canyon, with pines (*Pinus chihuahuana*, *Pinus* spp.), some oaks (*Quercus crassifolia* and *Quercus* spp.) and cypress (*Cupressus arizonica*), 27° 26.3'N, 107°29.3' W, 1800 m, steep rock wall, in some shade, 1994, Timdal, SON68/20 (O).

Squamules: up to 3 mm wide, rounded to elongate, adnate to partly ascending, adjacent to imbricate, weakly concave to weakly convex; **upper surface**: olivaceous to dark brown, dull, epruinose, smooth to sparingly fissured; **margin:** concolorous with upper side, straight or downturned, lobed; **upper cortex**: up to 150 µm thick (including up to 80 µm thick epinecral layer), composed of thin-walled hyphae with round lumina, not containing crystals of lichen substances or calcium oxalate; **medulla:** containing lichen substances but no calcium oxalate; **lower cortex:** poorly developed, of mainly periclinally oriented hyphae, not containing calcium oxalate; **lower surface**: medium brown, K-; **Apothecia**: up to 1.5 mm diam., laminal, immarginate even when young, medium brown, epruinose; **ascospores**: ellipsoid, 9.5-13.5 x 5-7 µm ; **Pycnidia**: unknown; **Spot tests:** upper cortex and medulla K-, C-, KC-, P-; **Secondary metabolites:** two unknown compounds (A5:B5-6:C6 and A5:B4:C6, both orange brown after charring).

Substrate and ecology: on soil and rock in open habitats, in Californian coastal scrub and Madrean evergreen woodland, from about sea-level up to 2000 m alt.; **World**

and **Sonoran distribution**: rare in California, Baja California and Chihuahua.



Notes: The species is most easily recognized by its unique chemistry. The small squamules and brown apothecia make it most likely to be confused with *P. pacifica* and *P. pruinosa*. Those species differ in being more or less pruinose. Furthermore, the former has more flat and marginate apothecia (at least when young), and the latter has squamules with a characteristic up-turned, epruinose margin.

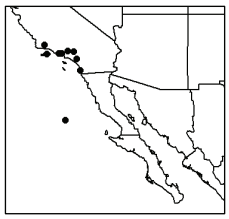
The identity of *Psora mexicana* de Lesd., described from the state of Puebla, Mexico, is still unsettled because the original material is missing. A specimen identified as that species by de Lesdain and examined by Timdal (1986) resembles *P. brunneocarpa* morphologically, but does not contain lichen substances.

Psora californica Timdal, Bryologist 89: 257 (1986).

Illustration: Timdal (1986), p. 257.

Squamules: up to 6 mm wide, elongate, adnate and dispersed to adjacent or imbricate, weakly concave to weakly convex; **upper surface**: castaneous brown, shiny, epruinose, smooth or sparingly fissured; **margin:** concolorous with upper side, often slightly down-turned, entire, crenulate or lobed; **upper cortex**: up to 140 µm thick, composed of thick-walled hyphae with angular lumina, containing crystals of lichen substances but no calcium oxalate; **medulla:** not containing crystals; **lower cortex:** of mainly periclinally oriented hyphae, not containing calcium oxalate; **lower surface**: medium brown, K-; **Apothecia**: up to 1.5 mm diam., laminal, immarginate or marginate when young and later immarginate, dark brown to black, epruinose; **ascospores**: ellipsoid, 12-14 x 5-7 µm; **Pycnidia**: laminal, immersed; **conidia**: bacilliform, 5-7 x 1 µm; **Spot tests:** upper cortex K-, C+ red, KC+ red, P-; medulla K-, C-, KC-, P-; **Secondary metabolites:** bourgeanic and gyrophoric acids, and trace of lecanoric acid.

Substrate and ecology: on soil and in crevices of rock, in open habitats in the lowlands, up to 980 m alt. in California, at 1250 m on Isla Guadalupe; **World distribution**: west coast of North America north to Washington; **Sonoran distribution:** fairly common in coastal California and Baja California.

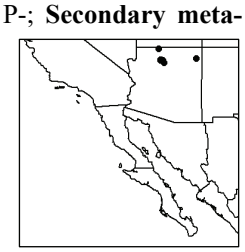


Notes: The C+ red and KC+ red reactions in the upper cortex are often difficult to observe. The present delimitation conforms with chemical strain I of Timdal (1986); strain II is here treated as *P. hyporubescens*.

Psora cerebriformis W. A. Weber, Mycotaxon 13: 104 (1981).

Illustrations: Timdal (1986), p. 259; St Clair (1999), p. 165; Brodo et al. (2001), p. 598.

Squamules: up to 8 mm wide, rounded, adnate and dispersed to adjacent or partly imbricate, weakly concave to weakly or strongly convex; **upper surface**: gray to olivaceous brown, dull, epruinose or partly to entirely pruinose, strongly fissured; **margin:** concolorous with upper side or white, straight, entire or crenulate; **upper cortex**: up to 140 µm thick, composed of thin-walled hyphae with round lumina, containing crystals of lichen substances and calcium oxalate; **medulla:** containing calcium oxalate; **lower cortex:** absent or poorly developed; **lower surface**: white to pale brown; **Apothecia**: up to 2 mm diam., marginal, immarginate even when young, black, epruinose or white pruinose; **ascospores**: ellipsoid, 10-17 x 6-8 µm; **Pycnidia**: laminal, immersed; **conidia**: bacilliform, 5-7 x 1 µm; **Spot tests:** upper cortex K+ yellow, C-, KC-, P+ yellow; medulla K-, C-, KC-, P-; **Secondary metabolites:** atranorin, sometimes trace of norstictic acid.



Substrate and ecology: on soil in open habitats at 1740-2130 m; **World distribution**: western North America; **Sonoran distribu-**

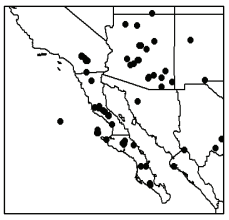
tion: locally fairly common in northern Arizona.

Psora crenata (Taylor) Reinke, Pringsh. Jahrb. Wiss. Bot. 28: 96 (1895).

Basionym: *Endocarpon crenatum* Taylor, London J. Bot. 6: 156 (1847); Synonyms: *Psora concava* B. de Lesd., *Psora coroniformis* Müll. Arg.; Illustrations: St. Clair (1999), p. 166; Timdal (1986), p. 260; Brodo et al. (2001), p. 599.

Squamules: up to 10 mm wide, rounded, adnate and dispersed to adjacent or imbricate, usually weakly to strongly concave; **upper surface**: orange to bright red or pink, more rarely reddish brown, dull, partly to entirely pruinose, sparingly fissured; **margin:** concolorous with upper side or white, down-turned or more rarely straight, more or less entire; **upper cortex**: up to 80-140 µm thick, composed of thin-walled hyphae with round lumina, containing crystals of calcium oxalate but no lichen substances; **medulla:** containing crystals of lichen substances and calcium oxalate; **lower cortex:** absent or poorly developed; **lower surface**: white to pale brown; **Apothecia**: up to 2 mm diam., marginal, immarginate even when young, black, epruinose or white pruinose; **ascospores**: ellipsoid, 12-16 x 6-8 µm; **Pycnidia**: unknown; **Spot tests:** upper cortex K-, C-, KC-, P-; medulla K+ red, C-, KC-, P+ orange; **Secondary metabolite:** norstictic acid.

Substrate and ecology: on soil in open habitats, from deserts to juniper-pinyon pine woodlands, up to 1840 m; **World distribution**: southern Africa, Australia and North America; **Sonoran distribution:** fairly common in Arizona, California, Baja California, Baja California Sur, Chihuahua, Sinaloa and Sonora.

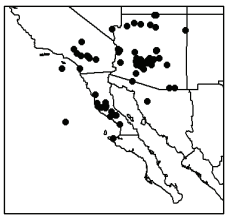


Psora decipiens (Hedwig) Hoffm., Descript. Adumbr. Pl. Lich. 2, 4: 63 (1794).

Basionym: *Lichen decipiens* Hedwig, Descript. Adumbr. Musc. Frond. 2: 7, Tab. 1B, Fig.1-6 (1789); Illustrations: Timdal (1986), p. 261; St. Clair (1999), p. 167; Brodo et al. (2001), p. 600.

Squamules: up to 6 mm wide, rounded, adnate and dispersed to adjacent or imbricate, weakly concave to weakly convex; **upper surface**: orange to bright red or rose, dull or shiny, epruinose or partly to entirely pruinose, smooth or sparingly fissured; **margin:** concolorous with upper side or white, straight or slightly up-turned, entire or often weakly crenulate (especially when young); **upper cortex**: up to 80-120 µm thick, composed of thin-walled hyphae with round lumina, containing crystals of calcium oxalate but no lichen substances; **medulla:** containing crystals of calcium oxalate, sometimes also lichen substances; **lower cortex:** absent or poorly developed; **lower surface**: white to pale brown; **Apothecia**: up to 2 mm diam., marginal, immarginate even when young, black, epruinose or white or yellow pruinose; **ascospores**: ellipsoid, 11-18 x 6-8 µm; **Pycnidia**: laminal, immersed; **conidia**: bacilliform, 6-7 x 1 µm; **Spot tests:** upper cortex and medulla K-, C-, KC-, P-; **Secondary metabolites:** none detected or rarely traces of norstictic acid.

Substrate and ecology: on more or less calciferous soil and crevices of rock in open habitats, from deserts to conifer forests, up to 1860 m; **World distribution**: Africa, Asia, Australia, Europe and North and South America; **Sonoran distribution:** common in Arizona, California, Baja California, Baja California Sur and Sonora.



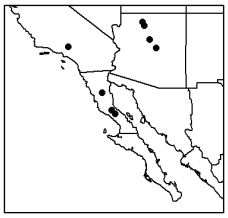
Notes: Specimens containing hyposalazinic and hypostictic acids occur in Colorado and Utah (plus Europe); these tend to have more rose colored squamules. In the Arctic, specimens with a high concentration of norstictic acid are common. There are other chemical strains in Australia and South Africa.

Psora globifera (Ach.) A. Massal., Ric. auton. lich. crost.: 91 (1852).

Basionym: *Lecidea globifera* Ach., Lichenogr. univers.: 213 (1810); Illustrations: Timdal (1986), p. 262; Brodo et al. (2001), p. 600.

Squamules: up to 5 mm wide, elongate, adnate to imbricate, weakly concave to weakly convex; **upper surface**: castaneous to dark brown, dull or shiny, epruinose or partly pruinose, sparingly to strongly fissured; **margin:** concolorous with upper side, straight or up-turned, crenulate to lobed; **upper cortex**: up to 60-120 µm thick, composed of thick-walled hyphae with more or less angular lumina, not containing crystals of lichen substances, sometimes containing calcium oxalate; **medulla:** not containing lichen substances or calcium oxalate; **lower cortex:** of mainly periclinally oriented hyphae, not containing calcium oxalate; **lower surface**: medium brown, K-; **Apothecia**: up to 1.5 mm diam., laminal, immarginate or marginate when young and later becoming immarginate, dark brown to black, epruinose or yellow pruinose; **ascospores**: ellipsoid, 10-13 x 5-7 µm; **Pycnidia**: laminal, immersed; **conidia**: bacilliform, 6-9 x 1 µm; **Spot tests:** upper cortex and medulla K-, C-, KC-, P-; **Secondary metabolites:** none detected.

Substrate and ecology: on soil or in crevices of rock in open habitats, mainly in conifer forests and woodlands at 550-2800 m.; **World distribution**: Asia, Europe and North America; **Sonoran distribution:** rare in Arizona, California and Baja California.

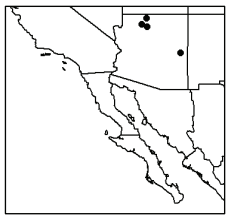


Psora himalayana (Church. Bab.) Timdal, Bryologist 89: 262 (1986).

Basionym: *Biatora himalayana* Church. Bab., Hookers J. Bot. 4: 251 (1852); Synonym: *Psora elenkinii* Räss.; Illustrations: Timdal (1986), p. 262; St. Clair (1999), p. 168; Brodo et al. (2001), p. 600.

Squamules: up to 4 mm wide, elongate, imbricate, weakly concave to weakly convex; **upper surface**: reddish brown or medium brown to dark brown, dull, epruinose or partly pruinose, smooth or sparingly fissured; **margin:** white, straight, lobed; **upper cortex**: up to 80-160 µm thick, composed of thick-walled hyphae with angular lumina, not containing crystals of lichen substances, sometimes containing calcium oxalate; **medulla:** not containing lichen substances, sometimes containing calcium oxalate; **lower cortex:** poorly developed, of anticlinally oriented hyphae, containing calcium oxalate; **lower surface**: white to medium brown, K-; **Apothecia**: up to 2 mm diam., laminal, immarginate even when young, black or dark brown, epruinose or white or yellow pruinose. **ascospores**: ellipsoid, 11-14 x 7-9 µm; **Pycnidia**: laminal, immersed; **conidia**: bacilliform, 6-7 x 1 µm; **Spot tests:** upper cortex and medulla K-, C-, KC-, P-; **Secondary metabolites:** none detected.

Substrate and ecology: on calciferous rock in open habitats, mainly in conifer forests at 1680-3000 m; **World distribution**: Asia, Europe (Urals) and western North America; **Sonoran distribution:** rare in northern Arizona.



Psora hyporubescens Timdal, **sp. nov.**

Diagnosis: *Species P. californicae et P. globiferae valde similis, sed cortice inferno croceo, K+ rubescenti.*

Type: U.S.A., California, Los Angeles Co., San Gabriel Mountains, 1.24 mi up Mt. Wilson Road from Angels Crest Hwy., 34°15'N, 118°05'W, 1500 m, 1988, Bratt and Timdal 7052 (O, holotype).

Selected additional specimens examined: U.S.A, California, Contra Costa Co.: Mt Diablo, near North Peak, 1175 m, Baltzo 768-69R (UC); - Los Angeles Co.: San Gabriel Mts, Mt Wilson, 1525 m, 1907, Hasse 902 (FH), San Antonio Mts, Cucamonga Canyon, 420 m, on thin

earth in rock crevices, 1918, Johnston 3157 (FH, POM) and San Antonio Mts, San Antonio Canyon, 1830 m, on cliff mainly in crevices, 1918, Johnston 3183 (FH); - Mendocino Co.: on Spyrock Rd, 4 mi from Rte 101, 39°48'N, 123°30'W, 1000 m, 1975, Anderegg et al. 3316 (ID); - Riverside Co.: Elsinore, [33°40'N, 117°19'W], 1908, Hasse (ASU) [Hasse, Lich. Exs. Rel. 108]; - Siskiyou Co.: Klamath Nat. Forest, Gold Flat, on road 7F01, about 6 mi SW of Scott Bar, 41°40.5'N, 123° 05.5'W, granite rocks, fir, maple, manzanita, 1989, Ryan 25008 (ASU); - Stanislaus Co.: Frank Raines Co. Park, Del Puerto Canyon, 1985, Thiers 48931 (SFSU); - Tulare Co.: Sequoia Nat. Park, 0.5 mi W of Atwell Mill Ranger Station along Mineral King Road, 1980 m, in conifer woods with fir, pine and sequoia near stream, 1984, Wetmore 50193 & 50219 (MIN) and South Creek just above the Johnsondale Bridge at Kern River off of county road M-99, 35°58'N, 118°29'W, 1160 m, on metamorphic rocks in a alder-ash riparian woodland, 1996, Shevock et al. 13015 (ASU).

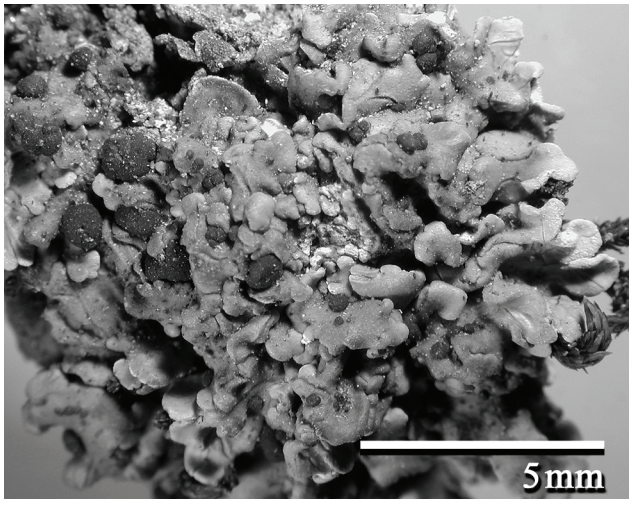
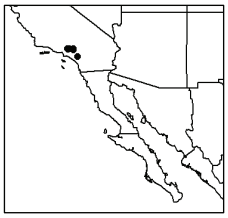


Fig. 86. *Psora hyporubescens*, photo E. Timdal.

Squamules: up to 5 mm wide, elongate, adnate to imbricate, weakly concave to weakly convex; **upper surface**: greenish brown to medium brown, dull, epruinose or pruinose near the margin, sparingly fissured; **margin:** concolorous with upper side, straight or up-turned, crenulate to lobed; **upper cortex**: up to 100 µm thick, composed of thick-walled hyphae with rather angular lumina, not containing crystals of lichen substances or calcium oxalate; **medulla:** containing lichen substances but no calcium oxalate; **lower cortex:** of mainly periclinally oriented hyphae, containing orange crystals (polarized light!) but not calcium oxalate; **lower surface**: orange brown, K+ red; **Apothecia**: up to 1.5 mm diam., laminal, convex and immarginate even when young, dark brown, epruinose; **ascospores**: ellipsoid, 9.5-11.5 x 4.5-7 µm; **Pycnidia**: not seen; **Spot tests:** upper cortex K-, C-, KC-, P-; medulla K-, C+red, KC+ red, P-; lower cortex K+ red, C-, KC-, P-; **Secondary metabolites:** gyrophoric acid and a series of undetermined anthraquinones.



Substrate and ecology: in crevices of rock in open habitats, mainly in conifer forests, at 1030-1980 m; **World distribution**: only known from California; **Sonoran distribution**: rare in the mountains of southern California.

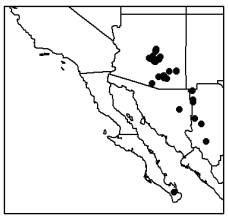
Notes: This species was treated as a chemotype of *P. globifera* by Timdal (1984a) and of *P. californica* by Timdal (1986). It is morphologically most similar to the former, and chemically most similar to the latter. It differs from *P. globifera* in having slightly paler and duller squamules with fewer fissures in the upper cortex, and in containing gyrophoric acid in the medulla and anthraquinones in the lower cortex. It differs from *P. californica* in having paler, duller, not down-turned, more crenulate, and more imbricate squamules with more fissures in the cortex; in containing anthraquinones in the lower cortex; and in lacking bourgeanic acid. *Psora californica* and *P. hyporubescens* are largely sympatric, but do not show altitudinal overlap: the former is known from 270-980 m in southern California (at 1250 m on Isla Guadalupe), the latter is known from 1030-1980 m.

Psora icterica (Mont.) Müll. Arg., Flora, Jena 71: 45 (1888).

Basionym: *Biatora icterica* Mont., Ann. Sci. nat., bot., Ser 2 2: 373 (1834); Illustrations: Timdal (1986), p. 264; St. Clair (1999), p. 169; Brodo et al. (2001), p. 601.

Squamules: up to 5 mm wide, rounded or elongate, adnate and dispersed to adjacent or slightly imbricate, weakly concave to weakly convex; **upper surface**: bright or greenish yellow, sometimes yellowish brown, dull, epruinose or partly pruinose, smooth or sparingly fissured; **margin:** concolorous with upper side, straight or up-turned, entire or crenulate to lobed; **upper cortex**: up to 50-80 µm thick, composed of thin-walled hyphae with round lumina, containing crystals of lichen substances, sometimes also calcium oxalate; **medulla:** containing calcium oxalate, not lichen substances; **lower cortex:** of mainly periclinally oriented hyphae, not containing calcium oxalate; **lower surface**: white to pale brown; **Apothecia**: up to 1.5 mm diam., laminal, immarginate even when young, black or dark brown, epruinose; **ascospores**: ellipsoid, 14-18 x 6-8 µm; **Pycnidia**: laminal, immersed; **conidia**: bacilliform, 7-8 x 1 µm; **Spot tests:** upper cortex and medulla K-, C-, KC-, P-; **Secondary metabolite:** rhizocarpic acid.

Substrate and ecology: on soil in open habitats, from deserts to conifer forests, at 540-2290 m; **World distribution**: North and South America; **Sonoran distribution:** fairly common in Arizona, Baja California Sur, Chihuahua and Sonora.

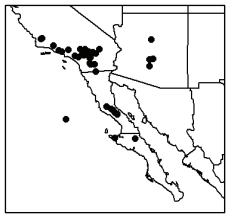


Psora luridella (Tuck.) Fink, Lich. Fl. U.S.: 213 (1935).

Basionym: *Lecidea luridella* Tuck., Proc. Amer. Acad. Arts Sci. 5: 418 (1862); Illustration: Timdal (1986), p. 265.

Squamules: up to 4 mm wide, rounded to elongate, adnate or ascending near the margin, rarely imbricate, weakly concave to plane; **upper surface**: medium brown to dark brown, dull, epruinose or faintly pruinose, smooth to sparingly fissured; **margin:** concolorous with upper side, straight to weakly up-turned, entire or lobed; **upper cortex**: up to 200 µm thick, composed of rather thin-walled hyphae with more or less round lumina, not containing crystals of lichen substances, sometimes containing calcium oxalate (mainly in the epinecral layer); **medulla:** not containing lichen substances or calcium oxalate; **lower cortex:** of mainly periclinally oriented hyphae, not containing calcium oxalate; **lower surface**: pale to medium brown, K-; **Apothecia**: up to 1.5 mm diam., laminal, convex and immarginate even when young, (medium-) dark brown to black, epruinose; **ascospores**: ellipsoid, 9-14 x 5-7 µm; **Pycnidia**: laminal, immersed; **conidia**: bacilliform, 6-9 x *c.* 1 µm; **Spot tests:** upper cortex and medulla K-, C-, KC-, P-; **Secondary metabolites:** none detected.

Substrate and ecology: on soil and rock, mainly in deserts, up to 1830 m; **World distribution**: western North America; **Sonoran distribution**: locally common in Arizona, California, Baja California and Baja California Sur.



Notes: The species is sometimes difficult to distinguish from *P. globifera* and *P. tuckermanii*. It differs from the former in its often smaller and more closely adnate squamules with a more smooth, dull, and paler brown upper surface, and in having more thin-walled hyphae with more rounded lumina in the upper cortex. The stainable layer of the upper cortex is roughly 10-15 cells thick in *P. globifera* and 15-25 cells thick in *P. luridella*. The apothecia of *P. luridella* are dark brown to pure black, rarely medium brown, and always epruinose; those of *P. globifera* are medium to dark brown, rarely black, and sometimes yellow pruinose. *Psora tuckermanii* differs morphologically in having generally larger, usually somewhat paler and more pruinose squamules and medium brown, sometimes white or yellow pruinose apothecia. Furthermore, it usually contains calcium oxalate in the

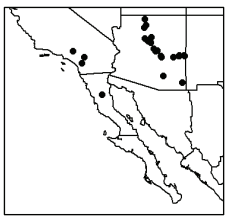
medulla. Timdal ([1986] p. 274) regarded some specimens from California and Baja California with dark brown to black apothecia and lacking calcium oxalate in the medulla as belonging to *P. tuckermanii*; these specimens are here regarded as belonging in *P. luridella*.

Psora nipponica (Zahlbr.) Gotth. Schneid., Biblioth. lichenol. 13: 117 (1980).

Basionym: *Lecidea nipponica* Zahlbr., Bot. Mag. Tokyo 41: 330 (1927); Synonym: *Psora novomexicana* de Lesd.; Illustrations: Timdal (1986), p. 267; St. Clair (1999), p. 170; Brodo et al. (2001), p. 602.

Squamules: up to 10 mm wide, elongate, ascending, concave to weakly convex; **upper surface**: olivaceous or reddish brown to medium brown, dull, epruinose or partly pruinose, smooth or sparingly fissured; **margin:** usually white, down-turned to up-turned, entire or lobed; **upper cortex**: up to 55-140 µm thick, composed of thick-walled hyphae with angular lumina, containing crystals of lichen substances but no calcium oxalate; **medulla:** containing crystals of lichen substances but no calcium oxalate; **lower cortex:** of anticlinally oriented hyphae, containing calcium oxalate; **lower surface**: white to medium brown; **Apothecia**: up to 2 mm diam., laminal, immarginate even when young, dark brown to black, epruinose; **ascospores**: ellipsoid, 10-14 x 5-7 µm; **Pycnidia**: laminal, immersed; **conidia**: bacilliform, 6-9 x 1 µm; **Spot tests:** upper cortex and medulla K-, C+ red, KC+ red, P-; **Secondary metabolites:** gyrophoric acid and trace of lecanoric acid.

Substrate and ecology: on soil or rock, usually in rock crevices in some shade, mainly in conifer forests and above tree line, at 1380-3540 m; **World distribution**: Japan and western North America; **Sonoran distribution:** fairly common in Arizona, California and Baja California.



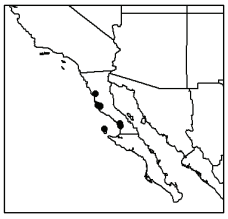
Notes: A chemical strain containing anthraquinones in the lower cortex is known from northern California and Idaho (Timdal 1986).

Psora nitida Timdal, Bryologist 89: 267 (1986).

Illustration: Timdal (1986), p. 268.

Squamules: up to 5 mm wide, rounded, adnate, dispersed to adjacent, usually concave; **upper surface**: castaneous brown, shiny, epruinose, smooth or sparingly fissured; **margin:** concolorous with upper side, down-turned, entire or lobed; **upper cortex**: up to 60-80 µm thick, composed of thin-walled hyphae with round lumina, not containing crystals of lichen substances or calcium oxalate; **medulla:** containing crystals of lichen substances but no calcium oxalate; **lower cortex:** of mainly periclinally oriented hyphae, not containing calcium oxalate; **lower surface**: white to pale brown; **Apothecia**: up to 1 mm diam., marginal, immarginate even when young, black, epruinose; **ascospores**: ellipsoid to broadly ellipsoid, 8-13 x 5-7 µm; **Pycnidia**: laminal, immersed; **conidia**: bacilliform, 5-7 x 1 µm; **Spot tests:** upper cortex K-, C-, KC-, P-; medulla K-, C+ red, KC+ red, P-; **Secondary metabolites:** gyrophoric acid and trace of lecanoric acid.

Substrate and ecology: on soil in Vizcaíno subdivision of Sonoran Desert, often in hillsides, up to 400 m; **World** and **Sonoran distribution**: rare in Baja California.



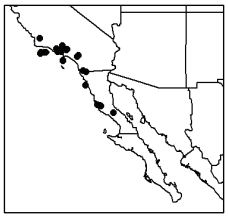
Psora pacifica Timdal, Bryologist 89: 268 (1986).

Illustrations: Timdal (1986), p. 268; Brodo et al. (2001), p. 603.

Squamules: up to 3 mm wide, elongate, imbricate to ascending, weakly concave to weakly convex; **upper surface**: medium to castaneous brown, dull or somewhat shiny, epruinose or partly pruinose, smooth; **margin:** concolorous with upper side, down-turned or straight, cren-

ulate or lobed; **upper cortex**: up to 35-65 µm thick, composed of thick-walled hyphae with angular lumina, containing crystals of lichen substances but no calcium oxalate; **medulla:** containing lichen substances but no calcium oxalate; **lower cortex:** poorly developed, composed of mainly periclinally oriented hyphae, not containing calcium oxalate; **lower surface**: white to pale brown; **Apothecia**: up to 1.3 mm diam., laminal, immarginate or marginate when young and later becoming immarginate, medium brown to reddish brown, epruinose; **ascospores**: ellipsoid, 10-14 x 5-7 µm; **Pycnidia**: unknown; **Spot tests:** upper cortex and medulla K-, C+ red, KC+ red, P-; **Secondary metabolites:** gyrophoric acid, trace of lecanoric acid, and usually small amounts of an apparently related compound.

Substrate and ecology: on soil in open habitats, often in coastal hillsides, up to 440 m; **World distribution**: west coast of North America; **Sonoran distribution:** uncommon in California and Baja California.



Notes: The C+ red and KC+ red reactions in the cortex are difficult to observe.

Psora peninsularis Timdal, **sp. nov.**

Diagnosis: *Squamae ad* 5 *mm latae, vulgo adnatae, castaneae, epruinosae, laeves vel leviter rimosae. Apothecia ad* 1.5 *mm lata, laminalia, immarginata, atra, nitida, epruinosa. Thallus acidum norsticticum continens.*

Type: MEXICO, Baja California, 10 km S of the bridge over El Rosario wash, 30°03'N, 115°35'W, 230 m, 1993, Timdal SON32/7 (O, holotype).

Additional specimens examined: U.S.A., California, Los Angeles Co., San Clemente Island, plateau between Thirst and Chukit Canyon (REWS site), *c.* 1650 ft, on soil, 1996, Bratt 9815 (O); - MEXICO, Baja California, 7 miles NE of El Rosario de Arriba, adjacent arroyo, 30°08'N, 115°38'W, on soil, 1974, Nash 8766 (ASU); - 23 km E of El Rosario along Rte 1, northern Vizcaíno Region of the Sonoran Desert, 30°02'0"N, 115°31'0"W, *c.* 200 m, 1989, Nash 26339 (ASU); - 10 km S of bridge over El Rosario wash, 30°03'N, 115°35'W, 230 m, on clay slopes above small valley, 1993, Wetmore 72348 (MIN).

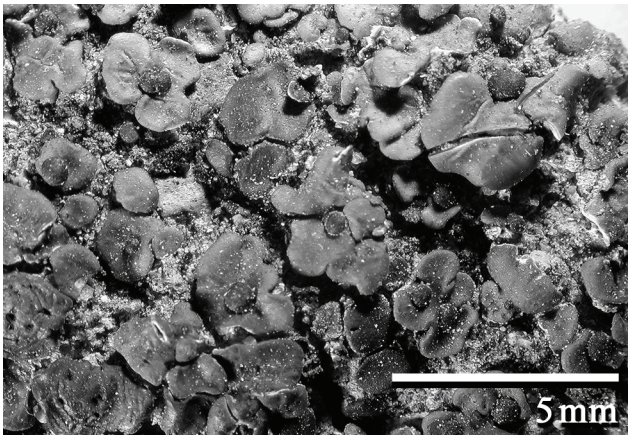
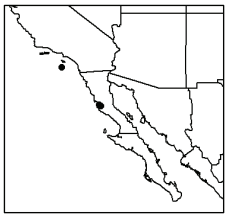


Fig. 87. *Psora peninsularis*, photo E. Timdal.

Squamules: up to 5 mm wide, elongate, adnate and dispersed to adjacent or slightly imbricate, plane to weakly convex; **upper surface**: castaneous brown, shiny, epruinose, smooth or sparingly fissured; **margin:** concolorous with upper side, more or less straight, entire, crenulate or lobed; **upper cortex**: up to 100 µm thick, composed of rather thin-walled hyphae with round lumina, sometimes containing some crystals of lichen substances but no calcium oxalate; **medulla:** containing crystals of lichen substances; **lower cortex:** of mainly periclinally oriented hyphae, not containing calcium oxalate; **lower surface**: medium brown, K-; **Apothecia**: up to 1.5 mm diam., laminal, immarginate even when young, black, shiny, epruinose; **ascospores**: ellipsoid, 10.5-13 x 5-6.5 µm; **Pycnidia**: laminal, immersed; **conidia**: bacilliform, 5-6 x 1 µm; **Spot tests:** upper cortex K-, C-, KC-, P-; medulla K+ red, C-, KC-, P+ orange; **Secondary metabolite:** norstictic acid.

Substrate and ecology: on soil in open habitats, in Vizcaíno subdivision of Sonoran Desert and in Californian coastal scrub, up to 500 m; **World** and **Sonoran distribution**: rare in southern California and Baja California.



Notes: The species resembles *P. californica* morphologically, but differs in forming somewhat smaller squamules without the often down-turned margin, in having an upper cortex composed of more thin-walled hyphae with more rounded lumina, in having pure black, more shiny apothecia, and in containing norstictic acid in the medulla. The Mediterranean-Macaronesian species *P. gresinonis* de Lesd. differs in forming smaller, more rounded and concave, olivaceous brown squamules with a slightly raised, often paler or grayish margin, and in having marginal to submarginal, smaller apothecia.

Psora pruinosa Timdal, **sp. nov.**

Diagnosis: *Squamae ad* 3 *mm latae, adnatae vel partim adscendentes, brunneae, pruinosae, laeves, margine epruinoso. Apothecia ad* 1.5 *mm lata, laminalia, immarginata, brunnea, epruinosa. Thallus pannarinum continens.*

Type: MEXICO, Baja California, 10 km S of the bridge over El Rosario wash, 30°03'N, 115°35'W, 230 m, 1993, Timdal, SON32/6 (O, holotype).

Additional specimens examined: U.S.A., California, San Diego Co., Camp Kearney Mesa, San Diego, 1932, Parks & Parks L115 (UC); - Los Angeles Co., Santa Catalina Island, 0.8 km NW of Catalina airfield at junction of road to Avalon and secondary road to the coast, 33°24'20"N, 118°24' 40"W, 440 m, on steep north facing hillside and ridgetop with oaks, Wetmore 73277 (MIN); - MEXICO, Baja California, El Rosario Arroyo, about 15 km ENE of El Rosario, 30°07'N, 115°08'W, 40 m, on hillside in Northern Vizcaíno region of the Sonoran Desert, with *Agave shawii* and *Opuntia molesta*, 1988, Wetmore 63737 (MIN).

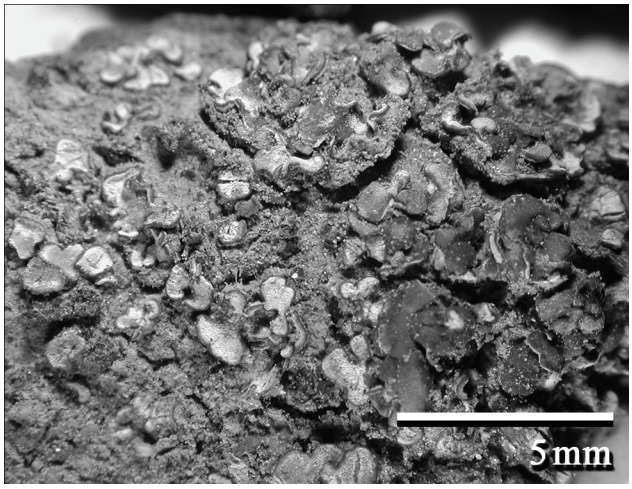
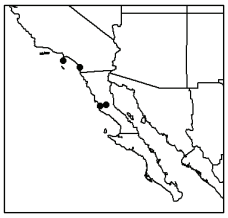


Fig. 88. *Psora pruinosa*, photo E. Timdal.

Squamules: up to 3 mm wide, elongate, adjacent or partly ascending, weakly concave to plane; **upper surface**: medium brown, dull, becoming densely pruinose, smooth; **margin:** concolorous with upper side, often slightly upturned, not pruinose, crenulate or lobed; **upper cortex**: up to 140 µm thick, composed of rather thick-walled hyphae with somewhat angular lumina, containing crystals of calcium oxalate but no lichen substances; **medulla:** containing lichen substances but no calcium oxalate; **lower cortex:** poorly developed, composed of mainly periclinally oriented hyphae, not containing calcium oxalate; **lower surface**: pale brown; **Apothecia**: up to 1.5 mm diam., laminal, convex and immarginate even when young, medium brown to reddish brown, epruinose; **ascospores**: ellipsoid, 11-15 x 5.5-7 µm (n=20); **Pycnidia** unknown; **Spot tests:** upper cortex K-, C-, KC-, P-, medulla K-, C-, KC-, P+ red; **Secondary metabolite:** pannarin.

Substrate and ecology: on soil in open habitats, in Vizcaíno subdivision of Sonoran Desert and in Californian coastal scrub, up to 440 m; **World** and **Sonoran distribution**: rare in southern California and Baja California.



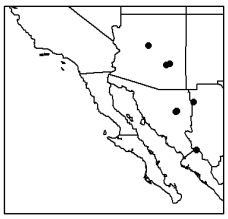
Notes: The species is recognized by the densely pruinose squamules with an up-turned, epruinose margin, and by the presence of pannarin which is unique in *Psora*.

Psora pseudorussellii Timdal, Bryologist 89: 269 (1986).

Illustrations: Timdal (1986), p. 269; Brodo et al. (2001), p. 603.

Squamules: up to 4 mm wide, elongate, imbricate, weakly concave to weakly convex; **upper surface**: medium brown, dull or shiny, epruinose or partly pruinose, smooth or sparingly fissured; **margin:** white, straight or up-turned, entire or lobed; **upper cortex**: up to 90-140 µm thick, composed of thick- to thin-walled hyphae with angular to round lumina, containing crystals of calcium oxalate; **medulla:** containing calcium oxalate; **lower cortex:** of mainly periclinally oriented hyphae, not containing calcium oxalate; **lower surface**: white to pale brown; **Apothecia**: up to 1.5 mm diam., laminal-submarginal, plane and marginate when young, later becoming more convex and often immarginate, reddish brown, epruinose or yellow pruinose; **ascospores**: ellipsoid, 8-12 x 5-7 µm; **Pycnidia**: unknown; **Spot tests:** upper cortex and medulla K-, C-, KC-, P-; **Secondary metabolites:** none detected.

Substrate and ecology: on calciferous rock in open habitats, at 790-1720 m; **World distribution**: mediterranean Europe and North America; **Sonoran distribution:** uncommon in Arizona, Chihuahua, Sinaloa and Sonora.



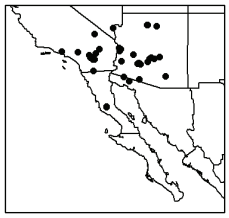
Notes: Some specimens are difficult to distinguish from *P. tuckermanii*. The apothecia of *Psora pseudorussellii* are more reddish brown, less convex and often partly marginate (especially when young); the squamules are generally smaller and usually somewhat darker than those of *P. tuckermanii*. The two species are largely allopatric: *P. pseudorussellii* has a mainly eastern and southern and *P. tuckermanii* a mainly western distribution in North America (Timdal 1986).

Psora russellii (Tuck.) A. Schneider, Textbook gen. Lichenol.: 141 (1897).

Basionym: *Lecidea russellii* Tuck., Proc. Am. Acad. Arts Sci. 5: 417 (1862); Synonym: *Psora nicolai* de Lesd.; Illustration: Timdal (1986), p. 272.

Squamules: up to 6 mm wide, rounded, adnate and dispersed to adjacent or imbricate, usually weakly to strongly concave; **upper surface**: medium to castaneous brown, dull or shiny, epruinose or partly pruinose, smooth or sparingly fissured; **margin:** concolorous with upper side or white, down-turned or straight, entire or lobed; **upper cortex**: up to 60-180 µm thick, composed of thin-walled hyphae with round lumina, containing crystals of lichen substances and calcium oxalate; **medulla:** containing lichen substances and calcium oxalate; **lower cortex:** of mainly periclinally oriented hyphae, not containing calcium oxalate; **lower surface**: white to medium brown; **Apothecia**: up to 1 mm diam., laminal-submarginal, immarginate, or marginate when young and later becoming immarginate, medium brown, epruinose or yellow pruinose; **ascospores**: ellipsoid, 11-15 x 5-8 µm; **Pycnidia**: unknown; **Spot tests:** upper cortex and medulla K+ red, C-, KC-, P+ orange; **Secondary metabolites:** norstictic acid and sometimes trace of gyrophoric acid.

Substrate and ecology: on soil or in crevices of rock in open habitats, mainly in deserts, rare in Californian coastal scrub and pinyon-juniper woodland, up to 1810 m; **World distribution**: North America; **Sonoran distribution:** rather common in Arizona, California, Baja California, and Sonora.

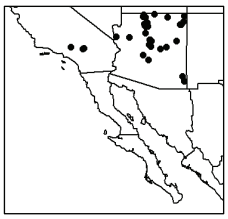


Psora tuckermanii Timdal, Bryologist 89: 273 (1986).

Illustrations: Timdal (1986), p. 273; Brodo et al. (2001), p. 604.

Squamules: up to 6 mm wide, elongate, imbricate, weakly concave to weakly convex; **upper surface**: light brown or medium brown, dull, epruinose or partly pruinose, smooth or sparingly fissured; **margin:** concolorous with upper side or white, down-turned or straight, entire or lobed; **upper cortex**: up to 60-120 µm thick, composed of thin-walled hyphae with round lumina, not containing crystals of lichen substances, sometimes containing calcium oxalate; **medulla:** not lichen substances, often containing calcium oxalate; **lower cortex:** of mainly periclinally oriented hyphae, not containing calcium oxalate; **lower surface**: white to medium brown; **Apothecia**: up to 1.5 mm diam., laminal, convex and immarginate even when young, medium brown, epruinose or white or yellow pruinose; **ascospores**: broadly ellipsoid, 8-11 x 6-8 µm; **Pycnidia**: unknown; **Spot tests:** upper cortex and medulla K-, C-, KC-, P-; **Secondary metabolites:** none detected.

Substrate and ecology: on soil and rock in open habitats, mainly in pinyon-juniper woodland, conifer forests, and Great Basin desert scrub, from 750 m to 2860 m alt. but rare below 1600 m; **World distribution**: western North America; **Sonoran distribution:** common in northern and central Arizona, scattered to rare in southern Arizona and California.



Notes: The specimens from Mexico and most of the specimens from southern California reported by Timdal (1986) are now considered belonging in *P. luridella*.

PSORINIA

by E. Timdal

Psorinia Gotth. Schneid., Biblioth. Lichenol. 13: 128 (1980).

Family: Lecanoraceae; Type: *Psorinia conglomerata* (Ach.) Gotth. Schneid.; No. species: two world-wide; Selected lit.: Thomson and Nash (1976), and Schneider (1979).

Notes: The second species, *P. lepidotella* (Nyl.) Gotth. Schneid., is apparently known only from the type collection. This specimen is in a poor condition, and could not be examined in detail by Schneider (1979), and consequently the generic description encompassing both species is not possible. The description given below is based on the type species, and it would be repetitious to have a separate generic description.

The Species

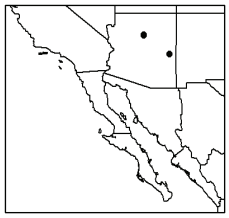
Psorinia conglomerata (Ach.) Gotth. Schneid., Biblioth. Lichenol. 13: 130 (1980).

Basionym: *Lecidea conglomerata* Ach., Lichenogr. Univ.: 201 (1810); Selected synonym: *Toninia conglomerata* (Ach.) Boistel; Illustration: Thomson and Nash (1976), p. 353.

Life habit: lichenized, not lichenicolous; **Thallus:** squamulose, attached by basal end of squamule when young, later by a well developed stipe; **squamules:** more or less dispersed when young, later becoming closely appressed, up to 5 mm wide, pulvinate, rounded, lacking vegetative dispersal units; **upper surface:** partly olivaceous brown and shiny in ± concave areas, partly pale gray and dull in ± convex areas, epruinose; margin: pale gray, dull, often

slightly raised in young squamules, later indistinct as the squamules become pulvinate and conglomerate; **upper cortex:** scleroplectenchymateous, composed of thick-walled, conglutinated hyphae with thread-like lumina, with cones or strands extending deep into the medulla and often merging with the stipe or lower cortex, covered by a thin epinecral layer, containing brown pigment and crystals dissolving in K in the uppermost 50-100 µm, not containing remnants of algae (chlor-zinc-iodine!); **algal layer:** in pockets below and between the upper cortex, approaching the upper surface below the gray, dull surface areas; **photobiont:** primary one a chlorococcoid alga; secondary photobiont absent; algal cells: 10-12 µm diam.; **medulla:** plectenchymatous, composed of rather thin-walled, only weakly conglutinated hyphae with thread-like lumina, filled with crystals dissolving in K and with remnants of algae (chlor-zinc-iodine!), I-; **lower cortex:** hardly differentiated from the upper cortex and continuous with this and the stipe; **lower surface:** pale gray to medium brown; **Ascomata:** apothecial, laminal, sessile, not or only slightly constricted at base, up to 1.5 mm diam., black, shiny, epruinose, simple or a few agglomerated, plane to moderately convex, with a narrow and often disappearing margin; exciple: annular, olivaceous green in the rim, colorless in inner part, composed of rather thick-walled, conglutinated, radiating hyphae with shortly cylindrical lumina, containing crystals dissolving in K; epithecium: olivaceous green, containing crystals dissolving in K-; hymenium: hyaline, I+ blue, 50-60 µm high; paraphyses: straight, sparingly branched and anastomosing, moderately conglutinated, apical cell not or only slightly swollen; hypothecium: colorless, composed of thick-walled, strongly conglutinated hyphae with thread-like lumina, lacking crystals, I+ blue, containing algae in the lower and lateral part; **asci:** broadly clavate, with a well developed, amyloid tholus containing an ocular chamber and a broad axial mass (*Lecanora*-type), 8-spored; **ascospores:** colorless, simple or 1-septate, narrowly ellipsoid, smooth, without halo, 9-15 x 4-6 µm; **Conidiomata:** pycnidial, laminal, immersed in the algal layer and medulla, with a dark green to black ostiole; **conidia**: acrogenous, filiform, straight to curved, 12-20 x *c*. 1 µm; **Spot tests:** upper cortex K+ yellow, C-, KC-, P+ yellow; medulla K+ yellow turning red, C-, KC-, P+ orange; **Secondary metabolites:** atranorin and norstictic acid.

Substrate and ecology: on exposed volcanic rock in the alpine zones, at 3530 - 3720 m alt.; **World distribution:** alpine zones of Europe and North America; **Sonoran distribution:** rare in northern and central Arizona (San Francisco Peaks and White Mountains).



Note: Two chemical strains occur in Europe: atranorin and either norstictic or stictic acid (plus related compounds).

PSOROMA

by P. M. Jørgensen

Psoroma Michx., Flora bor. Amer.: 321 (1803).

Family: Pannariaceae; Type: *Psoroma hypnorum* (Vahl) Gray; No. species: *c.* 10 world-wide; Selected lit.: Jørgensen (1978 and 2000a); Henssen and Renner (1981).

Life habit: lichenized, **Thallus:** squamulose, small (up to 0.5 mm wide in Northern Hemispheric material), with interspersed dark bluegreen granules, hypothallus indistinct; **upper surface:** green gray to yellow-brown or shining cinnamon brown but greenish when wet; isidia and soredia absent; **upper cortex:** paraplectenchymatous **medulla:** white, very thin, often indistinct; **photobionts**: primary one a chlorococcoid alga (*Myrmecia*?); secondary photobiont *Nostoc*, greenish to dark brown, in wart-like cephalodia; **lower cortex:** paraplectenchymatous; **Ascomata:** apothecial, common, large, sessile, up to 5 mm wide, often concave with brown disc; thalline margin: raised, persistent, squa-

mulose; hymenium: I+ dark blue; paraphyses: simple or branched near apices, apices not thicked or capitate; **asci:** narrowly ellipsoid or cylindrical, with internal amyloid apical tubes, apex K/I+ blue, the tholus staining paler, 8-spored; **ascospores:** simple, colorless, ellipsoid with distinctive, often with 1-2 large oil droplets, often warted epispore, ± apiculate; **Conidiomata:** pycnidial, pale brown; **conidia:** simple, bacilliform, colorless; **Secondary metabolites:** mostly without secondary products; **Geography**: pantemperate, in Northern Hemisphere but primarily in Southern Hemisphere, extending towards the subtropics in high montane areas; **Substrate**: on soil, often among mosses; also on bark in the Southern Hemisphere.

Note: This is primarily a temperate genus occurring in both hemispheres. All species have a green primary photobiont, external cephalodia and ascospores with warted perispores and correspond to what has been called the *Psoroma hypnorum* group. In the Southern Hemisphere many larger, squamulose or foliose species were placed in this genus, but they are now treated as *Pannaria* (Jørgensen 2000a).

Key to the species of ***Psoroma*** from the Sonoran region:

1. Apothecia large (to 5 mm), mostly concave with irregularly squamulose margins; spores 20-34 µm long .... ***P. hypnorum***
1. Apothecia smaller (to 2 mm), flat with ± continuous, granular margins; spores at most 22 µm long 2
   2. Thallus cinammon brown; spores 14-17 µm long; coastal ..... ***P. cinnamomeum***
   2. Thallus yellowish brown; spores 19-22 µm long; upper montane ..... ***P. tenue*** var. ***boreale***

The Species

Psoroma cinnamomeum Malme, Ark. Bot. 20A(3): 11 (1925).

Illustrations: Henssen and Renner (1981), pp. 444 & 446; Jørgensen (2000a), p. 701.

Thallus: small squamulose to granular, irregularly dispersed over the substrate; **squamules:** semiglobose, up to 1 mm wide; **upper surface:** cinnamon; **upper cortex:** paraplectenchymatous, 30-40 µm thick; **medulla:** composed of loosely reticulate hyphae; **lower cortex:** paraplectenchymatous, 20-30 µm thick; **cephalodia:** dark purplish brown, scarce in Californian material, mostly small, dark pustules beneath the apothecia (or squamules); **Apothecia:** common, up to 2 mm wide with a regular, thalline margin: up to 70 µm thick, initially smooth, becoming squamulose; disc: cinnamon-colored, often concave; exciple: poorly developed, subparaplechtenchymatous, 20-30 µm thick; hymenium hyaline but cinnamon above, I+ dark blue, *c.* 100 µm high; **asci:** clavate, with a distinct apical, amyloid ring structure, 8-spored; **ascospores:** simple, colorless, ellipsoid, 12-15 x 7-9 µm, with a distinct rugulose epispore; **Pycnidia:** not observed; **Spot tests:** all negative; **Secondary metabolites:** none detected except for an unidentified pigment.

Substrate and ecology: on detritus over soil, in moist, maritime heath; **World-distribution:** primarily a cool-temperate to subantarctic species from the Southern Hemisphere; **Sonoran distribution:** only known from Prince Island adjacent San Miguel Island in the Channel Islands of southern California.

Notes: It has a similar anatomy to *P. tenue*, but lacks the secondary products of that species. In addition, *P. cinnamomeum* has a more thick, urceolate apothecia when young and the cell-lumina of the corticate margin are smaller. The thalli of *P. cinnamomeum* is usually paler than *P. tenue*.

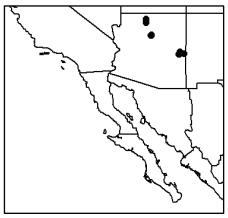
Psoroma hypnorum (Vahl) Gray, Nat. Arr. Br. Pl. I: 445 (1821).

Basionym: *Lichen hypnorum* Vahl, Fl. Dan.6 (16): 8 (1787); Illustrations: Goward et al. (1994), p. 122; McCune and Geiser (1997), p. 181; Jørgensen (1978), p. 28; Jørgensen (2000a), p. 701; Brodo et al. (2001), p. 605.

Thallus: squamulose, irregularly spreading over the substrate; **squamules:** small, 0.2-0.5 mm diam., sometimes almost granular; with interspersed darker (bluish), more granular squamules (containing *Nostoc*, i.e. the cephalodia); **upper surface:** mat gray to green-gray to yellow-brown when dry, bright green when wet (due to the green photobiont); **upper cortex:** paraplectenchymatous, 30-40 µm thick; **me-**

dulla: composed of loosely reticulate hyphae; **lower cortex:** paraplectenchymatous, 30-40 µm thick; **cephalodia:** frequent but sometimes few and inconspicuous, similar to thallus squamules or smooth, rounded, pale red-brown or bluish brown, scattered among the squamules or on the outher margin; **Apothecia:** frequent, usually large, up to 5 mm wide; disc: red-brown to dark brown, often concave; thalline margin: usually irregularly squamulose, 100-200 µm thick, rarely smooth, underside often with short, pale hairs; exciple: poorly developed, subparaplectenchymatous, 20-25 µm thick; hymenium: hyaline but brown above, I+ dark blue, 100-120 µm high; paraphyses: up to 4.5 µm wide, submoniliform, apices short-celled; **asci:** each with an internal apical amyloid tubes, clavate to subcylindrical, 70-90 x 11-15 µm, 8-spored; **ascospores:** simple, colorless, ellipsoid to narrowly ellipsoid, with an apiculus at one or both ends, with prominent, warted-ridged epispore, 20-34 x 8-12 µm (with epispore, otherwise 19-28 x 8-10 µm); **Pycnidia:** 0.1-0.2 mm diam., hyaline or pale brown; **conidia:** bacilliform, 5-6 x 1-2 µm; **Spot tests:** all negative; **Secondary metabolites:** none detected.

Substrate and ecology: moist habitats, among bryophytes or on soil, mostly in montane regions, particularly in spruce-fir forests; **World-distribution:** bipolar in cool-temperate and arctic-alpine regions of both hemispheres; **Sonoran distribution:** common in the high mountains of Arizona, most frequent above 3000 m.



Notes: If not checked when moist, it is often unneccesarily confused with *Protopannaria pezizoides*. Some material from Arizona has unusually large, greenish squamules and flat, dark brown apothecia. They have, however, spores and chemistry typical of the species and are regarded as being within its range of variation.

Psoroma tenue var. **boreale** Henssen, Mycotaxon 13: 441 (1981).

Illustrations: Henssen and Renner (1981), pp. 438, 440 & 444; Jørgensen (2000a), p. 701.

Thallus: small-squamulose to granulose, **squamules:** up to 1 mm broad, **upper surface:** shiny yellow-brown to brown with interspersed dark bluegreen granules (containing *Nostoc*, i.e. cephalodia); **upper cortex:** paraplectenchymatous, 20-30 µm thick; **medulla:** composed of loosely reticulate hyphae; **lower cortex:** paraplectenchymatous, 30-40 µm thick; **cephalodia:** frequent, dark purple brown, granular to coralloid branched, occurring singly or in clusters (often under the apothecia) up to 0.8 mm wide, corticated by one or two rows of cells; **Apothecia:** small, up to 2 mm diam., with granular thalline margin; discs: brown with concolorous margin or dark brown with a lighter brown margin, flat; hymenium: I+ dark blue, 95-120 µm high; hypothecium: 20-25 (-50) µm thick including ascogenous hyphae; subhymenium: varying thickness, frequently extending into a stipe of adglutinated hyphae with enlarged cells towards the base; **asci:** each with an internal amyloid apical tubes, 8-spored; **ascospores:** simple, colorless, ovoid with warted epispore, 19-24 x 7-12 µm; **Pycnidia:** inconspicuous; **conidia:** rod-shaped, 2-4 x 1 µm; **Spot tests:** K-, C-, KC-, P-; **Secondary metabolites:** thallus and apothecia with pannaric acid, porphyrilic acid methyl ester and a related unknown.

Substrate and ecology: wet soils near snowbeds in arctic-alpine environment; **World distribution:** widespread in arctic-alpine parts of the Northern Hemisphere; **Sonoran disribution:** rare, only collected a few times in the high mountains (above 3000 m) in Arizona, where it has the southernmost known locality in North America.

Notes: This taxon is separated from the similar *P. hypnorum* by its small flat apothecia and the shining brown, more granular thallus containing lichen metabolites. *Psoroma tenue* var. *tenue*, described from southern South America (Henssen and Renner 1981), has smaller lobes than *P. tenue* var. *boreale* and its cortex is less well developed.

PSORULA

by E. Timdal

Psorula Gotth. Schneid., Biblioth. lichenol. 13: 135 (1980).

Family: Psoraceae; Type: *Psorula rufonigra* (Tuck.) Gotth. Schneid.; No. species: one world-wide; Selected lit.: Schneider (1979), and Timdal (1984a).

Notes: *Psorula* differs from *Psora* mainly in the following characters: lichenicolous life habit, green pigments in the apothecium and pycnidium, absence of anthraxquinones from the epithecium, absence of calcium oxalate from the hypothecium, sessile pycnidia, intricately branched conidiophores, and pleurogenous, narrowly ellipsoid pycnoconidia (see Timdal 1984a).

Because the genus is now regarded as monotypic, it would be repetitious to have a separate generic description. Initially a second species, *P. scotopholis* (Tuck.) Gotth. Schneid. (Schneider 1979), was included in Psorula, but Timdal (1984a) placed that species in *Lecanora*.

The Species

Psorula rufonigra (Tuck.) Gotth. Schneid., Biblioth. Lichenol. 13: 136 (1980).

Basionym: *Biatora rufonigra* Tuck.. Proc. Amer. Acad. Arts Sci. 1: 250 (1847); Selected synonyms: *Psora brouardii* de Lesd., *Psora nigrorufa* de Lesd., *Psora rufonigra* (Tuck.) A. Schneid.; Illustration: Fig. 89 to right.

Life habit: lichenized, lichenicolous; **Thallus**: squamulose, attached by the whole lower surface or basal end of squamule; **squamules**: adnate and dispersed when young, later becoming ascending and imbricate, up to 2 (-3) mm wide, plane to concave, rounded to elongate, lacking vegetative dispersal units; **upper surface**: dark olivaceous brown, slightly shiny, epruinose, smooth; **margin**: entire or lobed, often slightly raised, dark brown to black; **upper cortex**: 30-50 µm thick, containing remnants of algae (chlor-zinc-iodine!), not containing crystals, consisting of a thin upper epinecral layer and a thicker lower stainable layer; stainable layer containing a brown pigment zone in the upper part, composed of rather thin-walled, anticlinally oriented hyphae with rounded lumina; algal layer: 50-100 µm thick, horizontally continuous;

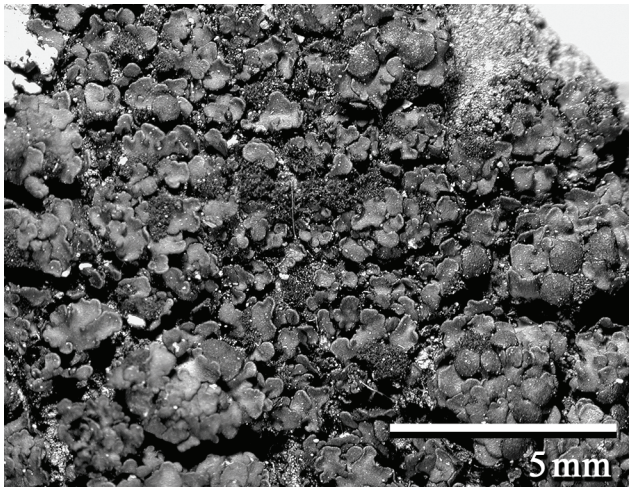
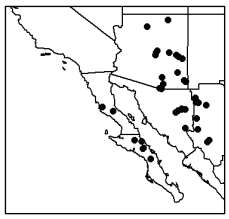


Fig. 89. *Psorula rufonigra*, photo by E. Timdal.

photobiont: primary one a chlorococcoid, secondary photobiont absent, but occurring on *Spilonema revertens*, a cyanolichen often thought to be a free-living cyanobacterium; algal cells: 10-15 µm diam.; **medulla**: thin or sometimes absent, white, of intricately interwoven hyphae, I-, not containing lichen substances or calcium oxalate; **lower cortex**: 20-40 µm thick, greenish black, often mixed with dark brown pigment, composed of anticlinally to periclinally oriented thick-walled hyphae with narrow lumina, not containing calcium oxalate; **lower surface**: dark green or brown to black; **Ascomata**: apothecial, marginal, sessile, with a constricted base, up to 1 mm diam., black, slightly shiny, epruinose, simple or more rarely a few agglomerated, plane to weakly convex,

with a narrow and often disappearing margin; exciple: annular, not continuous with upper cortex, greenish black in the rim, dark reddish brown in inner part, composed of thick-walled, strongly conglutinated, radiating hyphae with shortly cylindrical to rounded lumina; hypothecium: dark reddish brown, composed of strongly conglutinated hyphae, lacking crystals, I-; epithecium: dark green, often with a brown tinge, not containing crystals, K-; hymenium: hyaline to faintly green, I+ blue, 60-80 µm high; paraphyses: straight, sparingly branched and anastomosing, strongly conglutinated, apical cell not or only slightly swollen; **asci**: clavate, with a well developed, amyloid tholus containing a deeper amyloid tube and lacking an ocular chamber (*Porpidia*-type), 8-spored; **ascospores**: colorless, simple, ellipsoid, smooth, without halo, 9-12 x 5-7 µm; **Conidiomata**: pycnidial, marginal, sessile, black, with a dark green to brown wall and short-celled, intricately branched conidiophores; **conidia**: pleurogenous, narrowly ellipsoid, 3-5 x *c.* 1.5 µm; **Spot tests**: all negative; **Secondary metabolites**: none.

Substrate and ecology: on a filamentous cyanolichen (*Spilonema revertens*) over acidic rock in open habitats, up to 2350 m alt.; **World distribution**: widely distributed in arid and semi-arid areas in the temperate region in the northern hemisphere; **Sonoran distribution**: rather common in Arizona, Baja California, Baja California Sur, Chihuahua and Sonora; not known from southern California.



Notes: *Psorula rufonigra* is morphologically rather similar to *Toninia submexicana* de Lesd., but differs in anatomical feature of the apothecia, including the spores. *Psorula rufonigra* is associated with the cyanolichen *Spilonema revertens* and the *Toninia* usually grows independently.

PYRENULA

by A. Aptroot

Pyrenula Ach., Syn. meth. lich.: 125 (1814).

Family: Pyrenulaceae; Type: *Pyrenula nitida* (Weigel) Ach.; No. species: *c.* 200 world-wide; Selected lit.: Harris (1989 & 1995).

Life habit: lichenized or non-lichenized, saprophytic;.**Thallus:** crustose, usually immersed but sometimes superficial, sometimes areolate, occasionally with pseudocyphellae or pockets of crystals, often surrounded by a hypothallus; **photobiont:** primary one a trentepohlioid alga or absent, secondary photobiont absent; **Ascomata:** perithecial, black, often aggregated in pseudostromata; **involucrellum:** dark brown to black, clypeate, composed of fungal hyphae interspersed with bark cells and often K+ reddish or violet crystals; **ascomatal wall:** black, usually continuous below the hamathecium, often partly immersed in the thallus; true **exciple:** brown to pale brown, entire or not developed below the perithecial cavity, colorless or orange crystals often dense at the wall lining the locule; **hamathecium:** initially branched, anastomosed, sparsely septate paraphysoids; then replaced by unbranched paraphyses, not anastomosing, non-amyloid, hemiamyloid or amyloid; periphyses delveloped along the ostiolar canal; **asci:** bitunicate, clavate to cylindrical, long-stalked, with tholus, thickened at the apex with an internal apical beak, non-amyloid; **ascospores:** brown, ellipsoid to fusiform, transversely 2-30-septate, or muriform, with distosepta and often additional eusepta, 9-200 x 4-55 µm; walls: not ornamented; **Conidiomata:** pycnidial, black; **conidia:** filiform, simple, hyaline; **Secondary metabolites:** lichexanthone, or anthraquinones, or absent; **Geography:** cosmopolitan, but most diverse in the tropics; **Substrate:** mostly on bark, but also on non-calcareous rock.

Notes: the genus is in its current delimitation characterized by the combination of clypeate ascomata and brown, distoseptate ascospores and simple paraphyses.

Key to the species of ***Pyrenula*** from the Sonoran region:

1. Ascospores 3-septate; thallus with lichexanthone (UV + yellow) ..... ***P. occidentalis***
1. Ascospores (sub)muriform; thallus without lichexanthone (UV-negative, UV + whitish or UV + red due to anthraquinones) 2
   2. Thallus and ascocarps at least partly yellow due to anthraquinones (UV + red); ascospores shorter than 25 µm ..... ***P. ochraceoflava***
   2. Thallus and ascocarps without anthraquinones (UV-negative or + whitish); ascospores over 30 µm long 3
3. Ascospores mostly over 50 x 15 µm ... ***P. pyrenuloides***
3. Ascospores mostly below 50 x 15 µm ***P. thelomorpha***

The Species

Pyrenula occidentalis (R. C. Harris) R. C. Harris, in Ahti, Brodo and Noble, Mycotaxon 28: 96 (1987).

Basionym: *Pyrenula neglecta* subsp. *occidentalis* R. C. Harris, Michigan Bot. 12: 51 (1973).

Thallus: continuous, superficial on the substrate; **upper surface:** yellowish brown, smooth; pseudocyphellae absent; **photobiont:** a trentepohlioid alga; **Perithecia:** lenticular to hemispherical, black, semi-immersed in the thallus, *c.* 0.5-0.8 mm diam., K+ purplish in parts (but inside wall K-); **ascomatal wall:** black, continuous below the hamathecium; **hamathecium:** composed of unbranched pseudoparaphyses, not anastomosing; filaments: *c.* 1 µm wide, not inspersed with oil droplets; **asci:** cylindrical, with 8, irregularly arranged ascospores; **ascospores:** medium brown, narrowly ellipsoid, 3-septate with distosepta leaving angular lumina, end cells with the lumina directly against the outer wall, 18-25 x 8-12 µm; walls: not ornamented, without a gelatinous sheath; **Pycnidia:** often frequent, immersed; **conidia:** colorless, ± hooked, 20 x 1 µm; **Spot tests:** all negative or K+ yellowish, C-, KC-, P+ pale orange (of uncertain significance), UV+ yellow; **Secondary metabolite:** lichexanthone.

Substrate and ecology: on bark of various woody plants; **World distribution:** north temperate; **Sonoran distribution:** only recorded from southern California.

Pyrenula ochraceoflava (Nyl.) R. C. Harris, Mem. New York Bot. Gard. 49: 96 (1989).

Basionym: *Verrucaria ochraceoflava* Nyl., Expos. Syn. Pyrenocarp.: 50 (1858); Synonym: *Anthracothecium ochraceoflavum* (Nyl.) Müll. Arg.; Illustrations: Brodo et al. (2001), p. 613; Harris (1989), p. 107.

Thallus: continuous, superficial on the substrate; **upper surface:** yellow to orange or reddish, smooth; **photobiont:** a trentepohlioid alga; **Perithecia:** spherical, black, semi-immersed in the thallus, 0.3-0.5 mm diam.; **ascomatal wall:** black, continuous below the hamathecium; **hamathecium:** composed of unbranched pseudoparaphyses, not anastomosing; filaments: *c.* 1 µm wide, not inspersed with oil droplets; **asci:** cylindrical, with 8, irregularly arranged ascospores; **ascospores:** blackish brown, broadly ellipsoid, submuriform, distoseptate, 15-21 x 8-10 µm; walls: not ornamented, without a gelatinous sheath; **Spot tests:** all negative, UV+ red; **Secondary metabolites:** undetermined anthraquinones.

Substrate and ecology: on bark of *Avicennia*; **World distribution:** pantropical, especially abundant in coastal regions; **Sonoran distribution:** so far only collected once in Sinaloa.

Pyrenula pyrenuloides (Mont.) R. C. Harris, Mem. New York Bot. Gard. 49: 99 (1989).

Basionym: *Trypethelium pyrenuloides* Mont., Ann. Sci. Nat. Bot., sér. 2, 19: 69 (1843); Synonym: *Anthracothecium pyrenuloides* (Mont.) Müll. Arg.; Illustration: Harris (1989), p. 107.

Thallus: continuous, superficial on the substrate; **upper surface:** brownish, smooth, often with pseudocyphellae; **photobiont:** a trentepohlioid alga; **Perithecia:** spherical, black, immersed in the thallus, 0.5-0.8 mm diam.; **ascomatal wall:** black, continuous below the hamathecium; **hamathecium:** composed of unbranched pseudoparaphyses, not anastomosing; filaments: *c.* 1 µm wide, not inspersed with oil droplets; **asci:** cylindrical, with 8, irregularly arranged ascospores; **ascospores***:* blackish brown, narrowly ellipsoid, muriform with distosepta, 50-70 x 19-27 µm; walls: not ornamented, without a gelatinous sheath; **Spot tests:** all negative, UV negative; **Secondary metabolites***:* none detected.

Substrate and ecology: on bark of various woody plants; **World distribution:** pantropical; **Sonoran distribution:** only recorded from southern California.

Pyrenula thelomorpha Tuck., Gen. lich.: 275 (1872).

Synonym. *Anthracothecium thelomorphum* (Tuck.) Zahlbr.; Illustration: Harris (1989), p. 107.

Thallus: continuous, superficial on the substrate, **upper surface:** brownish, smooth, with pseudocyphellae; **photobiont:** a trentepohlioid alga or absent; **Perithecia:** spherical, black, immersed in the thallus, 0.4-0.6 mm diam.; **ascomatal wall:** black, continuous below the hamathecium; **hamathecium:** composed of unbranched pseudoparaphyses, not anastomosing; filaments: *c.* 1 µm wide, not inspersed with oil droplets; **asci:** cylindrical, with 8, irregularly arranged ascospores; **ascospores:** blackish brown, ellipsoid, muriform, distoseptate, 30-50 x 10-15 µm; walls: not ornamented, without a gelatinous sheath; **Spot tests:** all negative, UV negative; **Secondary metabolites***:* none detected.

Substrate and ecology: on bark of various woody plants; **World distribution:** neotropical or possibly nearly pantropical; **Sonoran distribution:** only recorded from southern California.

PYXINE

by K. Kalb

Pyxine E. A. Fr., Systema orbis vegetabilis. Pars I: 267 (1825).

Family: Physciaceae; Type: *Pyxine sorediata* (Ach.) Mont.; No. species: *c.* 60 world-wide; Selected lit.: Awasthi (1982), Imshaug (1957b), Kalb (1987 & 1994), Kashiwadani (1977a, b & c), and Swinscow and Krog (1975).

Life habit: lichenized; **Thallus:** foliose, lobate; **lobes:** radiating, but sometimes irregular; lobe tips: usually rotund, eciliate; **upper surface:** white, whitish gray to brownish-gray, leaden to bluish gray or stramineous, ± plane to convex or concave towards the periphery, sometimes reticulately ridged, shiny or dull, usually pruinose; with or without soralia, polysidiangia (= pustulate isidia) or isidia; pseudocyphellae: present in most species; **upper cortex:** paraplectenchymatous, formed by vertically arranged hyphae; **medulla:** separated into upper and lower layers, which are very often of different color and show different chemical reactions; **photobiont:** primary one a *Trebouxia*, secondary photobiont absent; **lower cortex:** prosoplectenchymatous, formed by longitudinally arranged hyphae; **lower surface:** usually black, whitish, brownish or bluish peripherally; attachment: by simple to multiple, furcately divided rhizines; cyphellae, pseudocyphellae and tomentum absent; **Ascomata:** apothecial, laminal, orbicular, sessile to elevated on a distinct internal stipe; thalline margin: prominent or reflexed, either distinct and persistent (*physciaeformis*-type), or in young apothecia distinct, then vanishing and giving the apothecia a lecid-

eine appearance (*cocoes*-type), or lacking such that all apothecia have a lecideine appearance from the beginning (*obscurascens*-type); exciple: present and persistent, sometimes blackened and/or substituted by a thickening parathecium; epithecium: bluish-black, K+ purple; hypothecium: brown; **asci:** lecanoral, with thickened apex wall layers (apex I+ blue), with distinct axial body, 8-spored; **ascospores:** brown, 1-3-septate, thick-walled, mischoblastiomorphic, ellipsoid, 10-23 µm x 4-8 µm; **Conidiomata:** usually present, pycnidial, laminal, immersed, conidiophore-type VI (Vobis 1980); **conidia:** ± bacilliform, formed pleurogenously, 3-4 x 0.8-1.2 µm; **Secondary metabolites:** upper cortex with atranorin and chloroatranorin) or lichexanthone, seldom (only in *P. nubila*) without acetone-soluble substances; medulla usually with terpenes and pigments [in old-world and Australasian species with norstictic acid (incl. satellites) often present], testacein (R_f-values: A 42, B' 25, C 20, pinkish after treatment with sulfuric acid and heat), a compound first detected in *Parmelia testacea* and of unknown structure and substance class present in some species; **Geography:** predominately tropical and subtropical with few species extending to temperate regions; **Substrate:** mostly bark, acidic rocks or mosses.

Key to the species of ***Pyxine*** from the Sonoran region:

1. Thallus K+ yellow or K- and UV- (atranorin present or in very low concentration) 2
1. Thallus K- and UV+ yellow (lichexanthone present) . 3

2. Thallus usually with soralia, rarely with polysidiangia; upper medulla (and sometimes soredia) yellow-orange, yellow or light yellow, lower medulla white; lobe margins with prominent white, linear pseudocyphellae distinctly contrasting with the dark lobe margins, pseudocyphellae rarely laminal; upper and lower medulla K-, P-; usually on acidic, mossy rocks, sometimes on bark ..... ***P. sorediata***
2. Thallus usually with polysidiangia, rarely with soralia; upper and lower medulla white; pseudocyphellae marginal and laminal; upper and lower medulla K+ yellow, P+ orange; on bark ..... ***P. mexicana***

3. Thallus without vegetative propagules 4
3. Thallus with soralia 5

4. Thallus whitish, whitish gray or stramineous; apothecia *cocoes*-type, with a distinct orange to orange-red internal stipe (K+ purple); ascospores 14-19 x 5-7.5 µm ..... ***P. petricola***
4. Thallus grayish-brown to grayish-green; apothecia *obscurascens*-type, with an indistinct, whitish internal stipe (K-); ascospores 10-17 x 4.5-7 µm .... ***P. pyxinoides***

5. Upper medulla lemon-yellow to creamish-yellow, lower medulla white; apothecia *obscurascens*-type; ascospores 13-19 x 6-8 µm ..... ***P. subcinerea***
5. Medulla white throughout; apothecia *cocoes*-type; ascospores 15-18 x 6-7 µm ..... ***P. cocoes***

The Species

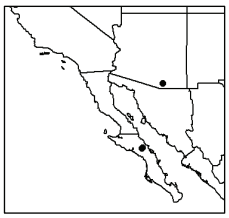
Pyxine cocoes (Swartz) Nyl., Mem. Soc. Imp. Sci. Nat. Cherbourgh 5: 108 (1857).

Basionym: *Lichen cocoes* Sw., Nov. Gen. Sp. Pl.: 146 (1788); Illustrations: Awasthi (1982), p. 368; Kalb (1987), p. 19; Brodo et al. (2001), p. 618.

Thallus: foliose, ± firmly appressed, up to 10 cm in diam. but usually much smaller (3-4 cm); **lobes:** flat, rarely slightly convex or concave, 0.4-0.8 mm wide; **upper surface:** light yellowish brown, gray or almost white; pseudocyphellae: sparse, usually restricted to the peripheral parts of the lobes, sometimes reticulately confluent; pruina: patchy, often glistening; **soredia:** always present, granular, rarely farinose, initially in marginal, fissural, then in laminal, orbicular soralia; isidia and polysidiangia lacking; **medulla:** white throughout; **lower surface:** black in center, paler towards lobe tips; rhizines: ± dense, blackish, furcately divided; **Apothecia:** *cocoes*-type, rare, laminal, 0.4-1.4 mm wide; disc: black, not pruinose; **internal stipe:** distinct, upper part brownish-red (rarely white: *P. cocoes* var. *pallida* - not yet known from the Sonoran region), lower part white; **ascospores:** one-septate, brown, 15-18 x 6-7 µm; **Pycnidia:** immersed; **conidia:** bacilliform, 3-4 x 1 µm; **Spot tests:** upper cortex K-, C-, KC-, P-; medulla upper and lower part K-, C-, KC-, P-; internal stipe upper part K+ red, C-, KC+ purple, P-; lower part K-, C-, KC-, P-; **Secondary metabolites:** upper cortex

with lichexanthone, medulla with a few terpenes in low concentration.

Substrate and ecology: on bark and wood near sea sides, rarely on acidic rock or in montane areas; **World distributon:** pantropical with scattered collections from the subtropics and insular Laurimacaronesia; **Sonoran distribution:** southern Arizona and Baja California Sur.



Pyxine mexicana Kalb, **sp. nov.**

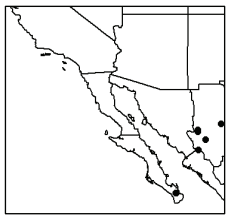
Diagnosis: *Similis P. coralligerae, sed differt medulla alba, marginibus apotheciorum pruinosis et terpenis aliis.*

Type: Mexico. Baja California Sur: Sierra Laguna just above Rancho La Victoria, oak forest, on *Quercus devia*; *c.* 1200 m, 23°36'43''N, 109°54'43''W, 6. I. 1998, leg.: T. H. Nash III 39585 (ASU, holotype; hb. Kalb, isotype).

Additional specimens examined: Baja California Sur: Cerro Blanco in NE foothills of the Sierra Laguna, on granite in thorn forest, Nash 39680 (ASU), Sierra Laguna just above Ranch La Victoria, on *Quercus devia*, Nash 39585 (ASU); top of ridge of Sierra Laguna and E of Cerro Verde, on granite, Nash 36619 (ASU); Chihuahua: Parque Nacional Cumbres des Majalca, 50 km NW of Ciudad Chihuahua, on acidic rock, Nash 31213 (ASU); Cascada de Basaseachic, on rhyolite, Nash 13538 (ASU); Durango: Sierra Madre Occidental, 47 km W of Durango, 23°56'N,104°57'30''W, on rocks, 2215 m, 26. 5. 1992, Kashiwadani 37144 (TNS); Sinaloa: 30 km NE of Choix, Cerro Solida above El Cajon, on *Quercus viminea*, Nash 12128 (ASU).

Thallus: foliose, ± firmly appressed, up to 5 cm in diam.; **lobes:** flat, slightly convex or concave towards the periphery, 0.8-2.0 mm wide; **upper surface:** gray brownish gray or almost white; pseudocyphellae: sparse to abundant, usually restricted to the peripheral parts of the lobes, initially marginal, then spreading laminally, sometimes reticulately confluent; pruina: punctiform, rarely confluent; **polysidiangia:** developing from marginal, later also from laminal pseudocyphellae, initially distinctly corticate, later bursting open and simulating nodular soralia; true soralia and isidia lacking; **medulla:** white throughout; **lower surface:** black in center, paler towards lobe tips; rhizines: ± dense, blackish, furcately divided; **Apothecia:** *obscurascens*-type, rare, laminal, 0.6-2.0 mm wide; exciple: outer part white pruinose (or rarely some apothecia without pruina); disc: black, not pruinose; **internal stipe:** distinct, white throughout; **ascospores:** one-septate, brown, 17-21 x 5.5-7 µm; **Pycnidia:** immersed; **conidia:** bacilliform, 3-4 x 1 µm; **Spot tests:** upper cortex K+ yellow, C-, KC-, P+ yellow; medulla upper and lower part K-, C-, KC-, P+ orange red; internal stipe upper and lower part K-, C-, KC-, P+ orange red; **Secondary metabolites:** upper cortex with atranorin; medulla with terpenes of a characteristic array on TLC plates, testacein.

Substrate and ecology: on bark and acidic rocks in montane areas from 1000-2200 m; **World distribution:** probably a Sonoran endemic; **Sonoran distribution:** southern mountains of Baja California Sur and the Sierra Madre Occidental region of Chihuahua.



Note: Previous collections of this species have been reported under the name *P. retirugella*.

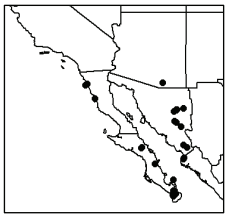
Pyxine petricola Nyl. in Cromb., Journ. Bot., London 14: 263 (1876).

Synonym: *Pyxine pringlei* Imshaug; Illustrations: Awasthi (1982), p. 375; Swinscow and Krog (1988), p. 290.

Thallus: foliose, ± loosely appressed, up to 5 cm in diam.; **lobes:** flat, usually distinctly concave towards the lobe tips, rarely convex throughout, 0.7-1 mm wide; **upper surface:** gray, greenish gray, almost white or stramineous; pseudocyphellae: sparse, laminal and marginal, usually restricted to the peripheral parts of the lobes, sometimes reticulately confluent; pruina: patchy, rarely punctiform, often glistening; soralia, isidia and polysidiangia lacking; **medulla:** white throughout; **lower surface:** black

in center, paler towards lobe tips; rhizines: ± dense, blackish, furcately divided; **Apothecia:** *cocoes*-type, often present, laminal, 0.5-1.5 mm wide; disc: black, not pruinose; **internal stipe:** distinct, upper part rose-red or orange-red (rarely white: *P. petricola* var. *convexula* - not yet known from the Sonoran region), lower part white; **ascospores:** one-septate, brown, 14-19 x 5-7.5 µm; **Pycnidia:** immersed; **conidia:** bacilliform, 3-4 x 1 µm; **Spot tests:** upper cortex K-, C-, KC-, P-; medulla upper and lower part K-, C-, KC-, P-; internal stipe upper part K+ blackish purple or purple, C-, KC-, P-; lower part K-, C-, KC-, P-; **Secondary metabolites:** upper cortex with lichexanthone; medulla with few terpenes in low concentration.

Substrate and ecology: on bark, wood and acidic rock from sea level to montane areas; **World distribution:** pantropical with scattered collections from the subtropics; **Sonoran distribution:** southern Arizona, Baja California, Baja California Sur, Sonora and Sinaloa, particularly common at low elevations in thorn forests.



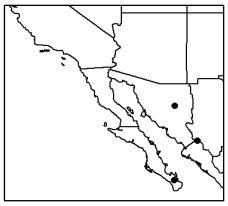
Notes: Populations with a stramineous and more closely appressed thallus with convex lobes have been described as *Physcia devertens* Nyl., Énumér. Lich. Annobon: 3 (1896) = *Pyxine devertens* (Nyl.) Vain., Add. Lichenograph. Antill. illustr.: 70 (1915), but examination of the holotype (H-Nyl. 31792) showed it to be identical, including the chemistry (no norstictic acid could be demonstrated by HPTLC, see however Swinscow and Krog 1975: 61) with typical *P. petricola* except for the differences mentioned above.

Pyxine pyxinoides (Müll. Arg.) Kalb, Bibl. Lich. 24: 66 (1987).

Basionym: *Catolechia pyxinoides* Müll. Arg., Flora 64: 509 (1881); Synonyms: *Pyxine minuta* Vain. and *Pyxine brachyloba* Müll. Arg.; Illustrations: Kalb (1987), figs. 22-24.

Thallus: foliose, very firmly appressed, up to 6 cm in diam.; **lobes:** flat, rarely slightly concave, 0.2-0.3 mm wide; **upper surface:** light gray or leaden, older thalli olivaceous to brownish gray; pseudocyphellae: sparse, usually restricted to the margins of peripheral parts of the lobes, rarely reticulately confluent; pruina: hardly visible; soralia, isidia and polysidiangia lacking; **medulla:** upper part light orange, lower part white or white throughout; **lower surface:** black in center, paler towards lobe tips; rhizines: ± sparce, blackish, furcately divided; **Apothecia:** *obscurascens*-type, often present, laminal, 0.25-0.6 mm wide; disc: black, not pruinose; **internal stipe:** indistinct, upper part creamish yellow or white, lower part white; **ascospores:** one-septate, brown, 13-17 x 4.5-7 µm (length-width-index: 2.2-3.2); **Pycnidia:** immersed; **conidia:** bacilliform, 3-4 x 1 µm; **Spot tests:** upper cortex K-, C-, KC-, P-; medulla upper and lower part K-, C-, KC-, P- or P+ orange-red caused by testacein; internal stipe upper part K-, C-, KC-, P-; lower part K-, C-, KC-, P-; **Secondary metabolites:** upper cortex with lichexanthone; medulla with terpenes of a characteristic array on TLC plates, with or without testacein (the latter present in all Sonoran collections).

Substrate and ecology: on acidic rocks in montane areas; **World distribution:** neotropical; **Sonoran distribution:** Baja California Sur and Sonora in tropical thorn forest to deciduous forest transition areas.



Notes: The difficulty of distinguishing *P. microspora* and *P. pyxinoides* has been mentioned by several authors (Swinscow and Krog 1975, Awasthi 1982, Kalb 1987), but spore dimensions (length-width-index: 2.2-3.2 in *P. pyxinoides* and 1.6-2.4 in *P. microspora*) are definitive. In addition, TLC results also helps to assign the correct species name to a collection. It cannot, however, be unequivocally concluded that only two species are involved in this difficult group. The presence or absence of testacein probably is of no taxonomic value, as has been demonstrated for *Parmelia testacea* (Elix 1994h).

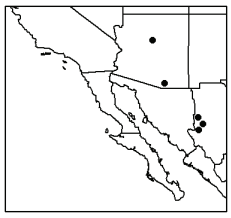
Pyxine sorediata (Ach.) Mont. in Sagra, Hist. Cuba 9: 188 (1842).

Basionym: *Lecidea sorediata* Ach., Syn. Meth. Lich.: 54

(1814); Synonym: *Pyxine cocoes* (Swartz) Nyl. var. *sorediata* (Ach.) Tuck.; Illustrations: Moberg (1983), p. 162; Hale (1979), p. 86; Brodo et al. (2001), p. 619.

Thallus: foliose, loosely appressed, up to 8 cm in diam.; **lobes:** flat or slightly concave, 0.6-1.3 mm wide; **upper surface:** beige gray, brownish gray, leaden or bluish gray; pseudocyphellae: very distinct along the lobe margins, sometimes gray pruinose and reticulately confluent; pruina: punctiform on the peripheral parts of the lobes; **soredia:** always present, granular, rarely farinose, initially in marginal, fissural, then in laminal, in orbicular soralia, sometimes secondarily with a cortex and then simulating polysidiangia; isidia and true polysidiangia lacking; **medulla:** upper part lemon yellow, ochraceous to orange yellow; **lower surface:** black in center, paler towards lobe tips; rhizines: ± dense, blackish to blackish blue, furcately divided; **Apothecia:** *obscurascens*-type, rare, laminal, 0.5-1.4 mm wide; disc: black, not pruinose; **internal stipe:** distinct, upper part dark orange, lower part white; **ascospores:** one-septate, brown, 14-19 x 6-8 µm; **Pycnidia:** immersed; **conidia:** bacilliform, 3-4 x 1 µm; **Spot tests:** upper cortex K+ yellow or K-, C-, KC-, P- or P+ pale yellow; medulla upper and lower part K-, C-, KC-, P-; internal stipe upper part K+ red, C-, KC+ purple, P-; lower part K-, C-, KC-, P-; **Secondary metabolites:** upper cortex atranorin (sometimes in very low concentration); medulla with terpenes of a characteristic pattern on TLC plates, and an unknown pigment.

Substrate and ecology: on bark, acidic rocks and over mosses from sea level to subalpine areas; **World distribution:** subtropical with collections from temperate regions (North America, Europe, Africa, Nepal, India, Japan, Australasia) and insular Laurimacaronesia; **Sonoran distribution:** Arizona and Sierra Madre Occidental region of adjacent Chihuahua in regions with high summer precipitation.

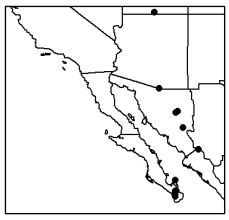


Pyxine subcinerea Stirt., Trans. New Zealand Inst. 30: 397 (1897).

Synonym: *Pyxine chrysanthoides* Vain.; Illustrations: Moberg (1983), p. 164; Kalb (1987), fig. 28; Swinscow and Krog (1988), p. 273.

Thallus: foliose, ± firmly appressed, up to 8 cm in diam., usually smaller (3-5 cm); **lobes:** flat to slightly concave, 0.3-0.6 mm wide; **upper surface:** (dark) gray to brownish or olivaceous gray; pseudocyphellae: distinct at margins, spreading on to lobe surface, rarely reticulately confluent; pruina: very distinct, very densely punctiform, sometimes patchy, often glistening; **soredia:** always present, farinose, initially in marginal, fissural, rarely later in laminal, orbicular soralia; isidia and polysidiangia lacking; **medulla:** upper part lemon to beige yellow, very thin lower part white; **lower surface:** black in center, paler towards lobe tips; rhizines: ± dense, blackish, furcately divided; **Apothecia:** *obscurascens*-type, common, laminal, 0.3-1.5 mm wide; disc: black, not pruinose; **internal stipe:** weakly developed, upper part brownish-red, lower part whitish; **ascospores:** one-septate, brown, 13-19 x 6-8 µm; **Pycnidia:** immersed; **conidia:** bacilliform, 3-4 x 1 µm; **Spot tests:** upper cortex K-, C-, KC-, P-; medulla upper and lower part K-, C-, KC-, P-; internal stipe upper part K+ purple, C-, KC-, P-; lower part K-, C-, KC-, P-; **Secondary metabolites:** upper cortex with lichexanthone; medulla with terpenes of a characteristic pattern on TLC plates, and an unknown pigment.

Substrate and ecology: on bark, wood, and rarely on acidic rocks from sea level to high montane areas; **World distributon:** pantropical with scattered collections from the subtropics and warm temperate regions, insular Laurimacaronesia and Europe/Italy; **Sonoran distribution:** Arizona, Baja California Sur, Sinaloa and Sonora, at low to intermediate elevations from thorn forests to oak forests.



Notes: Previously specimens belonging to this species have been reported under the names of *P. caesiopruinosa* and *P. meissneriana*.

RHIZOPLACA

by B. D. Ryan

Rhizoplaca Zopf, Mitt.-Ann. Chem. 340: 291 (1905).

Family: Lecanoraceae; Type: *Rhizoplaca opaca* (Ach.) Zopf (= *R. melanophthalma* (DC.) Leuckert & Poelt); No. species: at least eight world-wide; Selected lit.: Leuckert et al. (1976), Poelt (1958), McCune (1987), Moser-Rohrhofer (1975), and Ryan and Nash (1997b).

Life habit: lichenized; **Thallus:** squamulose, pulvinate, or peltate-umbilicate (to foliose or fruticose), monophyllous to strongly polyphyllous; attachment: by a single umbilicus or stalk per thallus or subunit, sometimes also with rhizinose strands; margins: entire to deeply lobed, **upper surface:** ± pale greenish yellow, to slightly brownish, or white; often blue-green-black; thallospores: sometimes present along edges; isidia, soredia and similar structures: absent; **upper cortex:** usually with structure difficult to see, due to gelatinization and to inspersion by granules; **medulla:** white, loose to ± hollow towards center, but often filled with granular or crystalline material; cell walls: with isolichenan; **photobiont:** primary one a chlorococcoid alga, secondary photobiont absent; **lower cortex:** usually thicker (and with thicker and more gelatinized hyphae) than upper one; **lower surface:** pale to dark brown, to blue-green black near edges; **Ascomata:** lecanorine apothecia, laminal to marginal, rounded to irregular, immersed to more often sessile or substipitate; exciple: ± hyaline; hymenium: ± hyaline or yellowish to orange; paraphyses: not (or scarcely) branched or anastomosing; **asci:** ± clavate, *Lecanora*-type, *c.* 8-spored; **ascospores:** non-septate, mostly ± ellipsoid (8-13 x 4-8 µm), but globose (10-12 x 7-10 µm) in one species and ovoid-oblong to crescent-shaped (15-20 x 4-5 µm) in another; wall: hyaline, smooth, non-halonate, without distinctly developed endospore thickening, not amyloid; **Conidiomata:** pycnidia, laminal or lateral, immersed; **conidia:** formed acrogenously, filiform, *c.* 15-40 x ≤ 1 µm, ± curved; **Secondary metabolites:** upper cortex: with usnic acids; medulla: with aliphatic acids, ± β-orcinol depsides, β-orcinol depsidones, or triterpenoids; **Geography:** circumpolar to temperate in both hemispheres, extending to the tropics in alpine areas, in ± dry areas; **Substrate:** non-calciferous or weakly to moderately calciferous rocks; some taxa also occurring on soil in cool, open and windy areas.

Notes: The usual lack of distinctly radiating marginal lobes, and the loose medulla and well-developed lower cortex, help to distinguish *Rhizoplaca* from *Lecanora*. The systematics and nomenclature of *Rhizoplaca* were reviewed briefly by Ryan and Nash (1997b), and more comprehensive and definitive treatments are in preparation by us. Information on distribution of chemotypes is given by Leuckert et al. (1976) and McCune (1987), but those treatments included *R. subdiscrepans s. lato* (and occasionally members of the *Lecanora opiniconensis* complex) under *R. chrysoleuca* (or occasionally *R. melanophthalma*). The here broadly treated taxa *R. chrysoleuca* and *R. melanophthalma* are extremely variable, often with several "morphotypes" or "color phases" appearing quite distinct when growing side by side, but no attempt is made here to account for the numerous published infraspecific taxa, nor any but the most commonly cited synonyms. Morphs growing loose on soil do not occur in the Sonoran region and are therefore not included in the present account.

Key to species of ***Rhizoplaca*** in the Sonoran region:

1. Upper surface distinctly whitish throughout, C+ yellow; containing only pseudoplacodiolic acid; apothecia mostly marginal; ascospores either over 7 µm wide or over 15 µm wide and then curved 2
1. Upper surface usually greenish yellow to yellowish brown, never entirely and purely white, always C- (but medulla can be C+ red in some species), without pseudoplacodiolic acid, or with it in addition to usnic acid; apothecia mostly laminal; ascopores under 7 µm long and under 15 µm wide, straight 3

2. Ascospores globose to broadly ellipsoid, 10-12 x 7-10 µm; thalli to 2 cm across; apothecia sessile, to 2

mm across, discs always densely pruinose, margins raised, thick and distinct (except when very young) ..... ***R. marginalis***

2. Ascospores oblong-ovoid to crescent-shaped, 15-20 x 4-5 µm; thalli mostly to 0.5 cm across; apothecia immersed to adnate, mostly to 1 mm across, discs often epruinose or weakly pruinose, margins level with disc, mostly thin or indistinct ..... ***R. glaucophana***

3. Thallus containing zeorin, and (in N. America) almost always pannarin (medulla P+ orange); without placodiolic and pseudoplacodiolic acids; upper surface often brownish, especially in herbarium; apothecia often long immersed; discs yellowish to reddish brown, epruinose; underside of thallus usually strongly cracked .... ***R. peltata***

3. Thallus without zeorin and pannarin (medulla P- or P+ yellow); often with various other substances; apothecia usually soon sessile to substipitate; discs variously colored but usually either at least partly pruinose or else greenish to bluish black; underside of thallus usually not distinctly cracked 4

4. Discs blue-black and epruinose, to greenish, brownish, or yellowish and then usually pruinose; paraphyses tips usually at least partly capitate and greenish to blue-black, N+ reddish; hymenium hyaline 5

4. Discs usually reddish, orangish, or yellowish and at least partly pruinose; paraphyses tips clavate, hyaline, N-; hymenium with yellowish to reddish tinges in thick section 6

5. Thallus or its subunits at least partly thin and concave to plane, with greenish to blue-black on the underside; upper surface usually rather deep greenish yellow, often with brownish tinges especially in herbarium, bare, not powdery-roughened except when pruinose; upper cortex with usnic acid only; lower surface usually blue-green-black near edges; ascospores ellipsoid (to globose), L: W < 2.5 ..... ***R. melanophthalma*** *s. lato*

5. Thallus and its subunits ± convex (never concave), brownish on underside; upper surface paler or grayish tinged, without brownish tinges even in old herbarium specimens, finely powdery-roughened; upper cortex (in Sonoran region specimens) with placodiolic acid, rarely usnic acid only; lower surface brownish; ascospores oblong-ellipsoid, L:W mostly > 2.5 .... uncommon color phase of ***R. subdiscrepans*** *s. lato*)

6. Thallus stipitate-squamulose, the squamules mostly convex and crowded into thick, turf-like or mound-like or cerebriform (sinuous-plicate) masses; underside brownish (to blackish but never greenish or bluish), sometimes with rhizinose strands .... ***R. subdiscrepans***

6. Thallus clearly umbilicate (or if appearing squamulose then squamules usually thin, concave to plane, not sinuous-plicate, and ± discrete, without rhizinose strands); underside usually at least partly greenish to blue-black ..... ***R. chrysoleuca*** *s. lato*

The Species

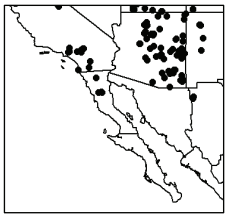
Rhizoplaca chrysoleuca (Sm.) Zopf, Ann. Chem. 34: (1905).

Basionym: *Lichen chrysoleucus* Sm., Trans. Linn. Soc. 1: 82 (1791); Synonyms: *Lecanora chrysoleuca* (Sm.) Ach., *Lecanora rubina* (Vill.) Ach. and also see Poelt (1958) and Leuckert et al. (1976); Illustrations: Hale and Cole (1988), pl. 9d; Wirth (1995), p. 451; McCune and Geiser (1997) p. 265; Brodo et al. (2001), p. 639.

Thallus: to 2-3.5 cm across, umbilicate, monophyllous, becoming deeply lobed, or ± polyphyllous and pulvinate; **lobes:** *c.* 1-3 mm across, plane to concave or less often convex, *c.* 0.5-1 (-1.5) mm thick, crenate-incised; **upper surface:** pale greenish yellow, light yellow, yellowish gray, pale yellowish green, or light gray to whitish, scarcely changed in herbarium, smooth or powdery; edges concolorous or often at least partly blackened; **Apothecia:** laminal or submarginal, often numerous and crowded, to 0.8-2.5 mm diam., adnate then sessile, constricted at base; disc: plane to convex, reddish orange to moderate or strong orangish yellow or yellow, at least partly weakly to densely pruinose and appearing light orange to light orange-yellow; thalline exciple: 0.1-0.4 mm wide, entire to flexuous or crenate towards inside, ± raised then level, persistent or excluded, concolorous with thallus or yellower, or slightly orangish when young; hymenium: *c.* (35-) 50-60 µm tall, ± yellowish or orangish, not inspersed, but usually with superficial layer of granules; paraphyses tips: hyaline, *c.* 2-3 µm wide; **ascospores:** ellipsoid to oblong-ellipsoid, *c.* 8.5-12 x 3.5-6 µm; **Pycnidia:**

rare; **conidia:** 15-20 (-30) µm long; **Spot tests:** upper cortex: K- or K+ yellow, C-, KC+ yellow, P-, UV-, medulla: K-, C- or C+ red, KC- or KC+ red, P-, or P+ yellow, UV-; **Secondary metabolites:** upper cortex: with usnic acid, ± either placodiolic or pseudoplacodiolic acid; medulla: with aliphatic acids or no substances, or, at lower latitudes (including the Sonoran region), occasionally psoromic or lecanoric acid chemosyndromes, or both.

Substrate and ecology: usually on hard, siliceous rocks (including granite, schist, quartz, mica, basalt), sometimes sandstone, and occasionally calcareous rocks; from pinyon-juniper woodland up into the alpine zone; frequently nitrophilous; **World distribution:** circumarctic, circumboreal to warm-temperate, Eurasia, North America (except temperate eastern N. America); reports from the Southern Hemisphere appear to be based on misidentifications; **Sonoran distribution:** Arizona, California, Baja California and Chihuahua; common at moderate to high elevations, 1200-3200 m.



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Notes: This species is distinguished from *R. melanophthalma* and *R. peltata* by the combination of persistently whitish to yellowish upper surface and reddish to yellowish pruinose discs (with correspondingly tinged hymenium). In contrast to the holotype of *R. chrysoleuca* (L!) and many other specimens from northern areas of North America and Eurasia, Sonoran region material usually has rather thick lobes with plane to down-turned and unthickened edges, with greenish, bluish, or blackish coloration absent or restricted to parts of the underside next to the edges, making the material occasionally difficult to distinguish from *R. subdiscrepans* (see notes under that species).

Rhizoplaca glaucophana (Nyl. *ex* Hasse) W. A. Weber, Mycotaxon 8: 559 (1979).

Basionym: *Lecanora glaucophana* Nyl. *ex* Hasse, Lich. S. California, ed. 2: 11 (1898); Synonyms: *Harpidium glaucophanum* (Nyl.) Hasse; Illustration: Fig. 90 to right.

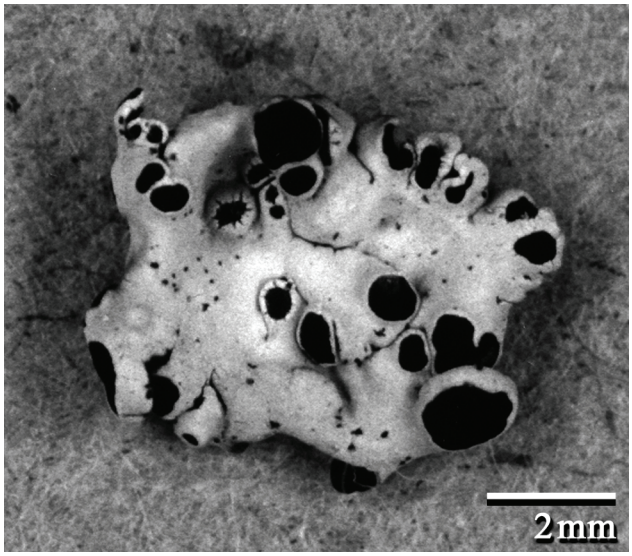
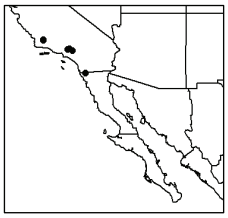


Fig. 90. *Rhizoplaca glaucophana*, photo by B. Ryan.

Thallus: 3-7 mm across, ± flat, monophyllous or marginally divided into rounded lobes, often closely appressed throughout; lobes 1-2 mm long, 0.5-1.5 mm wide; edges: turned downward and thickened on underside; **upper surface:** smooth, white with slight greenish tinge, unchanged in herbarium, somewhat mealy-roughened, sometimes with narrow black edges in places; **lower surface:** medium yellowish brown to orangish brown, to greenish black near edge; umbilicus distinct; **Apothecia:** common, mostly marginal (and often projecting somewhat beyond main edge of thallus), long immersed, finally broadly sessile but appressed and scarcely constricted at the base, to 1.0 (-1.4) mm diam.; disc: plane to slightly convex, matt, ± dark or deep brown, usually with reddish or grayish tinges, somewhat pruinose; thalline margin: concolorous with thallus, to 0.1-0.2 mm wide, level with disc, entire to slightly flexuous, occasionally crenate towards outside, finally excluded; hymenium: 50-60 (-80) µm high, hyaline, the uppermost 10 µm inspersed with brownish granules; paraphyses tips: to 4-6 µm thick, brown, olive in K; **ascospores:** oblong, often slightly to moderately curved, usually narrowed at one or both ends, (12-) 15-20 (-23) x (3-) 4-5 µm; **Pycnidia:** occasional; **conidia:** 20-30 µm long; **Spot tests:** upper cortex: K-, C+ yellow, KC+ yellow, P-, UV-; medulla: K-, C-, KC-, P-,

UV-; **Secondary metabolites:** upper cortex: with pseudoplacodiolic acid; medulla: none detected.



Substrate and ecology: on calcium poor siliceous rocks, apparently strongly nitrophilous, but growing in somewhat shaded areas; **World** and **Sonoran distribution:** California and Baja California, *c.* 1300 m.

Notes: This species is unlikely to be confused with any other lichen, except occasional small specimens of *R. marginalis*, from which it is easily separated especially by the elongated, curved spores.

Rhizoplaca marginalis (Hasse) W. A. Weber, Mycotaxon 8: 560 (1979).

Basionym: *Lecanora marginalis* Hasse, Bryologist 13: 112 (1910); Illustration: Fig. 91.

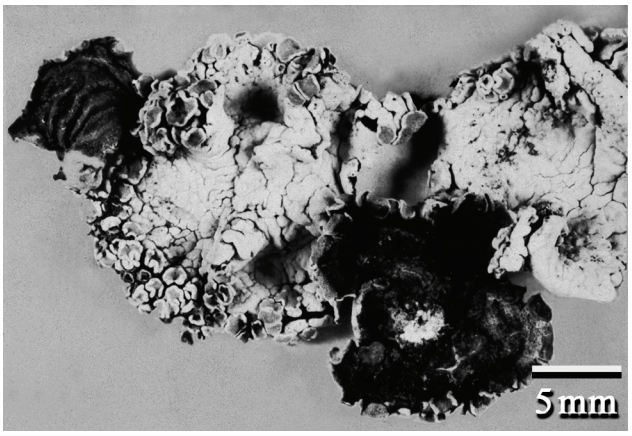


Fig. 91. *Rhizoplaca marginalis*, photo by B. Ryan.

Thallus: monophyllous, 0.7-1.5 cm across, entire or obscurely small-lobed, 0.5 mm thick (or slightly more towards circumference), edges: often rolled downward and convolutely folded; **upper surface:** smooth to wrinkled and warty, continuous to unevenly rimose, grayish yellow but uniformly and finely white-pruinose, appearing white or grayish white; **lower surface:** matt, light to moderate or dark yellowish brown or grayish brown (sometimes becoming blackish blue towards edge), sometimes strongly roughened and uneven; umbilicus: distinct; **Apothecia:** 0.7-1.6 mm diam., adnate to sessile, marginal or submarginal, often crowded and often irregular from pressure, occasionally turned toward the substrate through the downward-rolling of the thallus margin; disc: concave to plane or undulate, brownish black, usually densely grayish pruinose and appearing light bluish gray; thalline exciple: 0.2-0.3 mm wide, concolorous with thallus, raised or finally level with disc, becoming flexuous or crenate, persistent; hymenium: *c.* 50 (-60) µm high, ± hyaline; uppermost *c.* 10 µm partly dirty greenish (pale bluish gray in K), with surface layer of ± fine grayish granules; paraphyses tips: becoming dark-capitate; **ascospores:** globose to ovoid-ellipsoid, 9-14 x 6.5-8.5 µm; **Pycnidia:** generally numerous; **conidia:** 32-40 µm long; **Spot tests:** upper cortex: K+ weakly yellowish, C+ lemon yellow, KC+ yellowish, P-, UV-; medulla: K-, C-, KC-, P-, UV-; **Secondary products:** upper cortex with pseudoplacodiolic acid; medulla without substances.

Substrate and ecology: on non-calcareous rock (especially volcanic), on lower side of overhangs; **World distribution:** endemic to California (primarily central parts); **Sonoran distribution:** California, barely reaching the northern edge of the greater Sonoran Region (San Bernardino County).

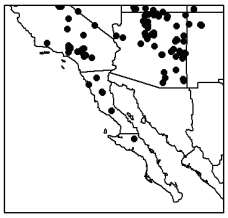
Notes: It is separated from *R. glaucophana*, which also has a white, C+ yellow upper cortex, by containing only pseudoplacodiolic acid, and having at least partly marginal apothecia (characters that distinguish these two species from other members of the genus), by the usually larger thalli and apothecia and especially by the broad, straight and rounded spores. The description of *Lecanora marginalis* given by Hasse (1910 & 1913) contains several statements that are inaccurate or at least misleading: 1) that the thallus is C-; 2) that the upper cortical cells are brown; 3) that the "hypothecium" is "of coarse cells and of the same hue with the the epithecium [i.e., "dull brownish black"]; and 4) that the paraphyses tips are "scarcely thickened".

Rhizoplaca melanophthalma (DC.) Leuckert & Poelt, Nova Hedwigia 28: 72 (1976).

Basionym: *Lichen melanophthalmus* DC., in Lam. & DC., Fl. Franç., ed. 3, 2: 377 (1805); Synonyms*: Lecanora melanophthalma* (DC.) Ramond, and see Poelt (1958) and Leuckert et al. (1976); Illustrations: Moberg and Holmåsen (1982), p. 114; Vitt et al. (1988), p. 190; McCune and Geiser (1997), p. 266; Brodo et al. (2001), p. 640.

Thallus: mostly 0.5-1.5 (-2.5) cm across, polyphyllous and often appearing squamulose or pulvinate, or rarely monophyllous and then usually deeply lobed; **lobes:** distinct to indistinct, usually to 0.5-5 (-10) mm long and 0.5-1.5 mm across, ± coarsely crenate-incised, ultimate segments: usually *c.* 0.5 mm across; thin and plane to concave, to sometimes thick and/or convex towards thallus center, sometimes plicate, edges: plane or down-turned; **upper surface:** dull to shiny, occasionally ± pruinose, usually light to moderate greenish yellow, in herbarium turning more yellowish or slightly brownish or grayish, edges: concolorous or blackening, smooth and shiny to roughened (occasionally forming black thallospores); **lower surface:** blue-black near edges, usually continuous, smooth to uneven or roughened; umbilicus: often rather broad and indistinct; **Apothecia:** 0.4-1.7 mm diam., immersed then sessile, or soon basally constricted to substipitate; disc: concave to plane or undulate, rarely convex, yellowish brown to moderate brown, olive, or greenish to bluish black, epruinose (especially when black) or weakly to densely pruinose, then appearing light yellowish brown to greenish yellow or bluish gray; thalline margin: variable in width, ± concolorous with thallus or paler, entire to flexuous or crenate, weakly to strongly raised and inflexed, persistently so or finally level; hymenium: ± hyaline, usually not inspersed, but the uppermost part often covered with granules; paraphyses tips: often becoming capitate and greenish brown to bluish black; **ascospores:** ± ellipsoid to subglobose but rather variable in size and shape, *c.* 8-13 x 4-7.5 µm; **Pycnidia:** often common; **conidia:** (15-) 20-25 (-30) µm long; **Spot tests:** upper cortex: K- or rarely + yellowish, C-, KC+ yellow, P-, UV-; medulla: K-, C- or occasionally C+ red, KC- or occasionally KC+ red, P- or P+ yellow, UV-; **Secondary metabolites:** upper cortex: with usnic acid only; medulla: with no substances or various fatty acids (pertusaric/constipatic acid complex), or with psoromic and/or occasionally lecanoric acid chemosyndromes and occasionally other unidentified substances.

Substrate and ecology: on rock, usually calcium-low (e.g., basalt, granite, schist), but sometimes on calcium-rich sandstone or even on limestone; usually on ± exposed and often somewhat nutrient-enriched surfaces, from pinyon-juniper communities up to the spruce zone and into the low alpine; **World distribution:** circumbipolar, circumboreal, circumaustral except for Australasia; extending to the tropics in alpine areas; Europe, Asia, northwestern and eastern Africa, North and South America, Antarctica; **Sonoran distribution:** Arizona, southern California, and Baja California from 1100-3000 m.



Notes: As treated here, *R. melanophthalma s. lato* can usually be recognized especially by the combination of: thallus ± squamulose to less often distinctly umbilicate, with at least some concave to flattened parts and distinct bluish black tinges on the margins or the underside towards edges (in contrast to *R. subdiscrepans*); upper surface usually relatively deeply yellowish green to olive or brownish; hymenium ± colorless below (never orange); absence of cortical substances other than usnic acid (all in contrast to *R. chrysoleuca* and *R. subdiscrepans*); and absence of terpenoids in the medulla (in contrast to *R. peltata*). For distinctions between *R melanophthalma* and lobate species of *Lecanora* (e.g., *L. weberi* Ryan), see the treatment of those taxa.

Rhizoplaca peltata (Ramond) Leuckert & Poelt, Nova Hedwigia 28: 73 (1976).

Basionym: *Lichen peltatus* Ramond, in Lam. & DC., Fl. Franc., ed. 3, 2: 377 (1805); Synonyms: *Lecanora peltata* (Ramond) Steud., *L. rubina* v. *heteromorpha* Ach. and see Poelt (1958) and Leuckert et al. (1976); Illustrations: Goward et al. (1994), p. 124; Brodo et al. (2001), p. 641 and Fig. 92 at top of next page.

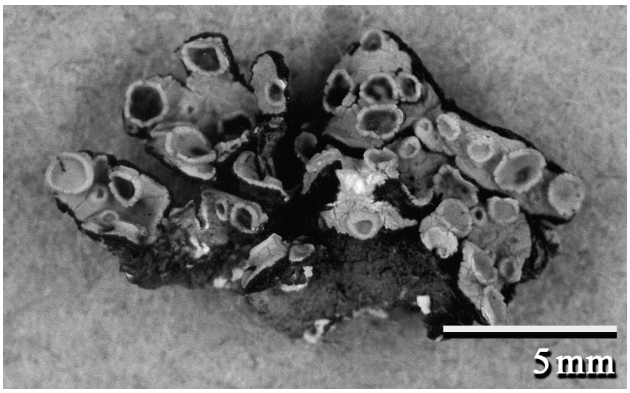
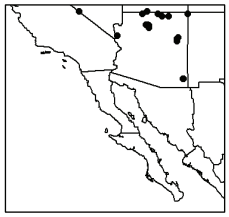


Fig. 92. *Rhizoplaca peltata*, photo by B. Ryan.

Thallus: to 3 cm across, distinctly umbilicate, usually monophyllous but sometimes strongly lobed; **lobes:** to 1.5-3 mm long, 2-3 mm wide, plane to slightly concave, entire to coarsely and shallowly crenate, ultimate segments: 0.5-1 mm wide, edges: not thickened, often rolled downward; **upper surface:** ± pale greenish yellow to yellow, sometimes grayish tinged, turning brownish or orange in herbarium, continuous to strongly rimose, epruinose to partly pruinose, matt or slightly nitid, edges: concolorous or blackened, sometimes with thallospores; **lower surface:** ± yellowish brown, to bluish black near edges, smooth to uneven, ± strongly cracked towards center, with medulla showing through; **Apothecia:** usually common, to 2-3 mm diam., long remaining immersed to broadly adnate (crater-like with broadly sloping rims), or at least finally sessile; disc: concave then plane or sometimes convex, epruinose, orangish yellow to yellowish or reddish brown; thalline margin: *c.* 0.1-0.4 mm wide, slightly to moderately raised or later level, usually persistent, entire to flexuous or coarsely crenate towards outside, ± concolorous with thallus; hymenium: hyaline, deeply inspersed with brownish granules; paraphyses tips hyaline, clavate, **ascospores** ± ellipsoid to subglobose, *c.* 9-12 x 5-8 µm; **Pycnidia:** sometimes present; **conidia:** 20-40 µm long; **Spot tests:** upper cortex K-, C-, KC+ yellow, P-, UV-; medulla (in Sonoran region material) K-, C-, KC-, P+ orange, UV-; **Secondary metabolites:** upper cortex: with usnic acid only (the report by Leuckert et al., 1976, of rare specimens with placodiolic acid, is dubious); medulla: with zeorin, and (in most sites in North America) pannarin, ± rangiformic acid or various unknowns; in other areas, specimens containing psoromic, lecanoric, norstictic, or hypoprotocetraric acid.

Substrate and ecology: on rock (often weakly to somewhat strongly calciferous, or at least exposed to calcareous dust), often on vertical or steep surfaces, often N-facing, or slightly protected, moderately nitrophilous, in pinyon-juniper and oak-pine woodlands, on basalt, schist, sandstone, and limestone; **World distribution:** southern Europe; SW to central Asia, northern Africa; temperate to boreal western North America; **Sonoran distribution:** Arizona, 1100-2400 m; also present in California (at least the northern parts).



Notes: Although frequently confused with *R. chrysoleuca* and *R. melanopthalma*, in the past, *R. peltata* is easily distinguished by the presence of terpenoids (and, in North America, almost always pannarin), and the discs are always epruinose and distinctly brownish, with the upper part of the hymenium densely inspersed. The cracked lower surface of thallus and the often crater-like apothecia are also helpful identifying characteristics. The illustration of *R. peltata* in Swinscow and Krog (1988, p. 291) is of a *Lecanora* species.

Rhizoplaca subdiscrepans (Nyl.) R. Sant., Lich. Sweden Norway: 278 (1984).

Basionym: *Squamaria chrysoleuca* var. *subdiscrepans* Nyl., Flora, 44: 718 (1861); Synonym: *Lecanora subdiscrepans* (Nyl.) Stizenb.; Illustration: Brodo et al. (2001), p. 641, and Fig. 93 on next page.

Thallus: to *c.* 3 cm across, to 2 mm thick in center, verrucose-squamulose, strongly polyphyllous; subunits scattered to contiguous or crowded, 0.3-1.3 mm across, convex, becoming ± sinuous and plicate; **lobes:** similar to central subunits or somewhat more flattened and becoming slightly elongated and divided, *c.* 1-1.5 mm long, ultimate segments *c.* 0.5 mm wide; **upper surface:** often somewhat powdery-roughened but not distinctly pruinose, pale yellowish green to somewhat whitish, edges concolorous;

lower surface: pale to dark brownish; umbilicus: indistinct, consisting of the narrowed base of the squamules; rhizinose strands: sometimes present; **Apothecia:** common, laminal, 0.7-1.5 (-3) mm diam., usually soon sessile and constricted at base; disc: plane or slightly concave, usually ± strongly orange, pruinose, and appearing light to moderate orange; in occasional specimens (especially from areas north of the Sonoran region) younger discs and ones exposed to strong light becoming bluish black and often epruinose; thalline margin: concolorous with thallus, 0.1-0.2 mm wide, entire to flexuous, often soon crenulate towards inside, somewhat raised and slightly inflexed especially when young, usually persistent; hymenium: pale yellowish or orangish, not inspersed, but the uppermost part usually covered with granules; paraphyses tips: hyaline and scarcely thickened, or occasionally becoming at least partly greenish-blue and ± capitate, to 3-5 µm;

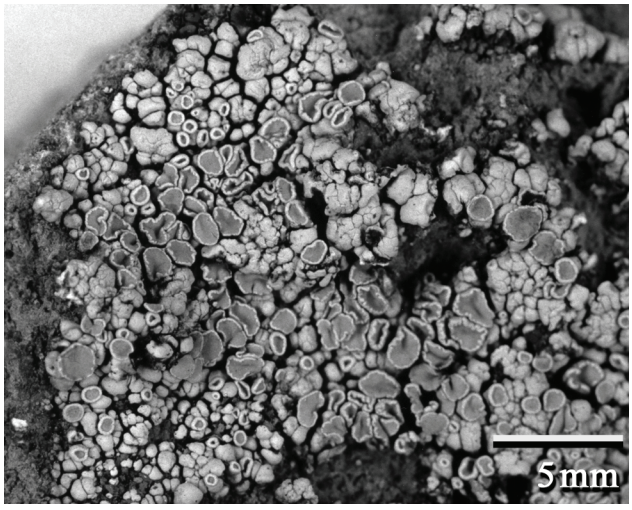
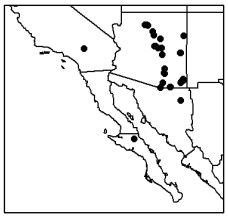


Fig. 93. *Rhizoplaca subdiscrepans*, photo by B. Ryan.

ascospores: (in material with placodiolic acid) ellipsoid to narrowly ellipsoid or slightly ovoid, (7-) 9-10 (-12) x (3-) 4 (-5) µm; **Pycnidia:** occasional; **conidia:** 15-25 µm long; **Spot tests:** upper cortex: K- or + yellowish, C-. KC+ yellow, P-, UV-; medulla: K- or (rarely, in non-Sonoran material, K+ yellow or red), C- or rarely C+ red, KC-, P- or occasionally P+ yellow, UV-; **Secondary metabolites:** upper cortex: in our region with placodiolic acid (major), usnic acid (minor); medulla: without lichen substances, or occasionally with psoromic or rarely lecanoric acid chemosyndromes or unidentified substances; the norstictic acid chemosyndrome occurs rarely (in Europe).

Substrate and ecology: on basalt, rhyolite, granite, and sandstone (including calciferous types); on exposed, dry, steep surfaces (in northern areas often south-facing), in pinyon-juniper and oak woodlands, and in pine forests, **World distribution:** chemotypes containing placodiolic acid (± other substances) occur in warm-temperate to boreal-arctic areas of Asia, Europe, and western North America; psoromic or rarely lecanoric acid occurs in some specimens (including ones from Arizona, but also from some northern localities); the report of "*Lecanora subdiscrepans*" from South America is dubious; **Sonoran distribution:** Arizona, Baja California Sur and Sonora at 1200-2900 m; southern California (San Bernardino Co.) at 1830 m.



Notes: Material from the Sonoran region is similar to that from other areas in western North America, and from Eurasia (and differs from that in eastern North America), in usually containing placodiolic rather than pseudoplacodioic acid, having relatively long and narrow ascospores, and including occasional specimens (e.g., one from Gila Co., Arizona) with discs that are at least partly bluish or bluish black as in *R. melanophthalma*. As treated here, *R. subdiscrepans* can be distinguished from both *R. melanopthalma* and *R. chrysoleuca* (with which it sometimes grows side by side) especially by the numerous and crowded, distinctly convex to plicate and at most vaguely umbilicate thallus subunits, with lower surface completely lacking greenish or bluish black tinges, and from *Lecanora opiniconensis* and related taxa (with which it is frequently associated in North America and Asia) especially by having pruinose discs and a more matt and grayish thallus lacking yellowish to orange lobe tips.

RIMELIA

by T. H. Nash III and J.A. Elix

Rimelia Hale & A. Fletcher, Bryologist 93: 23 (1990).

Family: Parmeliaceae; Type: *Rimelia cetrata* (Ach.) Hale; No. species: 12 world-wide; Selected lit.: Hale and Fletcher (1990) and Elix (1993a & 1994l).

Life habit: lichenized; **Thallus:** foliose, 4-20 cm wide, loosely adnate to adnate, lobate; **lobes:** irregular to sublinear, broad, 3-30 mm wide, often lacinate, elongate; apices: usually subrotund to rotund, ciliate (absent in one species); cilia: sparse to dense, simple to sparsely branched, not bulbate; **upper surface:** gray to dark gray, gray-green or pale green, conspicuously effigurate-maculate forming an intricate reticulate network, becoming cracked along the maculae but lacking true pseudocyphellae, pruinose or not towards the tips; with or without soredia or isidia; **upper cortex:** pored epicortex, vaulted paraplectenchymatous, **medulla:** white, relatively thick, hard and chalky, cell walls containing an intermediate type of lichenan; **photobionts:** primary one a *Trebouxia*, secondary photobiont absent; **lower surface:** glossy black centrally, brown peripherally, plane to papillate marginally, rhizinate; rhizines: simple but becoming sometimes squarrose, short ones throughout and longer ones in tufted groups; cyphellae, pseudocyphellae and tomentum absent; **Ascomata:** apothecial, becoming perforate, laminal, orbicular, cup-shaped, substipitate, perforate or imperforate; margin: prominent with thalloid rim, ciliate; exciple: gray or hyaline; epithecium: brown or brownish yellow; hypothecium: hyaline; **asci:** lecanoral, apex thickened and amyloid, with wide, axial body divergent towards apex, *c.* 8-spored; **ascospores:** simple, ellipsoid to broadly ellipsoid, 10-18 x 6-11 µm; wall: thin, hyaline; **Conidiomata:** pycnidial, laminal, immersed, punctiform; **conidia:** cylindrical to filiform, 9-16 x 1-1.5 µm; **Secondary metabolites:** upper cortex with atranorin and chloroatranorin; medulla with some combination of orcinol or ß-orcinol depsidones, ß-orcinol depsides, a xanthone or aliphatic acids; **Geography:** cosmopolitan with a major center in South America, temperate to tropical forests and woodlands; **Substrate:** mostly on bark, sometimes on acidic rock.

Notes: *Rimelia* is a segregate from *Parmotrema* that was initially recognized as a distinct group by Vainio in 1890, who later raised it to a sectional level [sect. Irregulares (Vainio 1923)]. The reticulate network of maculae on the upper suface is probably its most distinctive feature, which *Parmotrema* lacks. *Parmotrema* also does not have as well developed cracks in the upper cortex and has shorter, sublageniform conidia.

Key to the species of ***Rimelia*** from the Sonoran region:

1. Thallus sorediate or isidiate 2
1. Thallus lacking isidia and soredia ..... ***R. cetrata***

2. Thallus isidiate ..... ***R. subisidiosa***
2. Thallus sorediate 3

3. Medulla K+ yellow turning red (salazinic and consalazinic acids present) ..... ***R. reticulata***
3. Medulla K- (the fatty acid, caperatic acid present) ..... ***R. simulans***

The Species

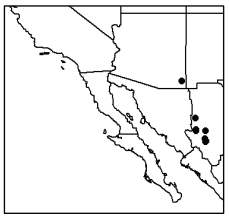
Rimelia cetrata (Ach.) Hale & A. Fletcher, Bryologist 93: 26 (1990).

Basionym: *Parmelia cetrata* Ach., Syn. Lich. 198 (18 14); Synonyms: *Parmelia herrei* Zahlbr., *Parmotrema cetratum* (Ach.) Hale and see Hale and Fletcher (1990); Illustrations: Hale (1979), p. 71 as *Parmotrema cetratum*; Brodo et al. (2001), p. 642.

Thallus: foliose, loosely adnate to adnate, 3-15 cm in diam., lobate; **lobes:** subirregular, elongate, slightly imbricate, plane, separate, 8-15 mm wide (very variable); margin: becoming dentate lacinate with age; lacinae: 5-10 x 1-2 mm; apices: rotund, ciliate; cilia: sparse, simple, up to 2.0 mm long; **upper surface:** ashy white to gray, smooth,

dull, strongly reticulate maculate, becoming reticulately cracked with age along the maculae; soredia, isidia and pustulae absent; **medulla:** white with continuous algal layer; **lower surface:** black with narrow brown zone peripherally, rhizinate to margin or narrowly erhizinate marginally; rhizines: scattered, simple to squarrosely branched; **Apothecia:** common, substipitate, up to 10 mm in diam.; margin: rugose, white maculate; disc: often perforate, concave or flat; **ascospores:** simple, hyaline, ellipsoid, 13-15 x 7-9; **Pycnidia:** common marginally; **conidia:** filiform, 10-14 x 1 µm; **Spot tests:** upper cortex K+ yellow, C-, KC-, P+ yellow; medulla K+ yellow turning deep red, C-, KC-, P+ orange; **Secondary metabolites:** upper cortex with atranorin and chloroatranorin; medulla with salazinic acid (major) and consalazinic acids (minor).

Substrate and ecology: usually on trees; **World distribution:** pansubtropical and pantemperate; common especially in SE USA and South Africa; **Sonoran distribution:** SE Arizona and adjacent Sierra Madre Occidental of Chihuahua, Sonoran and Sinaloa.

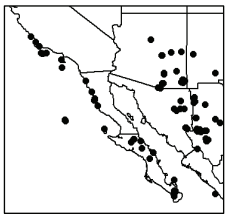


Rimelia reticulata (Taylor) Hale & A. Fletcher, Bryologist 93: 28 (1990).

Basionym: *Parmelia reticulata* Taylor, Fl. Hibern 148 (1836); Synonyms: *Parmotrema reticulatum* (Taylor) M. Choisy, and see Hale and Fletcher (1990); Illustrations: Elix (1994l), p. 194; Brodo (2001), p. 643.

Thallus: foliose, loosely adnate, 4-20 cm in diam., lobate; **lobes:** subirregular, elongate, slightly imbricate, plane, separate, 5-15 mm wide; margin: deeply crenate; apices: rotund, sometimes subascending, ciliate; cilia: simple, up to 3.0 mm long; **upper surface:** pale gray to gray-green, smooth, dull, strongly reticulately maculate; **soredia:** common, powdery to subpustular, laminal or marginal, in linear to orbicular soralia that are often subcapitate, or spreading and becoming somewhat diffuse; isidia, pustulae and dactyls absent; **medulla:** white with continuous algal layer; **lower surface:** black with narrow brown to rarely white, papillate zone peripherally, centrally rhizinate; rhizines: scattered to dense, mostly simple (to squarrose), black; **Apothecia:** rare, submarginal, substipitate, up to 8 mm in diam.; margin: thick, thalline, entire to crenulate, sorediate; disc: perforate, brown to dark brown, concave; **ascospores:** simple, hyaline, ellipsoid, 12-18 x 8-11 µm; **Pycnidia:** rare, punctiform; **conidia:** filiform, 12-16 x 1-1.5 µm; **Spot tests:** upper cortex K+ yellow, C-, KC-, P+ yellow; medulla K+ yellow turning deep red, C-, KC-, P+ orange; **Secondary metabolites:** upper cortex with atranorin and chloroatranorin; medulla with salazinic acid (major) and consalazinic acids (minor).

Substrate and ecology: commonly on rocks, also on trees in open habitats; **World distribution:** pansubtropical and pantemperate; North and South America, Africa, southern Asia, Australasia, Oceania; **Sonoran distribution:** common in SE Arizona and southwards in the Sierra Madre Occidental region of Chihuahua, Sonora and Sinaloa and southern mountains of Baja California Sur.



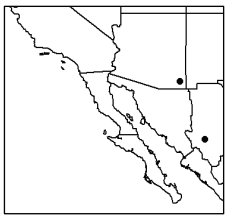
Rimelia simulans (Hale) Hale & A. Fletcher, Bryologist 93: 29 (1990).

Basionym: *Parmelia simulans* Hale, Phytologia 28: 339 (1974); Synonym: *Parmotrema simulans* (Hale) Hale and see Hale and Fletcher (1990); Illustration: Hale and Fletcher (1990), p. 24.

Thallus: foliose, loosely adnate, 3-15 cm in diam., lobate; **lobes:** subirregular, elongate, slightly imbricate, plane, separate, 4-10 mm wide; margin: strongly laciniate, apices: rotund, ciliate; cilia: simple, up to 2.0 mm long; **upper surface:** gray, smooth, dull, strongly reticulately maculate; **soredia:** common, coarse and granular, often on the lacinae, in orbicular soralia or spreading and becoming somewhat diffuse; isidia, pustulae and dactyls absent; **medulla:** white with continuous algal layer; **lower surface:** black with brown zone peripherally, rhizinate to the margin; rhizines: scattered to dense, mostly simple, black; **Apothecia:** rare, substipitate, up to 5 mm in diam.;

margin: entire to crenulate, sorediate, disc: perforate, brown, concave; **ascospores:** simple, hyaline, ellipsoid, 12-17 x 6-9 µm; **Pycnidia:** common, punctiform; **conidia:** sublageniform, 4-6 x 1 µm; **Spot tests:** upper cortex K+ yellow, C-, KC-, P+ yellow; medulla K-, C-, KC-, P-; **Secondary metabolites:** upper cortex with atranorin and chloroatranorin; medulla with caperatic acid (major).

Substrate and ecology: commonly on rocks, also on trees in open habitats; **World distribution:** North and tropical America; **Sonoran distribution:** common in SE Arizona and southwards in the Sierra Madre Occidental region of Chihuahua.

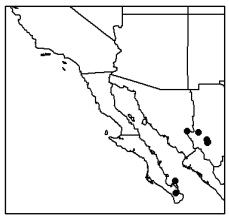


Rimelia subisidiosa (Müll. Arg.) Hale & A. Fletcher, Bryologist 93: 29 (1990).

Basionym: *Parmelia cetrata* var. *subisidiosa* Müll. Arg., Engler Bot. Jahrb. 20: 256 (1894); Synonym: *Parmelia subisidiosa* (Müll. Arg.) C. W. Dodge and *Parmotrema subisidiosum* (Müll. Arg.) Hale; Illustrations: Brodo et al. (2001), p. 643; Hale (1979), p. 67 as *Parmotrema subisidiosum*.

Thallus: foliose, loosely adnate to adnate, 3-10 cm in diam., lobate; **lobes:** subirregular, elongate, slightly imbricate, plane, separate, 5-12 mm wide; margin: becoming dentate or lacinate with age; lacinae: 5-10 x 1-2 mm; apices: rotund, ciliate; cilia: sparse, simple, up to 2.0 mm long; **upper surface:** gray to green-gray, smooth, dull, strongly reticulate maculate, becoming reticulately cracked with age along the maculae, isidiate; **isidia:** laminal and marginal, cylindrical, simple to branched, tips often bearing cilia, more common marginally; soredia and pustulae absent; **medulla:** white with continuous algal layer; **lower surface:** black with brown zone peripherally, rhizinate to margin; rhizines: scattered, mostly simple, sometimes bifurcate to squarrose; **Apothecia:** rare, up to 5 mm wide; margin: thalline, isidiate; disc: brown, imperforate or perforate; **ascospores:** simple, hyaline, ellipsoid, 12-14 x 6-10 µm; **Pycnidia:** common, immersed; **conidia:** filiform, 10-12 x 1 µm; **Spot tests:** upper cortex K+ yellow, C-, KC-, P+ yellow; medulla K+ yellow turning deep red, C-, KC-, P+ orange; **Secondary metabolites:** upper cortex with atranorin and chloroatranorin; medulla with salazinic acid (major) and consalazinic acids (minor).

Substrate and ecology: usually on trees; **World distribution:** Arizona to Central America, east Africa; **Sonoran distribution:** Sierra Madre Occidental of Chihuahua and Sonoran and southern Baja California Sur.



ROCCELLA

by A. Tehler

Roccella DC, Fl. Franc. ed. 3 (2): 334 (1805).

Family: Roccellaceae; Type: *Roccella fusiformis* (L.) DC; No. species: *c.* 30 world-wide; Selected lit.: Darbishire (1898).

Life habit: lichenized; **Thallus:** fruticose, pendent, sparsely dichotomously branched, main and terminal branches flattened or terete, branches 2-5 -(10) mm thick and usually 5-15 cm long; **lobe surface:** creamy white-grayish to grayish-brown, smooth or wrinkled, sparsely pruinose or epruinose; soredia (often in soralia) present or absent, isidia absent; **cortex:** hyphae anticlinally arranged, 40-70 µm thick; **medulla:** loose above, byssoid or chalky; below plectenchymatous in area of the basal plate (holdfast) and often (yellowish) brown; **photobionts**: primary one a *Trentepohlia*, seconddary photobiont absent; **attachment:** by holdfasts, including an hypomedulla

which is usually brown to dark brown (sometimes with a yellowish tinge); **Ascomata:** apothecioid, lateral, circular in outline, immersed or sessile with constricted base, up to 2.5 mm diam.; disc: exposed, white with a rimose, pruinose layer; exciple: initially with algae and a cortex, later the algae often displaced and the cortex eroded; proper exciple: a thin parathecium, sometimes inconspicuous; epithecium: 40-50 µm, brown, with paraphysoids intertwined, sparsely branched; hymenium: 70-90 µm high; paraphysoids: sparsely branched, hyaline, 1-2 µm diam.; hypothecium: distinct, dark brown (carbonaceous), not extending down into medulla; **asci:** clavate, 60-85 x 12-14 µm; **ascospores:** fusiform, curved, smooth, 3-septate, hyaline; **Conidiomata:** pycnidial, solitary, immersed, black, 0.1 mm diam.; **conidia:** filiform, curved, 16-21 x <1 µm; **Secondary metabolites**: orcinol and ß-orcinol depsides, aliphatic acids; **Geography:** a pantropical genus and extending into adjacent temperate regions, especially those with Mediterranean climates; **Substrate:** on bark or rock.

Notes: In the checklist of North American lichens Esslinger and Egan (1995) list as many as nine species of *Roccella*, all of which have been reported from California (Darbishire 1898; Hasse 1913; Tuckerman 1882). Some of the names such as *Roccella fuciformis*, *R. phycopsis* and *R. tinctoria* are European species, that have been incorrectly reported from North America. The other species, *Roccella babingtonii*, *R. decipiens*, *R. difficilis*, *R. fimbriata*, *R. montagnei* and *R. peruensis*, are all part of a difficult species complex with a distribution that extends down to mediterranean Chile in South America and include adjacent islands such as the Galapagos and with an offshoot into the Caribbean region. They may even have a global distribution. This treatment agrees with Hale and Cole (1988) that only two taxa from that species complex should be recognized from California, although different names are used here. A third taxon, *R. portentosa*, is reported from southern Baja California Sur.

Key to the species of ***Roccella*** from the Sonoran region:

1. Thallus sorediate ..... ***Roccella peruensis***
1. Thallus not sorediate 2
2. Branches flattened, C+ red ..... ***Roccella decipiens***
2. Branches terete, C- ..... ***Roccella portentosa***

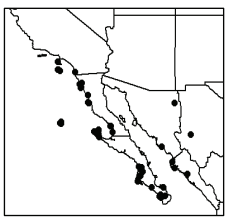
The Species

Roccella decipiens Darb., Ber. Dtsch. Bot. Ges. 15: 5 (1897) nom. nud. Monogr. Roccell., Bibl. Bot. 9: 49 (1898).

Synonym: *Roccella fimbriata* Darb.; Illustrations: Darbishire (1898), figs. 92 & 93; Hale (1979), p. 221 as *Roccella fimbriata*.

Thallus: fruticose, pendent, main branches flattened, usually 5-20 cm long; **lobe surface:** grayish to grayish-brown, often uneven with ridges and wrinkles; without soredia; **medulla:** white but brown in the holdfast zone, usually with a yellowish tinge; **"Apothecia":** usually present; circular in outline but often with undulating margin, sessile with constricted base, rarely immersed, up to 2.5 mm diam.; hymenium: 70-90 µm; paraphysoids: sparsely branched, hyaline, <2 µm diam.; **asci:** clavate, 60-85 x 12-14 µm, 8-spored; **ascospores:** fusiform, curved, hyaline, 3-septate, 22-27 x 5-6 µm; walls: smooth; **Spot tests:** cortex K+ more or less yellowish red (sometimes inconspicuous), C+ red, KC+ red, P-; medulla K-, C-, KC-, P-; **Secondary metabolites:** erythrin and lecanoric acid.

Substrate and ecology: grows near the sea on any suitable substrate, such as the vertical rocks and cliffs and on the trunks, branches and twigs of various trees and shrubs; **World distribution:** uncertain, but probably extending from California to south central Chile, and possibly also the Carribean and pantropical; **Sonoran distribution:** along the western coast of California from San Francisco south to the tip of Baja California along the Pacific coast. It is also present on the Mexican mainland in the southern part of Sonora and adjacent Sinaloa.



Notes: *Roccella decipiens* is characterized by the fertile, non-sorediate thallus and feels somewhat stiffer and more

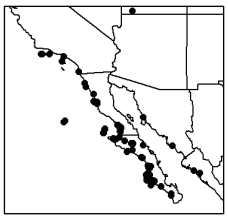
robust than *R. peruensis* probably due to the lack of soralia that weaken the cortex. The name *R. fimbriata* (Darbishire 1935) has been frequently utilized for this taxon in California and Mexico (e.g. Hale 1979). However, *R. decipiens* (Darbishire, 1898) is an older name and thus take precedence over *R. fimbriata* (also see Notes under *R. peruensis* below). *Roccella decipiens* was described from southern California by Darbishire (1898) as being a constantly fertile species without soralia. Furthermore, morphological, chemical and molecular investigations (Myllys et al., 1999) indicate that *Roccella decipiens* may be the fertile counterpart in a species pair relationship with the sorediate *Roccella peruensis* (below). Thus the name *Roccella decipiens* may be subject to change when the the genus *Roccella* is revised.

Roccella peruensis (Krempelh.) Darb., Bull. Herb. Boiss. 5: 763 (1897).

Basionym: *Roccella montagnei* var. *peruensis* Krempelh., Verh. Zoo.-bot. Ges. 26: 442 (1877), type: Peru, Lima, 1868-71, Barranca (*lectotype* M-0024563, selected here); Synonym: *Roccella babingtonii* Mont., *Roccella difficilis* Darb. (*type*: Peru, Payta, 1836, Gaudichaud [lectotype PC selected here]), *Roccella mexicana* Vain.; Illustrations: Darbishire (1898), fig. 89; Hale (1979), p. 220; Brodo et al. (2001), p. 648, both as *Roccella babingtonii*; and the front cover of this book.

Thallus: fruticose, pendent, main branches flattened, usually 5-15 cm long; **lobe surface:** grayish, often uneven with ridges and wrinkles; **soredia:** farinose, in maculiform soralia which may often fuse to cover much of the lobe surface; **medulla** white but brown in the holdfast zone, usually with a yellowish tinge; **"Apothecia":** not seen; **Spot tests:** cortex K+ more or less yellowish red (sometimes inconspicuous), C+ red, KC+ red, P-; medulla K-, C-, KC-, P-; **Secondary metabolites:** erythrin and lecanoric acid.

Substrate and ecology: grows near the sea on any suitable substrate, such as the vertical rocks and cliffs and on the trunks, branches and twigs of various trees and shrubs; **World distribution:** uncertain, but probably from California to south-central Chile, and possibly Carribean and pantropical; **Sonoran distribution:** extending from southern California south to the tip of Baja California along the Pacific coast and also occurring in southern parts of Sonora and adjacent Sinaloa.



Notes: *Roccella peruensis* is characterized by its sterile, sorediate thallus. *Roccella peruensis* feels somewhat softer and less robust than *R. decipiens*, probably due to the presence of soralia. The name and *R. babingtonii* Mont. (Montagne 1852) has been frequently used for this taxon in California and Mexico. *Roccella babingtonii*, however, was described by Montagne as having apothecia only; soredia were not mentioned by him. Thus, Montagne's description cannot be applied to the sterile, sorediate taxon *R. peruensis* (Krempelh.) Darb. The description of *R. babingtonii* Mont. better fits to the fertile *R. decipiens* Darb. above and may in fact be the oldest name for that taxon. Morphological, chemical and molecular investigations (Myllys *et al.*, 1999) indicate that *Roccella peruensis* may be the sterile counterpart in a species pair relationship with the fertile *R. decipiens* (above). Thus, the name *R. peruensis* may be subject to change when the the genus *Roccella* is revised.

Roccella portentosa (Gay) Darb., Ber. Dtsch. Bot. Ges. 15: 10 (1897).

Basionym: *Roccella tinctoria* var. *portentosa* Mont. *ex* Gay, Flora Chilena 85 (1854, ["1852"]).

Thallus: fruticose, erect or pendent, both main and terminal branches terete, 5-10 cm long; **lobe surface:** white grayish, smooth; **medulla:** white but brown in the holdfast zone, usually with a yellowish tinge; **"Apothecia":** usually present, circular in outline with slightly undulating margin, sessile with constricted base, up to 2 mm diam.; hymenium: 70-90 µm; paraphysoids: sparsely branched, hyaline, <2 µm diam.; **asci:** clavate, 60-85 x 12-14 µm, 8-spored; **ascospores:** fusiform, curved, hyaline, 3-septate, 23-27 x 5-6 µm; walls: smooth; **Spot tests:** cortex K-, C-, KC-, P-; medulla K-, C-, KC-, P-; **Secondary metabolites***:* not investigated.

Substrate and ecology: on rocks near the sea; **World distribution:** South America, from central Chile to the Galapagos Islands, and northwards to Baja California; **Sonoran distribution:** only known on cliffs near Todos Santos in southern Baja California Sur.

Notes: *Roccella portentosa* is distinguished from *R. decipiens* and *R. peruensis* mainly by its terete and smooth branches and its C- thallus reaction. No representative from the *R. portentosa* complex has been described from the Sonoran region. The specimens collected from Baja California have clearly sessile apothecia and the thallus cortex and medulla are C-. South American specimens have apothecia which are usually more or less immersed and their thallus C reaction is variable ranging from fully C+ or, C- cortex but C+ medulla, or rarely completely C-. In South America sorediate specimens may also be involved in species pair complexes. The identification of the Baja Californian specimens as *R. portentosa* should be considered as provisional until the genus *Roccella* has been revised.

ROCCELLINA

by A. Tehler

Roccellina Darb., Bibl. Bot. 9: 54 (1898).

Family: Roccellaceae; Type: *Roccellina condensata* Darb.; No. species: 24 world-wide; Selected lit.: Tehler (1983 & 1994).

Life habit: lichenized; **Thallus:** crustose or sometimes nearly subfruticose, effuse, smooth to slightly verrucose; **surface:** creamy white to white-grayish to brown to green-brown, epruinose to slightly pruinose; soralia often developed (in species outside the Sonoran region); isidia not seen; **cortex:** with mixed and intertwined hyaline hyphae in a brownish gelatinous substance; **medulla:** white, chalky with or without brown hypomedulla in lower parts; **photobionts:** primary one a *Trentepohlia*, secondary photobiont absent; **Ascomata:** apothecioid, numerous, solitary to aggregated, circular in outline, sessile, 0.8-1.2 mm diam.; disc: exposed, convex or flat, pruinose, white-gray; exciple: entire or slightly undulating to strongly undulating; epithecium: brown or brownish; hymenium: hyaline; hypothecium: extending down to the substrate; **asci:** clavate, 70-110 µm, 8-spored; **ascospores:** fusiform, curved, smooth, 3-septate, hyaline, 25-31 x 4-5 µm; **Conidiomata:** pycnidial, solitary, immersed, dark-brown; **conidia:** filiform, curved or semi-circled, hyaline, 9-17 µm long less than 1 µm thick; **Secondary metabolites:** ß-orcinol depsides and depsidones, dibenzofurans, aliphatic acids; **Geography:** coastal regions of Mediterranean and subtropical climates; **Substrate:** on bark or rock.

Key to the species of ***Roccellina*** from the Sonoran region:

1. Thallus predominantly brownish and K+ yellow, ascomata sessile with constricted base .... ***Roccellina conformis***
1. Thallus predominantly whitish and K-, ascomata immersed or sessile with base not constricted .... ***Roccellina franciscana***

The Species

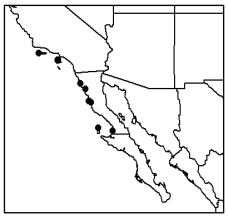
Roccellina conformis Tehler, Opera bot. 70: 50 (1983).

Illustrations: Tehler (1983), p. 50; Brodo et al. (2001), p. 648.

Thallus: crustose, effuse, smooth to slightly verrucose, 0.3-0.7 mm diam.; **surface:** creamy brown to green-brown; soredia: not seen; **cortex:** 20-40 µm thick; **medulla:** white, chalky; **"Apothecia":** numerous, circular in outline, sessile, 0.8-1.2 mm diam.; exciple: entire or slightly undulating, protruding above the disc; epithecium, light brown to brown, 25-60 thick; hymenium: hyaline; **asci:** clavate, 70-110 µm, 8-spored; **ascospores:** fusiform, curved, smooth, 3-septate, hyaline, 25-31 x 4-5

µm; **Spot tests:** thallus: K+ yellow turning red, C-, KC-, P+ yellow-red; **Secondary metabolites:** an unknown substance.

Substrate and ecology: growing on bark of trunks, twigs and branches of different trees and shrubs near the ocean; **World and Sonoran distribution:** *Roccellina conformis* is found only from a few sporadic localities near the sea from Santa Catalina Island, California, down to Laguna Manuela in southern Baja California.



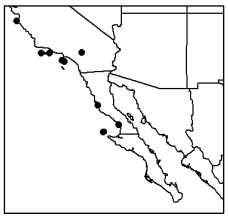
Notes: *Roccellina conformis* is similar to *Dirina paradoxa* subsp. *approximata* which also grows on the trunks and branches of various trees and shrubs near the sea. *Roccellina conformis* is easily distinguished from the latter by its C- thallus reaction. *Roccellina franciscana* differs in its K- and P- reaction and in the more pruinose, grayish white thallus and much more undulating, nearly stromatoid, subimmersed ascocarps with an unconstricted base.

Roccellina franciscana (Zahlbr. *ex* Herre) Follmann in Huneck & Follmann, Philippia 4: 119 (1979).

Basionym: *Dirina franciscana* Zahlbr. *ex* Herre, Bot. Gaz. 43: 270 (1907); Synonym: *Schismatomma cupressum* Herre (1952); Illustration: Tehler (1983), p. 49.

Thallus: crustose, bullate and, especially when epilithic often forming small cushions, effuse, smooth to slightly verrucose, 0.3-0.7 mm diam.; **surface:** grayish white, often with slightly brownish parts; soralia not seen; **cortex:** 20-40 µm thick; **medulla:** white, chalky; **"Apothecia":** sometimes nearly stromatoid, numerous, circular in outline, sessile or subimmersed with base not constricted, 0.5-3 mm diam.; exciple: entire or slightly undulating, in level with or only slightly protruding above the disc; epithecium: light brown to brown, 25-60 thick; hymenium: hyaline; **asci:** clavate, 70-110 µm, 8-spored; **ascospores:** fusiform, curved, smooth, 3-septate, hyaline, 25-31 x 4-5 µm; **Spot tests:** thallus K-, C-, KC-, P-; **Secondary metabolites:** roccellic acid.

Substrate and ecology: most common on bark and wood of various trees and shrubs near the sea, but is also found on rocks; **World and Sonoran distribution:** found only in California from San Francisco in the north down to San Diego and farther south in Baja California to Rosario de Arriba.



Notes: *Roccellina franciscana* is distinguished from *Roccellina conformis* by its white-grayish thallus with K- and P- reactions and the apothecia which are much more undulating or nearly stromatoid and are often subimmersed and without a constricted base.

SCHISMATOMMA

by A. Tehler

Schismatomma A. Massal., Ric. auton. lich. crost.: 56 (1852).

Family: uncertain; Type: *Schismatomma pericleum* (Ach.) Branth & Rostr.; No. species: eight world-wide; Selected lit.: Tehler (1993a).

Life habit: lichenized; **Thallus**: crustose, coherent but when in bark usually incoherent, 0.05-0.2 mm wide; **surface:** white to whitish-gray to gray brownish-gray, smooth or finely rugose, epruinose; soredia present or absent; **cortex:** inconspicuous or missing; **medulla:** absent or indiscernible; **photobionts**: primary one a *Trentepohlia*, secondary photobiont absent; **Ascomata:** apothecioid, numerous, solitary, elongated or circular in outline, sessile rarely immersed with base usually not constricted, between (0.15-) 0.5 (-1.3) mm diam.; disc: exposed, convex to nearly flat, rarely concave, pruinose rarely epruinose

but pruina may disappear with age in some species; exciple: present but usually poorly developed and on old ascomata often dislocated; cortex: absent; algae: missing or sporadically present; proper exciple: a thin parathecium, rarely inconspicuous, plectenchyma in most species of loosely intertwined hyphae or in some species with hyphae anticlinally arranged; epithecium: brown; hymenium: up to 80 µm thick, paraphysoids unbranched or only sparsely branched, hyaline; hypothecium: dark-brown (carbonaceous) rarely pale brown or hyaline, extending down to substrate; **asci:** clavate, 50-80 x 10-15 µm; **ascospores:** fusiform or acicular-fusiform, hyaline, 3-septate; walls: smooth; **Conidiomata:** pycnidial, solitary, immersed or slightly sessile, black or brown, *c.* 0.05-0.15 mm diam.; **conidia:** bacilliform rarely filiform, curved, hyaline or rarely pale brownish olive-green; **Secondary metabolites:** aliphatic acids, ß-orcinol depsides; **Geography:** subtropical to temperate regions; **Substrate:** on bark.

Notes: Tehler (1993a) reported only one species in *Schismatomma* for California. Several other species formerly placed in *Schismatomma* were excluded from the genus, but were not recombined to their proper genera because their taxonomic placement was unknown. One of those species, *Schismatomma pluriloculare* (Zahlbr.) Zahlbr., occurs in the Sonoran region and thus is provisionally treated here.

Key to the species of ***Schismatomma s.l.*** from the Sonoran region:

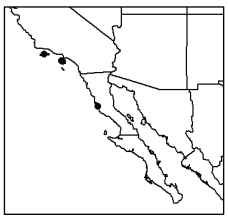
1. Thallus C+ red (lecanoric acid present), spores 7-11 septate ..... ***"Schismatomma" pluriloculare***
1. Thallus C-, spores 3 septate ... ***Schismatomma rediunta***

The Species

"Schismatomma" pluriloculare (Zahlbr.) Zahlbr.

Basionym: *Platygrapha plurilocularis* Zahlbr., Annal. Naturhist. Hofmuseum Wien 26: 169 (1902).

Thallus: crustose, verruculose, rimose, coherent, 0.2-1 mm thick; **upper surface:** greenish-white; soralia often developed, at first punctiform to maculiform but when old often confluent; **cortex:** hyphae mixed and intertwined but sometimes more or less anticlinally arranged in the upper part, 20-40 µm thick; **"Apothecia":** numerous or absent, circular in outline, sessile with constricted base, 0.5-2 mm diam; disc: exposed, flat or concave, white pruinose; exciple: crenulate or strongly crenulate, conspicuously protruding above the disc, algae and cortex present; proper exciple: conspicuous, dark-brown (carbonaceous), up to 100 thick; epithecium: 10-15 µm thick, pale brown; hymenium: 50-65 µm high, paraphysoids: richly branched and intertwined, tips 2 µm diam. but *c.* 1 µm diam. below; hypothecium: dark-brown (carbonaceous); **asci:** clavate, 50-60 x 10-15 µm; **ascospores** fusiform, straight or curved, hyaline, multi-septate usually with 7-11 septa, 22-38 x 4-6 µm; **Pycnidia:** not seen; **Spot tests:** thallus K-, C+ red, KC+ red, P-; **Secondary metabolite:** lecanoric acid.



Substrate and ecology: mostly found on dead twigs and branches but also on bark of different shrubs and trees near the ocean; **World** and **Sonoran distribution:** sparsely distributed along the coast from Monterey County, California, in the north to central Baja California in the south.

Notes: This species is often wholly sorediate but then usually with rudimentary apothecia also present. Completely sorediate individuals may be difficult to distinguish from sorediate individuals of *Sclerophyton californicum* which may grow in the same habitat. However, the thallus of "*Schismatomma" pluriloculare* is verruculose and is more greenish. The use of the quotes about the generic name indicate that the placement in this genus is not completely certain.

Schismatomma rediunta (Hasse) Tehler, Lichenologist 17: 211 (1985).

Basionym: *Lecanora rediunta* Hasse, Bull. Torrey Bot. Club 24: 446 (1897); Synonym: *Dirina rediunta* (Hasse)

Zahlbr.; Illustrations: Tehler (1993a), p. 210; Tehler (1985), p. 211.

Thallus: not well developed, 0.1 mm thick; **surface:** white; soredia not developed; **"Apothecia":** developing erumpently, immersed to sessile, 0.2-0.5 mm diam; disc: convex; exciple: level with the disc, algae missing; proper exciple: sometimes inconspicuous; epithecium: 10-15 µm thick with hyphae richly branched and intertwined, verrucose, tips 2 µm diam.; hymenium: 55-65 µm high; hypothecium: dark-brown (carbonaceous); **asci:** clavate, 50-60 x 13 µm, 8-spored; **ascospores:** fusiform, curved, hyaline, 19-22 x 4-5 µm; **Pycnidia:** 0.1 mm diam; **conidia:** bacilliform, curved, 6-9 x 1<2 µm; **Spot tests:** thallus K-, C-, KC-, P-; **Secondary metabolite:** roccellic acid.

Substrate and ecology: *Schismatomma rediunta* has been found on bark of *Juglans californica*, *Umbellularia californica* and *Heteromeles arbutifolia*; **World and Sonoran distribution:** *Schismatomma rediunta* is restricted to southern California on Santa Catalina and Santa Cruz Islands and on the nearby mainland in Santa Monica.

Notes: Because it is inconspicuous, it is very rarely collected. The first recollection of *Schismatomma rediunta* since 1907 was made 1994.

SCHIZOPELTE

by A. Tehler

Schizopelte Th. Fr., Flora, 58: 143 (1875).

Family: Roccellaceae; Type: *Schizopelte californica* Th. Fr.; No. species: one world-wide; Selected lit.: Darbishire (1898), and Tehler (1990a).

Note: Because the genus is monotypic, a generic description would simply recapitulate the specific description given below.

The Species

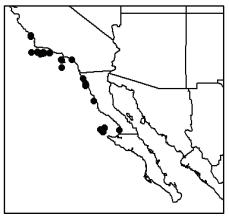
Schizopelte californica Th. Fr., Flora 58: 143 (1875).

Synonym: *Combea californica* (Th. Fr.) Follmann & Geyer; Illustrations: Hale (1979), p. 228; Brodo et al. (2001), p. 652.

Life habit: lichenized; **Thallus:** fruticose, epilithic, erect, sparsely dichotomously branched, both main and terminal branches terete, branches up to 3 mm thick; **lobe surface:** creamy white, grayish-white, smooth with old parts sometimes rugose, sparsely pruinose; soredia and isidia absent; **cortex:** 50-65 µm thick, with hyphae interwovenly arranged; **medulla:** white, cretaceous, except in top of young branches where it is brown and byssoid; **photobiont:** primary one a *Trentepohlia*, secondary photobiont absent; **attachment:** holdfast included in a small crustose or suffruticose, effuse, primary thallus with brown or in parts reddish hypomedulla; **Apothecia:** numerous, solitary, terminal on branches, circular in outline but when old sinuate, sessile to stipitate, with constricted base, up to 2 cm diam.; disc: exposed, concave, gray with a smooth pruinose layer; thalline exciple: prominent with algae and cortex; proper exciple: a thin parathecium, sometimes inconspicuous; epithecium: brown, 20-30 µm thick; hymenium: 70-100 µm thick with sparsely branched, paraphysoids: hyaline, intertwined, richly branched; hypothecium: distinct, dark-brown (carbonaceous), extending down into medulla; **asci:** clavate, 70 x 14 µm, 8-spored; **ascospores:** slightly fusiform, straight or slightly curved, verrucose, brown, 5-7 septate, 19-23 x 3-5 µm; **Conidiomata:** pycnidial, aggregated in groups in well defined, white-pruinose, ascomata-like synpycnidia, 2 mm in diam.; solitary pycnidia: sometimes present; immersed, black, 0.1 mm diam.; **conidia:** filiform, curved in a semicircle, 11-13 x < 1 µm; **Spot tests:** cortex K-, C+ red turning yellow, KC+ red, P-; medulla K-, C-, KC-, P-; **Secondary metabolites:** dibenzofurans, orcinol depsides [schizopeltic acid, erythrin (both major), and lecanoric

acid, isoschizopeltic acid, pannaric acid, 3-*O*-methylpannaric acid, pannaric acid 2-methyl ester and pannaric acid 6-methyl ester (all trace)-according to Elix et al. (1995].

Substrate and ecology: grows near the ocean on vertical and overhang cliffs exposed to the north, above the littoral and away from direct sea spray; **World and Sonoran distribution:** *Schizopelte californica* has been found as far north as San Luis Obispo Co., California, and as far south as central Baja California. Thus, it is essentially restricted to maritime parts of the Sonoran region.



Notes: *Schizopelte californica* is very charactaristic with its terminal apothecia and brown spores. It was transferred to *Combea* by Follmann and Geyer (1986), primarily on the basis of the shared secondary products erythrin, lecanoric acid, and schizopeltic acid, although these substances are also present in other genera of the family (see Tehler [1990a] for further discussion).

SCLEROPHYTON

by J. M. Egea and P. Torrente

Sclerophyton Eschw., Syst. Lich. 14 (1824).

Family: Opegraphaceae; Type: *Sclerophyton elegans* Eschw.; No. species: 8 world-wide; Selected lit.: Egea and Torrente (1995).

Life habit: lichenized; **Thallus:** crustose, heteromereous; **upper surface:** cream or pale brown to dark brown, dull, epruinose, smooth or roughened or fissured (in one species); **upper cortex:** interwoven hyphae with hyaline tips, or with epinecral layer embedded in a yellow-brown gelatinous substance; **medulla:** white and cretaceous, plectenchymatous, interspersed with granules and crystals of unknown nature (K soluble); **photobiont:** primary one a trentepohlioid alga, secondary photobiont absent; **lower cortex:** lacking; **lower surface** pale or blackish, attached by rhizoidal web, partly with additional rhizines of longitudinally arranged hyphae; **Ascomata:** dendroid-elongate, perithecioid to stellate and lirellate, aggregated or not, usually surrounded by a slightly elevated white rim (false thalline margin), rarely apothecioid with true thalline margin; proper exciple: thin, up to 15 µm thick, pale to dark brown, composed of plectenchyma of conglutinated hyphae with individual hyphae not easily discernable; hypothecium: hyaline; paraphysoids: richly branched, anastomosing; **asci:** bitunicate with fissitunicate dehiscence, *c.* 80 x 17 µm, endoascus: two layered, both layers hemiamyloid (K/I+ blue), but with thin, strongly amyloid band in the internal endoascus, with ± distinguishable ring structure and small ocular chamber, 8-spored; **ascospores:** simple, septate or muriform, constricted at one or more septa, thick-walled, oblong-ovoid to elongate-fusiform, the upper apex rounded and narrowing to lower end, hyaline to dark brown, usually with thick gelatinous sheath; **Conidiomata:** pycnidial, punctiform, laminal, immersed or subimmersed, unilocular, with colorless walls or reddish brown in the upper part; **conidia:** filiform and curved or rarely straight; **Secondary metabolites:** ß-orcinol depsides or depsidones and/or pigments; **Geography:** SW North America, the Carribean, Brazil, western and SW Europe; **Substrate:** on bark or rocks.

Key to the species of ***Sclerophyton*** in the Sonoran region:

1. Ascomata dendroid; ascospores triseptate, brownish when old, with a large terminal cell ..... ***S. incriptum***
1. Ascomata not dendroid; ascospores pluriseptate, brown when old, without large terminal cell 2

2. Ascomata lirellate or apothecioid at maturity; thallus C+ reddish 3
2. Ascomata punctiform; thallus C- 4

3. Ascospores 22-30 (-32) x 4-8 (-9) µm, with (3-) 5-7 transverse septa; thallus P- ..... ***S. californicum***

3. Ascospores 30-40 x 8-12 µm, with 6-9 (-10) transverse and 1-2 longitudinal septa; thallus P+ orange .... ***S. cerebriforme***

4. Thallus P-; ascospores 6-8 (-.9) septate, hyaline, becoming brown when old ..... ***Sclerophyton*** sp.
4. Thallus P+ orange; ascospores 4-7 septate, brown at maturity 5

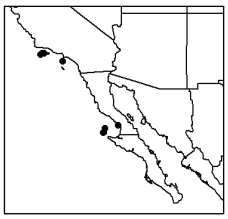
5. Ascospores 30-42 (-45) x 6-8 µm, 5-7 septate, on trees . ..... ***S. rostratum***
5. Ascospores 17-19 (-26) x 5-7 µm, 4-6 (-7) septate; on rocks ..... ***S. circumscriptum***

The Species

Sclerophyton californicum (Tuck.) Hasse, Bryologist 12: 101 (1909).

Basionym: *Chiodecton californicum* Tuck., Syn. North Amer. Lich. 2: 135 (1888); Illustration: Egea and Torrente (1995), p. 209.

Thallus: crustose, effuse, continuous to cracked-areolate, sometimes bullate, up to 1.5 mm thick; **upper surface:** creamy white to yellowish or geenish, smooth to slightly verrulose; **upper cortex:** up to 25 µm thick, composed of interwoven hyphae with hyaline tips; **medulla:** white, cretaceous; **lower cortex:** absent; **prothallus:** often present, thin, smooth, black; **Ascomata:** perithecioid and lirellate or apothecioid, usually aggregated into stroma-like structures, 1-3 mm diam., with slightly constricted base, usually with more than 7 ascomata surrounded by a thin slightly elevated thalline margin; lecanoroid ascomata: roundish to ± irregular, 0.4-1.2 mm diam., sessile with a constricted base, smooth, entire or crenulate; disc: plane, black, with whitish pruina; proper exciple: up to 15 µm thick, dark brown; hypothecium: carbonaceous or dark brown, extending to medulla or substrate; hymenium: 140-160 µm thick, I+ reddish, K/I+ pale blue; **asci:** 56-70 x 16-19µm, 8-spored; **ascospores:** ellipsoid to oblong-fusiform, hyaline when young, brown at maturity, 22-30 (-32) x 5-8 (-9) µm, (3-) 5-7 septate, constricted at each septum, with thick gelatinous sheath; **Pycnidia:** laminal, pyriform, up to 0.25 mm tall and 0.18 mm wide; walls: colorless or reddish brown at upper part; **conidia:** filiform, curved, 18-25 x 1 µm; **Spot tests:** thallus and medulla K- or K+ yellowish, C+ reddish, KC-, P-; **Secondary metabolites:** lecanoric acid (major) and erythrin.



Substrate and ecology: on bark and rocks; **World** and **Sonoran distribution:** along the coast (including the Channel Islands) from San Luis Obispo County, California, southwards to Baja California.

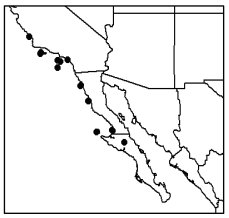
Notes: At an early stage of development the ascomata resemble those of *S. circumscriptum*, but they become quite different with age.

Sclerophyton cerebriforme Egea & Torrente, Bryologist 98: 211 (1995).

Illustration: Egea and Torrente (1995), p. 210.

Thallus: crustose, effuse, continuous to rimose or verrucose, sometimes bullate, up to 0.6 mm thick; **upper surface:** white to geenish, smooth to slightly verrulose; **upper cortex:** up to 40 µm thick, composed of interwoven hyphae with hyaline tips; **medulla:** white, cretaceous; **lower cortex:** absent; **prothallus:** often present, thin, smooth, black; **Ascomata:** lirellate to dendroid, immersed, usually aggregated into rounded or elongate, slightly elevated stroma-like structures, usually with many ascomata surrounded by a thin, white rim; disc: plane, narrow, slit-like, black, with whitish pruina; proper exciple: up to 15 µm thick, dark brown; hypothecium: dark brown, extending to the substrate; hymenium: 300-350 µm thick, I+ reddish, K/I+ pale blue; **asci:** 125-160 x 25-30µm, 8-spored; **ascospores:** oblong-fusiform to fusiform, hyaline when young, brown at maturity, 30-40 x 8-12 µm, 6-9 (-10) septate transversely and 1-2 septate logitudinally, constricted at each septum, with thick gelatinous sheath; **Pycnidia:** laminal, subglobose, up to 0.25 mm tall and 0.20 mm wide; walls: colorless or reddish brown at upper part; **conidia:** filiform, curved, 13-20 x 1 µm; **Spot tests:** thallus and medulla K- or K+ yellowish, C+ reddish, KC-, P-; **Secondary metabolites:** lecanoric acid (major) and erythrin.

Substrate and ecology: on rocks in coastal habitats; **World** and **Sonoran distribution:** along the coast (including the Channel Islands) from San Luis Obispo County, California, southwards to Baja California.



Notes: At an early stage of development the ascomata resemble those of *S. circumscriptum*, but they become quite different with age.

Sclerophyton circumscriptum (Taylor) Zahlbr., Engler & Prantl, Natürl. Pflanyenfam. I: 10 (1905).

Basionym: *Verrucaria circumscripta* Taylor, Syn. Fl. Hibern. 2: 96 (1836); Illustration: Egea and Torrente (1995), p. 212.

Thallus: crustose, effuse, continuous to rimose or verrucose, sometimes bullate, up to 0.3 mm thick; **upper surface:** white; creamy or grayish, smooth, slightly farinose; **upper cortex:** lacking but with an epinecral layer with some scattered, hyaline hyphae; **medulla:** white, cretaceous; **lower cortex:** absent; **prothallus:** often present, thin, smooth, black; **Ascomata:** perithecioid, up to 0.3 mm diam., immersed, rounded, oval or elongate, usually numerous, scattered or often in groups or dispersed in flexuose or radiating lines, not aggregated into stroma-like structures; thalline margin: undifferentiated; disc: plane, black, with whitish pruina; proper exciple: up to 15 µm thick, brown above, pale below; hypothecium: pale brown, fusing with medulla; hymenium: 100-150 µm thick, I+ blue, K/I+ pale blue; **asci:** cylindrical, 70-95 x 15-19µm, 8-spored; **ascospores:** oblong-ovoidal to oblong-fusiform, dark brown, (17-) 19-26 x 5-7 µm, 4-6 (-7) septate, constricted at each septum, with thick gelatinous sheath; **Pycnidia:** not seen; **Spot tests:** thallus and medulla K- or K+ yellowish, C-, KC-, P+ yellow (orange); **Secondary metabolites:** psoromic acid (major) and 2'-*O*-demethylpsoromic acid (minor).

Substrate and ecology: on rocks in coastal habitats; **World distribution:** SW North America, western Europe and the Carribean **Sonoran distribution:** Baja California.

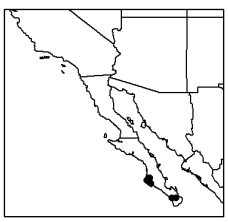
Notes: Specimens from Baja California have slightly fewer septa than European specimens, but no other differences have been found.

Sclerophyton rostratum Egea & Torrente, Bryologist 98: 214 (1995).

Illustration: Egea and Torrente (1995), p. 213.

Thallus: crustose, effuse, rimose to areolate, sometimes bullate, up to 0.4 mm thick; **upper surface:** creamy white to greenish, smooth to verrulose; **upper cortex:** up to 30 µm thick, composed of interwoven hyphae with hyaline tips; **medulla:** white, cretaceous; **prothallus:** often present, thin, smooth, black; **Ascomata:** perithecioid, punctiform, up to 0.5 mm diam., immersed or subimmersed, rounded, oval, or elongate, scattered or often united and lirellate, aggregated into stroma-like structures without a constricted base, surrounded by a thin thalline margin or undifferentiated; disc: plane, black, with whitish pruina; proper exciple: up to 10 µm thick, pale brown; hypothecium: pale brown, fusing with the medulla; hymenium: hyaline, 300-350 µm thick, I+ reddish, K/I+ pale blue; subhymenium: pale brown, up to 50 µm thick; **asci:** 100-120 x 20-23µm, 8-spored; **ascospores:** ellipsoid-fusiform, with lower end tapering to narrow apex, hyaline when young, brown at maturity, 30-42 (-45) x -8 µm, (3-) 5-7 septate, constricted at one (rarely more) septum, with thick gelatinous sheath; **Pycnidia:** laminal, subglobose, up to 0.35 mm tall and 0.25 mm wide; walls: colorless or reddish brown at upper part; **conidia:** filiform, curved, 14-18 x 1 µm; **Spot tests:** thallus and medulla K- or K+ yellowish, C-, KC-, P+ yellow (orange); **Secondary metabolites:**. psoromic acid (major) and 2'-*O*-demethylpsoromic acid (minor).

Substrate and ecology: on bark in the Magdalena region of the Sonoran Desert; **World** and **Sonoran distribution:** only known from two nearly coastal localities in Baja California Sur.



Note: The submuriform spores are unique among the group.

Sclerophyton sp., Bryologist 98: 214 (1995).

Illustration: Egea and Torrente (1995), p. 214.

Thallus: crustose, effuse, rimose, up to 0.2 mm thick; **upper surface:** white to yellowish, smooth to verrulose; **upper cortex:** lacking but with an epinecral layer with some scattered, hyaline hyphae; **medulla:** white, cretaceous; **lower cortex:** absent; **prothallus:** often present, thin, smooth, black; **Ascomata:** perithecioid, up to 0.4 mm diam., immersed, rounded, oval, or elongate, not aggregated into stroma-like structures; thalline margin: undifferentiated; disc: plane, black; proper exciple: up to 10 µm thick, hyaline to pale below; hypothecium: hyaline to pale below, fusing with the medulla; hymenium: up to 150 µm thick, I+ blue, K/I+ pale blue; **asci:** *c.* 80 x 17 µm, 8-spored; **ascospores:** oblong-fusiform to fusiform, hyaline when young, brown in inner part at maturity, 24-33 (-35) x 5-7 (-8) µm, 6-8 (-9) septate, constricted at one septum, with thick gelatinous sheath; **Pycnidia:** not seen; **Spot tests:** thallus and medulla K- or K+ yellowish, C-, KC-, P-; **Secondary metabolites:** an unknown.

Substrate and ecology: on bark; **World** and **Sonoran distribution:** only known from one coastal locality in Orange County in southern California.

SIGRIDEA

by A. Tehler

Sigridea Tehler, Crypt. Bot. 3: 145 (1992).

Family: Roccellaceae; Type: *Sigridea californica* (Tuck.) Tehler; No. species: five world-wide; Selected lit.: Tehler (1993b).

Life habit: lichenized; **Thallus:** crustose, effuse; **surface:** white, 0.1-0.5 mm thick, smooth to rugose to verrucose, epruinose or finely pruinose; soredia absent; **cortex:** usually present but sometimes absent, 10-25 µm thick; hyphae interwovenly arranged, hyaline; **medulla:** very thin sometimes indiscernible; **photobiont**: primary one a *Trentepohlia*, secondary photobiont absent; **Ascomata:** apothecioid, numerous, solitary, circular in outline, sometimes undulating, elevated with constricted base, (0.2) 0.5-1 (1.6) mm diam.; disc: exposed, pruinose; exciple: cortex and algae usually present but sometimes absent; proper exciple: parathecial, but sometimes thin; epithecium: brown or brownish, branched or richly branched hyphae; hymenium: 70-100 µm thick with paraphysoids parallel, sparsely branched, hyaline, 1 µm diam.; hypothecium: dark-brown (carbonaceous), extending down to substrate; **asci:** clavate, 50-80 x 10-15 µm, 8-spored; **ascospores:** fusiform, curved, 3-septate, hyaline; **Conidiomata:** pycnidial, solitary, immersed or slightly elevated, dark brown; **conidia:** bacilliform, curved, simple, hyaline; **Secondary metabolites:** ß-orcinol depsides; **Geography:** predominantely subtropical regions and occurring in some mediterranean areas; **Substrate:** on bark.

The Species

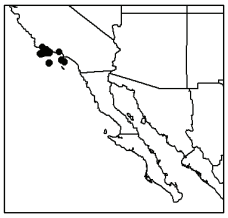
Sigridea californica (Tuck.) Tehler, Crypt. Bot. 3: 145 (1993).

Basionym: *Dirina californica* Tuck., Lichens of California, 422 (1866); Synonyms: *Dirina hassei* Zahlbr. and *Schismatomma californicum* (Tuck.) Zahlbr.; Illustrations: Tehler (1985), p. 210 as *Schismatomma californica* and Tehler (1993b), p. 430.

Thallus: crustose, effuse; **upper surface:** white, 0.1-0.3 mm; **cortex:** 10 µm thick, sometimes poorly developed; **medulla:** white; **"Apothecia":** sometimes slightly undulating, sessile, 0.2-1 mm diam.; disc: convex, strongly white pruinose; exciple: protruding above the disc, with cortex and algae but sometimes without cortex; proper

exciple: thin; epithecium: 10-20 µm thick, light brown to brown; hymenium: 60-70 µm high; paraphysoids: sparsely branched, parallel, hyaline, *c.* 1 µm in diam.; **asci:** clavate, 50-60 x 10-15 µm, 8-spored; **ascospores:** 13-15 x 3-4 µm; **Pycnidia:** 0.1 mm diam; **conidia:** bacilliform, 2-4 x 1-2 µm; **Spot tests:** thallus K- or yellowish, C-, KC-, P+ yellow; **Secondary metabolite:** psoromic acid.

Substrate and ecology: growing on the trunks of trees and shrubs, such as *Quercus*, *Heteromeles*, *Adenostoma*, and *Pinus* but it is also lignicolous and often found on fence poles or unpainted wood, very rarely on rocks; **World distribution:** distributed in coastal regions from southern Oregon southwards to northern Baja California; **Sonoran distribution:** southern California.



SOLENOPSORA

by B.D. Ryan & E. Timdal

Solenopsora A. Massal., Frammenti lichenografici: 20 (1855).

Family: Catillariaceae; Type: *Solenopsora requienii* A. Massal. (= *S. holophaea* (Mont.) Samp.); No. species: 10-15 world-wide; Selected lit.: Ryan and Timdal (in prep.).

Life Habit: lichenized, not lichenicolous or sometimes possibly on cyanophilic lichens; **Thallus:** crustose, effigurate, squamulose, or placodioid, attached by the lower surface or by rhizines, appressed or with free lobe tips; **hypothallus:** present or absent; **areoles/squamules:** dispersed or adjacent or imbricate, up to 1.5 mm wide, rounded, crenulate, lobed or with incised margins, blastidia and soralia present or absent; **upper surface:** white, gray, light green, or light to dark brown; dull or shiny, smooth, pruinose or not; **upper cortex:** usually well developed and consisting of an upper epinecral layer and a lower stainable layer, the latter composed of irregularly or predominantly anticlinally oriented hyphae, containing remnants of algae (chlor-zinc-iodine!) and often crystals of secondary metabolites; **medulla:** white, of intricately interwoven hyphae, not amyloid or weakly amyloid; **photobiont:** primary one a chlorococcoid alga, secondary photobiont absent; algal cells: 10-15 µm in diam.; algal layer: horizontally continuous or interrupted by strands of cortical tissue; **lower cortex:** present or absent; **lower surface:** white to pale brown; **Ascomata:** apothecial, lecanorine, circular, laminal to submarginal, subimmersed, sessile, or substipitate, with a more or less prominent, often disappearing thalline margin; up to 1 mm in diam.; disc: medium brown to brownish black, pruinose or not; exciple: pale to medium brown; hypothecium: hyaline to pale brown, lacking crystals; epithecium: pale to medium brown, K-, N-; hymenium: hyaline, amyloid, 40-70 µm high; paraphyses: weakly conglutinated, thin-walled, sparingly branched and anastomosing, often with a swollen apical cell, often with a sharply delimited, brown cell wall pigment in the upper part of the apical cell; **asci:** clavate, with a well developed, evenly deeply amyloid tholus lacking an ocular chamber (*Catillaria*-type), 8-spored; **ascospores:** 1-septate, ellipsoid to shortly bacilliform, often slightly constricted at the septum, hyaline, smooth, 6-20 x 3-6 µm; **Conidiomata:** pycnidial, laminal, immersed; **conidia:** pleurogenously formed, shortly bacilliform, 2-6 x *c.* 1 µm; **Secondary metabolites:** orcinol and β-orcinol depsidones, triterpenes and unidentified compounds; **Geography:** temperate and subtropical regions of the world, center of diversity in Mediterranean Europe and North Africa; **Substrate:** rock and soil, especially calcareous substrates.

Notes: The *Catillaria*-type ascus and the pleurogenous, bacilliform conidia place *Solenopsora* in the Catillariaceae. The genera *Catillaria* A. Massal. and *Placolecis* Trevis. differ in having lecideine apothecia. In addition, *Placolecis* has simple ascospores. *Halecania* M. Mayrhofer differs in having halonate ascospores.

Some *Solenopsora* species (e.g. *S. candicans* and *S. olivacea*) have effigurate, placoidioid thalli, but none of these are known from the Sonoran region.

Key to the species of ***Solenopsora*** in the Sonoran region:

1. Squamules brittle, ascending from the base, often forming cushions; algal layer forming major part of squamule; medulla lacking; upper cortex poorly defined ..... ***S. cladonioides***
1. Squamules not brittle, not ascending from the base, not forming cushions; upper cortex and medulla well developed 2
   2. Squamules convex, crenulate or minutely lobed, appressed or at most with free lobe tips; spores narrowly ellipsoid to shortly bacilliform, 13-21 µm long ..... ***S. crenata***
   2. Squamules concave to plane, with well developed lobes, usually with the major part of the underside free from the substrate; spores medium ellipsoid, 9-12 µm long ..... ***S. chihuahuana***

The Species

Solenopsora "chihuahuana" B. D. Ryan & Timdal, in prep.

Illustration: Fig. 94 to right.

Thallus: squamulose; **squamules**: up to 1.5 mm diam., concave to plane, deeply lobed, usually with the major part of the underside free from the substrate; **hypothallus**: absent; **upper surface**: light green to light brown, more or less pruinose towards the lobe tips; margins: not thickened; vegetative diaspores: absent; **upper cortex**: up to 45 µm thick, composed of anticlinally oriented hyphae covered by crystals which are, at least partly, insoluable in K, containing scattered remnants of algae (chlor-zinc-iodine!), with a thin epinecral layer; **medulla**: containing crystals which are, at least partly, not dissolving in K, I+ faintly blue; **algal layer:** continuous; **lower cortex**: poorly developed; **lower surface**: whitish; rhizines absent; **Apothecia**: up to 1 mm diam., more or less immersed when young, becoming sessile and often constricted at the base, plane and marginate when young, becoming more or less convex and immarginate, medium to dark brown, pruinose; **ascospores**: ellipsoid, 1-septate, hyaline, 9-12 x 3.5-5 µm; **Pycnidia**: immersed; **conidia**: shortly bacilliform, 3-4 x *c.* 1 µm; **Spot tests**: K-, C-, KC-, P+ orange (medulla) or P- (cortex); **Secondary metabolites**: pannarin, zeorin, and undetermined secondary products.

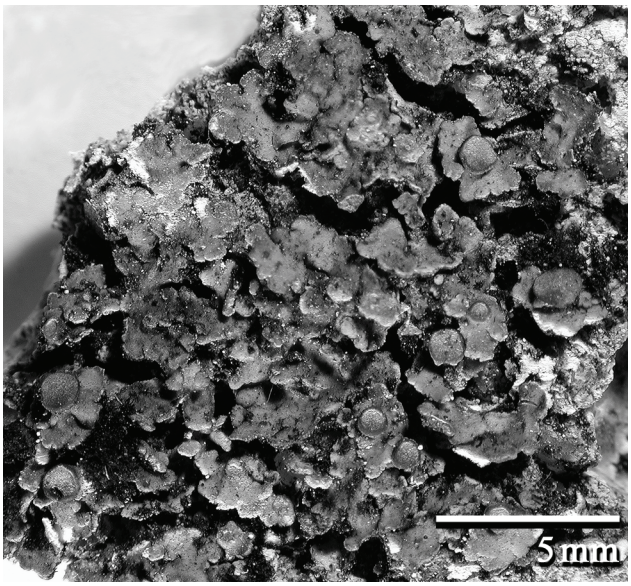


Fig. 94. *Solenopsora chihuahuana*, photo by E. Timdal.

Substrate and ecology: on or among cyanolichens on a steep to overhanging rock face, in Madrean oak-pine forest at 1800 m (single locality); **World** and **Sonoran distribution**: Barranca del Cobre, Chihuahua.

Notes: *Solenopsora chihuahuana* has flattened to concave squamules in contrast to the convex squamules of *S. crenata*, and the spores of *S. chihuahuana* are substantially shorter than those of *S. crenata*. Neither of the species are as brittle as the upright *S. cladonioides* (below).

Solenopsora "cladonioides" B. D. Ryan & Timdal, in prep.

Illustration: Fig. 95 on next page.

Thallus: squamulose, often forming small cushions; **squamules**: up to 1.5 mm diam., concave or plane, brittle, as-

cending from the base; **hypothallus**: absent; vegetative diaspores: absent; **upper surface**: light green to light brown, epruinose; **upper cortex**: poorly developed, containing crystals which are, at least partly, not dissolving in K; **medulla**: lacking; **algal layer**: forming major part of squamule, consisting of algal colonies interspersed by strands of chondroid hyphae, containing crystals which are, at least partly, not dissolving in K, I-; **lower cortex**: similar to upper cortex; **lower surface**: pale brown to white; rhizines: absent; **Apothecia**: up to 1 mm diam., constricted at the base, sometimes substipitate, plane and marginate when young, sometimes becoming convex and immarginate, medium brown to brownish black, pruinose; **ascospores**: ellipsoid, 1-septate, hyaline 9-11 x 4-4.5 µm; **Pycnidia**: immersed; **conidia**: shortly bacilliform, 2.5-3 x *c.* 1 µm; **Spot tests**: K-, C-, KC-, P+ orange; **Secondary metabolites**: pannarin, zeorin, and undetermined secondary products.

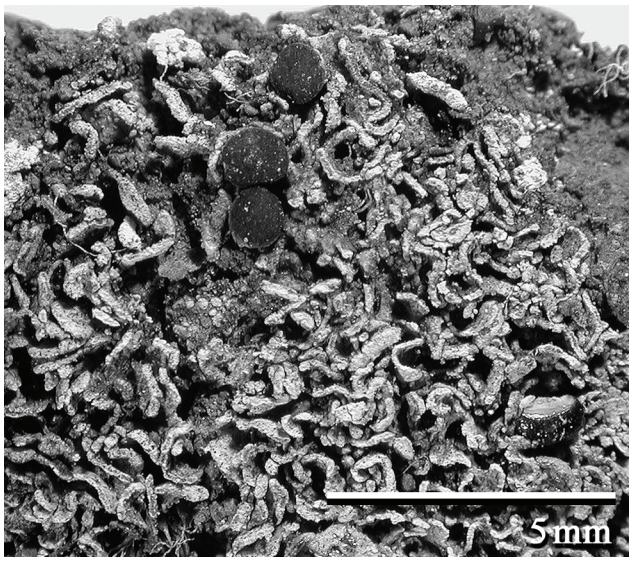
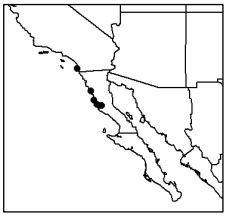


Fig. 95. *Solenopsora cladonioides*, photo by E. Timdal.

Substrate and ecology: on soil in open habitats, in Vizcaino subdivision of Sonoran desert and in Californian coastal scrub, up to 500 m; **World** and **Sonoran distribution**: California and Baja California, rare.



Notes: *Solenopsora cladonioides* has upright squamules that are reminiscent of basal *Cladonia* squamules. Furthermore, its algal layer forms a major portion of the squamules and is inspersed with strands of chondroid hyphae. Its medulla is more clearly defined than in other *Solenopsora* species.

Solenopsora crenata (Herre) Zahlbr., Catal. lich. univers. 5: 755 (1928).

Basionym: *Placolecania crenata* Herre, Proc. Wash. Acad. Sci. 12: 190. 1910; Illustration: Fig. 96 below.

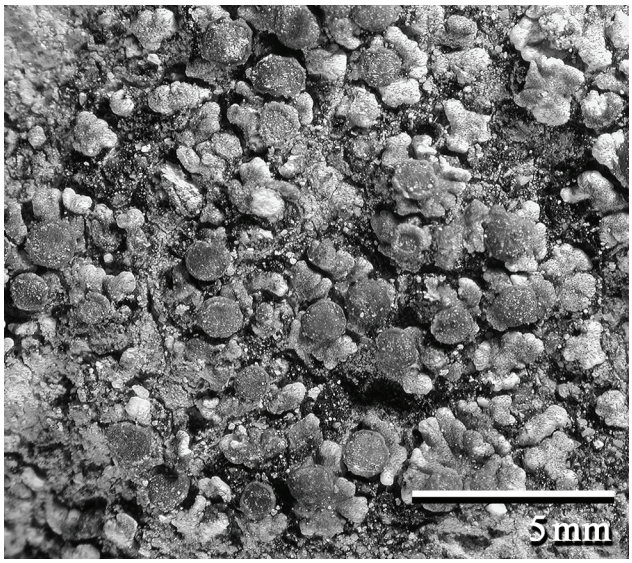


Fig. 96. *Solenopsora crenata*, photo by E. Timdal.

Thallus: squamulose; **squamules**: up to 1 mm diam., thick, convex, crenulate or minutely lobed, appressed or at most with free lobe tips; **hypothallus**: absent; **upper surface**: white to light gray or pale yellowish-brownish, epruinose or pruinose; vegetative diaspores: absent; **upper cortex**: well developed, up to 100 µm thick, stainable layer composed of mainly anticlinally oriented hyphae interspersed with algal remnants (chlor-zinc-iodine!) and crystals which, at least partly, do not dissolve in K, with a thick epinecral layer; **medulla**: I+ faintly blue, containing crystals which, at least partly, do not dissolve in K; **algal layer:** dis-

continuous, interrupted by conical strands of upper cortex; **lower cortex**: thick, white, poorly defined from medulla; **lower surface:** pale brown to white, rhizines: absent; **Apothecia**: up to 1 mm diam., sessile, becoming constricted at the base, plane and marginate when young, becoming convex and immarginate, dark brown, pruinose; **ascospores**: narrowly ellipsoid to shortly bacilliform, 1-septate, hyaline 13-21 x 4-5 µm; **Pycnidia**: immersed; **conidia**: shortly bacilliform, 3-3.5 x *c.* 1 µm; **Spot tests**: K-, C-, KC-, P+ orange; **Secondary metabolites**: pannarin, zeorin, and undetermined secondary products.

Substrate and ecology: on soil and rock in open habitats near the coast, up to 150 m; **World distribution**: southern and central coast of California; **Sonoran distribution**: Channel Islands, southern California, rare.

Notes: *Solenopsora crenata* is characterized by its small, white to light gray, crenulate to minutely lobed squamules. It is morphologically similar to *S. carpatica*, but that species has more ascending squamules and shorter spores.

SPILONEMA

by M. Schultz

Spilonema Bornet, Mem. Soc. Imp. Scienc. Nat. Cher. 226: (1856).

Family: Coccocarpiaceae; Type: *Spilonema paradoxum* Bornet; No. species: four world-wide; Selected lit.: Henssen (1963a).

Note: Because the genus is monotypic, a generic description would simply recapitulate the specific description given below.

The Species

Spilonema revertens Nyl., Flora 48: 601 (1865). Synonyms: see Henssen (1963); Illustrations: Henssen (1963a), plates 24e & 25d, and Fig. 97 to right.

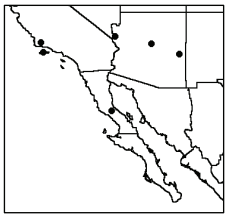
Life habit: lichenized; **Thallus:** filamentous, subfruticose to dendroid, composed of tiny erect or rarely decumbent lobules which carry numerous, minute side branches, with roundish to angular, convex cushions, sometimes becoming areolate and then appearing crustose, attached to the substrate by a hypothallus composed of interwoven bluish-black hyphae, gelatinous when wet; **upper surface:** dark olive to blackish, rough, sometimes granulose, rarely shiny, rough or granulose, rarely shiny; **lower surface:** dark blue-green, brownish, dark purple to blackish due to the presence of colored hypothallus, rarely with pale rhizines; **anatomy:** ecorticate, homoiomerous, a dense network of thick hyphae, in basal parts sometimes paraplectenchymatous;

Fig. 97. *Spilonema revertens*, photo by M.Schultz.

photobionts: a filamentous cyanobacterium, *Stigonema* or *Hyphomorpha*, secondary photobiont absent; **Ascomata:** apothecial, sessile, lecideine, lateral on the thallus lobules, usually hidden within the cushions, up to 0.5 mm wide; disc: black, convex from the beginning, thalline margin absent; exciple**:** violaceous, thin, becom-

ing excluded, composed of radially orientated hyphae; epihymenium: brownish to dark violaceous; hymenium: greenish or partly violaceous, amyloid; paraphyses: robust, distinctly septate, sparingly branched, with pointed tips; hypothecium: violaceous; **asci:** lecanoral, wall thick, with amyloid tip, 8-spored; **ascospores:** at first simple, later septate, rarely mature, hyaline, ellipsoid, 7-9 (11) x 2.5-3.5 (-6) µm; wall: thin, hyaline; **Conidiomata:** pycnidial, sessile, simple, globose, up to 0.2 mm wide; **conidia:** small, bacilliform or ellipsoid, *c.* 2.5 x 1 µm; **Spot tests:** all negative; **Secondary metabolites:** none detected.

Substrate and ecology: on siliceous rock, on sheltered, steep faces of boulders in damp places or along lake shores, often associated with *Psorula rufonigra*; **World distribution:** cosmopolitan, mostly arctic to temperate regions of the Northern Hemisphere; **Sonoran distribution:** Arizona, southern California, Baja California, Baja California Sur, Sonora and Chihuahua, mostly between 1000 and 2700 in montane areas.



Notes: The species is distinguished from other cyanolichens by the tiny fruticose, ecorticate lobes and the presence of a bluish-black hypothallus. *Spilonema paradoxum* is very similar but the cushions are less tightly aggregated, the lobes are rarely erect and the apothecia and pycnidia are usually not hidden in the cushions. *Spilonema revertens* is the host of the parasitic lichen *Psorula rufonigra*.

Some species of *Ephebe* and *Lichinella* are similar, however, they never develop a dark hypothallus and always possess a thalline margin surrounding the apothecia. *Thermutis* lacks a thalline apothecial margin but the photobiont is a species of *Scytonema* whose filaments are surrounded by hyphae. *Polychidium* is also similar but is distinguished by its corticate lobes.

SQUAMARINA

by B. D. Ryan

Squamarina Poelt, Mitt. Bot. Staatssaml. München 2: 524 (1958) [emend Hafellner, Beih. Nova Hedwigia 79: 342 (1984)].

Family: "Squamarinaceae" Hafellner (1984); Type: *Squamarina gypsacea* (Sm.) Poelt; No. species: *c.* 20 worldwide; Selected lit.: Poelt (1958), Hafellner (1984) and Feige et al. (1997).

Life habit: lichenized; **Thallus:** squamulose or placodioid-subfoliose, tightly to somewhat loosely attached, most species 1.5-2.5 cm wide (but some species up to 10 cm wide), usually 1-2 mm thick (some species forming mats up to 2 cm thick); **thallus center:** rimose-areolate to squamulose; **lobes:** usually large (compared to those of lobate species of *Lecanora*), very stiff; **upper surface:** usually ± greenish yellow when fresh, to brownish or grayish, often at least partly white due to pruina, continuous to rimose, ± smooth; isidia and soredia: absent, phyllidia-schizidia: present or absent; cephalodia: absent; **upper cortex:** evenly very thick (compared to most lobate species of *Lecanora*; 50-100 µm or more), sharply delimited, without dead algal cells; inspersed with yellowish granules (soluble in K); **medulla:** prosoplectenchymatous, thick, chalky; hyphae: strongly conglutinated, ± thick-walled, with wide to narrow lumina; **photobiont:** primary one a trebouxioid alga, secondary photobiont absent; algal layer: well-delimited, continuous, rather narrow; **lower cortex:** absent; **lower surface:** pale or dark; rhizinose strands, varying from taproot-like branched cords with compact medulla and firm outer surface (*Squamarina*-type) to a looser rhizohyphal felt (*Placidium*-type), depending on the species; **Ascomata:** apothecial, usually laminal, circular or irregular, subimmersed to sessile, lecanorine to occasionally biatorine (varying on the same thallus); disc: mostly yellow-brown to red-brown, pruinose or not; thalline margins: prominent or not,: thick, similar in structure to that of thallus; algal layer: present

under hypothecium, often absent from the margin; true exciple: sometimes evident externally, hyaline or ochraceous-yellowish; hymenium: gel hyaline, euamyloid; uppermost part hyaline or ochraceous-yellowish, inspersed with fine granules or (when discs pruinose) covered with coarser granules; paraphyses: septate, not (or scarcely) branched and anastomosing; hypothecium: hyaline or ochraceous-yellowish, thick; **asci:** ± narrowly clavate, lecanoral; wall: euamyloid; tholus: appearing uniformly amyloid and lacking non-amyloid axial body but with small ocular chamber (Hafellner 1984), and with a regular, narrowly cylindric, deeply amyloid central tube (Timdal 1991; Haugan and Timdal 1992), 8-spored; **ascospores:** biseriately arranged, simple, ellipsoid or cylindrical-ellipsoid or oblong, 9-15 (-19) x 4.5-7.5 µm; wall: hyaline, smooth, thin, non-halonate, not amyloid; **Conidiomata:** pycnidial, immersed; **conidia:** formed acrogenously, filiform, ± curved, *c.* 15-40 x ≤ 1 µm; **Secondary metabolites:** cortex with usnic acids (sometimes only traces); medulla with or without ß-orcinol depsidones or (in an undescribed species) terpenoids; **Geography:** Northern Hemisphere in arid and semi-arid regions; **Substrate:** bryophytes, soil, detritus, or usually calcium-rich rock.

Notes: For an introduction to the difficult nomenclatural and taxonomic history of this genus, see Ryan and Nash (1997b); in this Flora the present treatment covers only the core group of *Squamarina*; the species of "sect. *Petroplaca*", which have a *Lecanora*-type ascus (with distinct non-amyloid axial mass) will be treated in Volume II, potentially as a different genus with the Lecanoraceae.

The Species

Squamarina lentigera (G. H. Weber) Poelt, Mitt. bot. Staats. München 2: 536 (1958).

Basionym: *Lichen lentigerus* G. H. Weber, Spic. Fl. Goetting: 192 (1778); Synonyms: *S. kansuensis* (H. Magn.) Poelt; for further synonomy see Poelt (1958); Illustrations: Hale (1979), p. 230; Vitt et al. (1988), p. 189 [highly pruinose form]; McCune and Goward (1995), p. 160; Brodo et al. (2001), p. 661; and Fig. 98 to right.

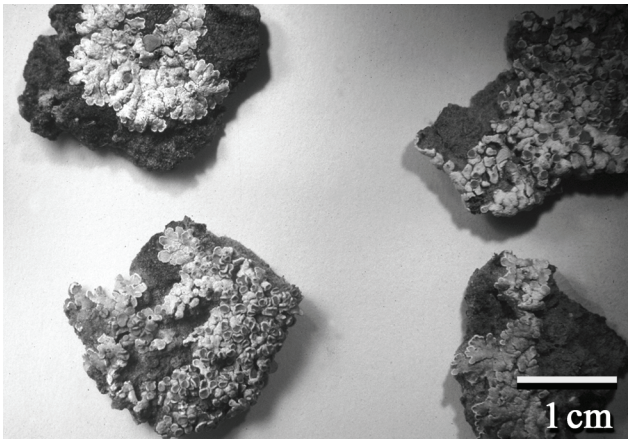


Fig. 98. *Squamarina lentigera*, photo by B. Ryan.

Thallus: tightly adnate, up to 3 cm across, up to 1-2 mm thick, ± distinctly rosetted, not imbricated, not mat forming; thallus center: areolate; **areoles:** plane to convex, 0.5-1 mm across, sometimes strongly wrinkled to verrucose (partly due to abundant apothecial primordia); **lobes:** 2-4 mm long, 0.5-2 (-3) mm wide, coarsely crenate-incised; edges: raised and thickened; **upper surface:** pale or light greenish yellow to grayish greenish yellow, mostly epruinose except on lobe edges, or appearing yellowish white from pruina, especially on lobe edges and spottily in thallus center, sometimes wrinkled, especially in thallus center; **upper cortex** *c.* 50 µm thick, ± gelatinized, of mostly anticlinal hyphae; epinecral layer *c.* 10 µm thick; **medulla** with grayish granules (insoluble in K); algal layer: *c.* 30 µm thick [up to 50 µm or more in non-Sonoran material], ± continuous; algae *c.* 10-12 µm diam.; **lower surface:** pale, rarely darkening; rhizinose strands: rather few and inconspicuous, 0.5 mm long, *Psora*-type (intermediate between *Squamarina*-type and rhizohyphal felt); **Apothecia:** usually common and crowded in thallus center, up to 1 mm diam., but often smaller; disc: epruinose, plane to slightly convex, moderate orangish yellow, yellowish brown or with pinkish-orange tinges, sometimes darkened by parasites, plane to convex; thalline margin: 0.1 mm wide, entire, pruinose, soon excluded; amphithecial hyphae: radially arranged; algal layer: mainly below hypothecium, thick, continuous; true exciple: not evident externally; hymenium: *c.* 65-75 µm high, uppermost *c.* 10-20 µm pigmented; paraphyses: ± loosely coherent, *c.* 2-2.5 µm thick; tips: hyaline, little thickened;

hypothecium: of unoriented hyphae; **asci:** narrowly clavate, *c.* 35-45 x 10-12 µm, 8-spored; **ascospores:** mostly immature, in ascus ellipsoid, 10 x 4.5 µm [mature spores in non-Sonoran material *c.* 8-12 x 5-6 µm]; **Pycnidia:** uncommon or inconspicuous; ostioles: yellowish to dark olivaceous brown; **conidia:** *c.* 18-35 x ≤ 1 µm [based on non-Sonoran material]; **Spot tests:** cortex: K+ yellow or K-, C-, KC+ yellow, P-; medulla: K-, KC-, C-, P- or P+ yellow; **Secondary metabolites:** cortex: with usnic acid (major), and sometimes also isousnic acid (minor); medulla: with or without psoromic acid chemosyndrome or various unidentified substances; psoromic and non-psoromic chemotypes present in the Sonoran region and other warm areas; reports of atranorin (e.g., by Hale 1979) are apparently based on misidentification of isousnic acid.

Substrate and ecology: on sandy, calcareous soil in arid areas, montane **World distribution:** Europe, Asia, North America; **Sonoran distribution:** northern Arizona, 910-1615 m.

Notes: Although the map in Hale (1979) suggests that the species extends into southern California, I have seen no material of *Squamarina* s. str. from that state. As discussed by Ryan and Nash (1997b), Röser (1996) and Feige et al. (1997), this species includes specimens with P+ yellow medulla (psoromic acid), which in China has gone under the name of *S. kanusensis*. Although the species can be rather variable and sometimes problematic (especially in more northern parts of North America), the limited amount of Sonoran material seems to be rather uniform and quite similar in morphology and anatomy to most European material.

STAUROTHELE

by J. W. Thomson

Staurothele Norm. Nom. Conserv., Nyt. Mag. Naturvid. 7: 240 (1853).

Family: Verrucariaceae; Type : *Staurothele fuscocuprea*; No. species: *c.* 40 world-wide; Selected lit.: de Lesdain (1932), Swinscow (1963) and Thomson (1991).

Life habit: lichenized**; Thallus:** crustose, sometimes embedded in substrate and nearly invisible, or smooth or rimose-areolate to bullate areolate, sometimes with radiating marginal areoles, some species very dendroidly arranged; **upper surface:** gray or various shades of brown, smooth; **upper cortex:** lacking or rudimentary, algae often found within upper thallus layers; **medulla:** white; **photobiont:** primary one an alga (*Stichococcus*), secondary photobiont absent; cells: irregularly distributed throughout; **lower cortex:** absent; **hypothallus:** present or absent (most North American species); **Ascomata:** perithecial, simple (without a separate involucrellum) or compound (with darker involucrellum covering the exciple to the base), or subcompound (with a small involucrellum limited to the ostiole region), either embedded in substrate, sessile on the substrate, or within areoles of thicker thalli; apical ostioles: present; periphyses: present; paraphyses: lacking; hymenial gelatin: usually I+ blue in 2-spored species, I+ yellow or red in 8-spored species; hymenium: containing photobiont (*Stichococcus mirabilis* Lagerheim) which may be spherical or elongate; **asci:** saccate, verrucarioid, without a distinct ocular chamber, 1-(-8)-spored (when 2-spored the distal spore is usually larger than the basal one); **ascospores:**, hyaline or becoming brown, muriform, with many cells; **Conidiomata:** pycnidial, laminal, of *Dermatocarpon*-type; **conidia:** bacilliform, simple, colorless; **Secondary metabolites:** none detected; **Geography:** widespread in temperate to polar regions wherever open rock surfaces occur; sometimes submerged; **Substrate:** on or in various rocks (including calcareous and siliceous rocks) and made-made substrates (bricks, mortar, etc.).

Key to the speices of ***Staurothele*** in the Sonoran region:

1. Spores 1-2 per ascus 2

1. Spores 4-8 per ascus; thallus of tiny granular verrucules combined into areolate appearing units, greenish gray or ashy gray; perithecia with dimidiate involucrellum; spores hyaline, 18-32 x 10-25 µm ..... ***S. verruculosa***

2. Thallus with radiate areolae at margins 3
2. Thallus lacking radiate areolae at margins 4

3. Marginal areolae narrow and high convex .... ***S. drummondii***
3. Marginal areolae flattened ..... ***S. effigurata***

4. Perithecia surficial on the rock, thallus whitish or lacking ..... ***S. elenkinii***
4. Perithecia within the thallus areolae 5

5. Thallus with continuous zone toward periphery, interior smooth or chinky or areolate; perithecia immersed ..... ***S clopimoides***
5. Thallus entirely areolate or chinky areolate 6

6. Areolae more or less narrowed at base to appear somewhat spherical, sterile and fertile areoles of same size, ostiole with black involucrellum conspicuous around it ..... ***S. areolata***
6. Areoles rimose, not narrowed at base; perithecial mouth dark but neither ring-like nor pruinose 7

7. Thallus dark brown, smooth, often with radiate-lobed appearance, the "lobes" contiguous or widely separate, areoles rounded above, fertile larger than sterile peripheral ones ..... ***S. drummondii***
7. Thallus black or dark brown (in that case rough above), or greenish-yellow to olive gray or ashy, chinky areolate, the areoles rounded or flat 8

8. Thallus dark brown, of tiny angular areoles 0.1-0.2 mm broad; perithecium completely immersed and only tip of involucrellum visible; hymenial gelatin I-; spores 23-39 x 10-18 µm; on noncalcareous rocks ..... ***S. polygonia***
8. Thallus greenish yellow to olive gray, areoles 0.1-0.3 mm broad; perithecia with involucrellum projecting conspicuously above thallus and only partly embedded in thallus; hymenial gelatin I+ blue; spores 37-52 x 13-20 µm; on calcareous rock ..... ***S. monicae***

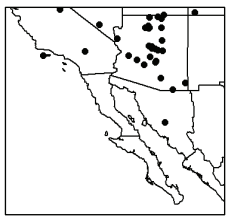
The Species

Staurothele areolata (Ach.) Lettau., Hedwigia 52: 84 (1912).

Basionym: *Pyrenula areolata* Ach., Synopsis Lich. 122 (1814); Synonyms: see Thomson (1991); Illustration: Thomson (1991), p. 353.

Thallus: crustose, of deeply cracked areolate to subsquamulose; **areoles:** strongly convex, 0.3-0.7 mm thick, from contiguous to dispersed, similar whether sterile or fertile; **surface:** dark brown or blackish brown; smooth; **prothallus:** absent; **Perithecia:** within larger areoles, only mouth showing with part of involucrellum which is thickened only near mouth (subcompound), black or dark brown, merging with thallus tissue; exciple: hyaline to pale brown, blackening toward mouth; **asci:** saccate, 2-spored; **ascospores:** ellipsoid or ovoid, dark brown, muriform with many cells, 20-50 x 15-25 µm; **Spot tests:** all negative; **Secondary metabolites:** none detected.

Substrate and ecology: on acid or basic rocks often near but not in water; **World distribution:** circumpolar temperate and boreal; western montane specimens range up to 3600 m and extending to central Mexico; **Sonoran distribution:** common in Arizona and scattered in southern California and Sonora where limestone occurs and on gneiss, schist and sandstone.



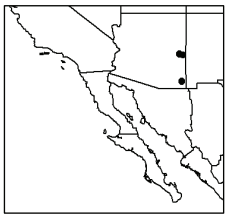
Staurothele clopimoides (Anzi *ex* Arnold) Stein., Ann. Naturh. Hofmuseum Wien 20: 383 (1907).

Basionym: *Sphaeromphale clopimoides* Anzi, Verh. Zool. -Bot. Ges. Wien 24: 250 (1874); Illustration: Thomson (1991), p. 353.

Thallus: crustose, areolate; **areoles:** smooth to deeply chinky; **surface:** coppery brown, smooth; **prothallus:** absent; **Perithecia:** entirely immersed in thallus with only flattened mouth projecting; **involucrellum:** pale-brown; exciple: pale-brown, dark above and merging with the in-

volucrellum for about 1/3 of the upper part; hymenial gelatin: blue then violet with I; **asci:** saccate, 2-spored; **ascospores:** ellipsoid or narrowly ellipsoid, finally dark brown, muriform, many celled, 38-50 x 14-21 µm; **Spot tests:** all negative; **Secondary metabolites:** none detected.

Subtrate and ecology: on granites and gneiss not far from water; **World distribution:** North America: Alaska to Arizona in the mountains; **Sonoran distribution:** only known from eastern Arizona.

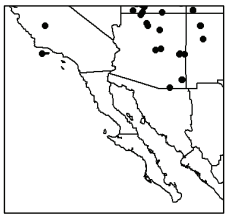


Staurothele drummondii (Tuck.) Tuck., Genera Lich. 257 (1872).

Basionym: *Verrucaria drummondii* Tuck., Proc. Amer. Acad. Arts & Sci. 6: 286 (1864); Synonyms: see Thomson (1991); Illustrations: Thomson (1991), p. 353; Brodo et al. (2001), p. 662.

Thallus: crustose, thin or thick; **areoles:** central ones thicker and larger than the peripheral ones, marginal ones may be contiguous and appearing radiate or becoming separate and dispersed-radiate; **surface:** brown or blackish brown, shining or dull; **prothallus:** sometimes present (particularly on quartz substrates), blackish, cobwebby; **Perithecia:** entirely within the central thallus verrucules, 0.4-0.6 mm wide, only the mouth visible, simple; exciple: hyaline, surrounded by a dark thalloid layer between it and the involucrellum; **involucrellum:** prominent and black, curving around most of the exciple; hypothecium: hyaline; hymenium: I+ blue; **asci:** saccate, 2-spored; **ascospores:** ellipsoid or narrowly ellipsoid, brown, muriform, up to 9-septate transversely and 3-septate longitudinally, 24-50 x 11-21 µm; **Spot tests:** all negative; **Secondary metabolites:** none detected.

Substrate and ecology: a species of irrigated depressions; **World distribution:** Eurasia, Greenland and western North America; **Sonoran distribution:** Arizona and California in the mountains from 150 to 3700 m.



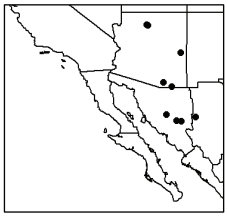
Notes: As noted in Thomson, (1991), when growing on smooth substrata this species is easily distinguished from *Staurothele areolata*, but on rough substrata the distinguishing smaller areoles of the periphery are harder to note. The fruiting and sterile areoles in *S. areolata* are nearly of the same size and abruptly cease at the margin, unlike the presence of the smaller, more rotund marginal areoles in *S. drummondii*. In Hasse's Exsiccati 237, it is reported as *Endocarpon wilmsoides*.

Staurothele effigurata J. W. Thomson, Bryol. 94: 397 (1991).

Illustration: Thomson (1991), p. 358.

Thallus: crustose, areolate; **areoles:** 0.3-1.0 mm broad, marginal ones forming radiating flattened squamules up to 2 mm long and 1 mm broad, black below; **surface:** gray; **prothallus:** absent; **Perithecia:** up to 0.3 mm wide, within the central areoles, only the mouth visible as an inconspicuous small projection of the areole; exciple: dark; hymenial algae predominately short, 3-4 µm; **asci:** saccate, 2-spored; **ascopores:** ellipsoid to narrowly ellipsoid, pale brown, muriform to 7-septate transversely, 3-septate longitudinally, 40-45 x 15-20 µm; **Spot tests:** all negative; **Secondary metabolites:** none detected.

Substrate and ecology: on acidic rocks, from the deserts to lower montane regions; **Worldwide and Sonoran distribution:** apparently restricted to the southwestern in Arizona, Sonora and western Chihuahua.

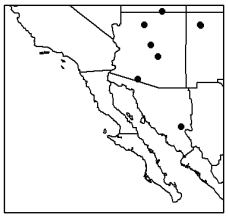


Staurothele elenkinii Oksn., Bull. Jard. Bot. Kieff 5-6: 76 (1927).

Synonym: *Staurothele sessilis* Magn.; Illustration: Thomson (1991), p. 358.

Thallus: crustose, at least partially endolithic, verruculate; **verrucules:** scant, tiny or lacking,; perithecial warts subspherical with the base constricted, to 0.7 mm broad; **surface:** (if visible) black, sometimes a paling of the substrate is only visible; **prothallus:** absent; **Perithecia:** single in the verrucule, up to 0.5 mm broad; **involucrellum:** black carbonaceous and constricted below, algae visible in lower portion, subcompound in the sense of Swinscow, dark reddish brown; hymenium: interior I+ blue; **asci:** saccate, 2-spored; **ascopores:** ellipsoid, dark brown, muriform, up to 8-septate transversely and 3-septate longitudinally, 33-62 x 18-33 µm; **Spot tests:** all negative; **Secondary metabolites:** none detected.

Substrate and ecology: on calcareous rocks, shales or sandstones; altitudes for western specimens range from 900 to 2800 m; **World distribution:** western North America; **Sonoran distribution:** scattered throughout Arizona and southwards into Sonora.



Staurothele lecideoides de Lesd, Annal. Crypt. Exot. 5: 98 (1932).

Illustration: Thomson (1991), p. 358.

Thallus: crustose, quite thin, chinky-areolate; **areoles:** minute, angular, flat, confluent; **surface:** bluish-ashy; **hypothallus:** lacking; **Perithecia:** single in areoles, tiny, up to 0.2 mm wide, apex flat, pruinose; exciple: black, entire; hymenium: I+ blue, turning red; **asci:** saccate, 2-spored; **ascospores:** ellipsoid to narrowly ellipsoid, hyaline, muriform, many celled, 29-38 x 12-18 µm; **Spot tests:** all negative; **Secondary metabolites:** none detected.

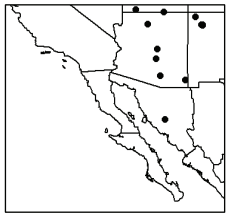
Substrate and ecology: on siliceous rocks; **World and Sonoran distribution:** only known form western North America in the Sonoran region of Arizona (and in adjacent New Mexico) and Sonora, Mexico.

Staurothele monicae (Zahlbr.) Wetmore, Mycotaxon 23: 247 (1985).

Basionym: *Endocarpon monicae* Zahlbr., Beih. Bot. Centralbl. 13: 153 (1902); Illustration: Thomson (1991), p. 358.

Thallus: crustose, areolate; **areoles:** angular, sides vertical, closely compacted, 0.1-0.3 mm broad; **surface:** dull greenish-brown varying to orange-brown, in the mass the color is nearly greenish yellow or olive-gray; usually only slightly convex; **Perithecia:** with base partly immersed in the areoles; **involucrellum:** black, very prominently projecting above the areoles (not within as in *S. areolata*); exciple: black; hymenial gelatin: I+ blue; **asci:** broadly clavate, 2-spored; **ascospores:** ellipsoid to narrowly ellipsoid, greenish initially, soon becoming dark brown, muriform 7-8 (-12)-septate transversely, 2-3 septate longitudinally, 26-60 x 10-26 µm; **Spot tests:** all negative; **Secondary metabolites:** none detected.

Substrate and ecology: on calcareous rocks at altitudes ranging from 700-3600 m; **World distribution:** North America, from California to Minnesota; **Sonoran distribution:** Arizona to Sonora, 100 to 2300 m.



Notes: In Hasse's Lich. Exs. 212 (W, ASU), it is reported as *Endocarpon monicae* Zahlbr. In comparison with *S. areolata, S. monicae* is duller and the areoles are not as convex.

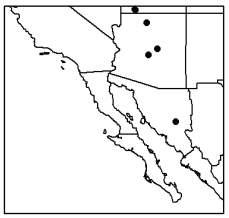
Staurothele polygonia de Lesd., Lich. Mexique 29 (1914).

Illustration: Thomson (1991), p. 359.

Thallus: crustose, areolate; **areoles:** tiny, angular, flat, 0.1-0.2 mm broad; **surface:** dark-brown, becoming slightly more olive-brown when moist; surface minutely rough, marginal areoles showing a slight tendency to become sorediate; **medulla:** dark; **hypothallus:** dark; **Perithecia:** 0.6-1.0 mm wide, immersed, one per areole, a broadened black flat involucrellar tip visible; ostiole: not noticeable,

involucrellum: black, wrapping around the dark exciple; hymenial gelatin: I-; **asci:** saccate, 1-2-spored; **ascopores:** ovoid, pale brown, muriform, up to 6-11-septate transversely, 1-2-septate longitudinally, 23-39 x 10-18 µm; **Spot tests:** all negative; **Secondary metabolites:** none detected.

Substrate and ecology: on granitic rocks or non calcareous rocks in montane area, 1400-2000m; **World distribution:** from central Mexico to California, Texas and southern Utah; **Sonoran distribution:** scattered in Arizona and southwards to Sonora.



Staurothele verruculosa J. W. Thomson, Bryol. 94: 364.

Illustration: Thomson (1991), p. 359.

Thallus: crustose, verruculose; **verrucules:** combined into angular areolate-appearing areas; **surface:** greenish gray to greenish ashy; usually only slightly convex; subisidiose; **Perithecia:** with base partly immersed in the areoles, black, 0.3-0.5 mm wide; **involucrellum:** dark red to reddish black, dimidiate, 125-150 µm thick; exciple: dark red, *c.* 50 µm thick; hymenial gelatin: I+ blue; **asci:** broadly clavate, 4 (-8)-spored; **ascospores:** broadly ellipsoid, hyaline, muriform, 7-septate transversely, 1 (-2)-septate longitudinally, 18-32 x 12-25 µm; **Spot tests:** all negative; **Secondary metabolites:** none detected.

Substrate and ecology: on conglomerate,1600 m; **World** and **Sonoran distribution:** thus far only known from central Arizona.

STEREOCAULON

by B. D. Ryan

Stereocaulon (Schreb.) Hoffm., Deutschl. Flora 2: 128 (1796), *nom. cons.*

Family: Stereocaulaceae; Type: *Stereocaulon paschale* (L.) Hoffm. (1796); No. species: 123 world-wide; Selected lit.: Lamb (1951, 1977 & 1978).

Life Habit: lichenized; **Thallus:** fruticose, occasionally reduced and more crust-like, attached by the whole lower surface or by basal holdfasts; **primary thallus:** usually rudimentary and disappearing early but in some species persistent, composed of basal granular or squamule-like structures (phyllocladia); **secondary thallus:** shrubby, erect to decumbent, composed of stalks (pseudopodetia), developing from a ± well-developed holdfast in some species, **Pseudopodetia:** solid, ± terete, weakly to strongly branched, fruticose in appearance, usually corticate; central axis: cartilaginous, composed of thick-walled, longitudinal hyphae; **surface:** grayish, ochraceous-yellowish, olivaceous, brownish, rose or white, contiguous or granular-farinose to spongiose-filamentous, with or without tomentum; **phyllocladia** or phyllocladioid branchlets: verrucose to granular, cylindrical, squamulose or foliose, containing the algae and a loosely interwoven medulla, sometimes appearing dorsiventral; with or without soredia; **photobiont:** primary one a chlorococcoid alga, secondary photobiont a cyanobacterium (*Nostoc* or *Stigonema* or occasionally *Scytonema* or *Chroococcus*) usually present in cephalodia on the pseudopodetia; cephalodia: mostly irregularly globose; **lower surface:** tomentose to glabrous; **Ascomata:** apothecial, terminal or lateral, roundish, sessile or substipitate or stipitate; disc: plane to often convex, pale brown to red-brown, dark brown or black, without a thalline margin; exciple: prominent (raised) to ± soon disappearing, sometimes pale and appearing almost thalloid; hymenium: hyaline below, brown, or

ochraceous-yellowish above; paraphyses: unbranched, not (or scarcely) anastomosing, apices mainly with a brown cap; hypothecium: hyaline or ochraceous-yellowish (to brown in some species); **asci:** clavate to cylindrical, unitunicate, tholus I+ blue; in K/I with a blue outer layer, and a blue apical dome with a ± central, darker blue tube, *c.* 8-spored; **ascospores:** ellipsoid, hyaline, clavate, or fusiform to cylindrical, acicular, or vermiform, transversely 1-13 septate, (12-) 16-100 (-200) x 2-7 µm, hyaline, smooth, thin walled, without distinctly developed endospore thickening, I-; **Conidiomata:** sometimes present, terminal or lateral, immersed in the tips of phyllocladia, ovoid to spherical, darkened around ostiole; **conidia:** formed acrogenously, filiform to cylindrical, straight or curved, simple; **Secondary metabolites:** orcinol and ß-orcinol depsides, orcinol and ß-orcinol depsidones and aliphatic acids; **Geography:** arctic-alpine, boreal and montane regions of Northern and Southern Hemispheres; **Substrate:** on soil, bryophytes, detritus, or non-calciferous, siliceous rock; in cool to cold, humid areas.

Notes: The genus is not likely to be confused with any other, except perhaps *Leprocaulon*, which has very fine, ecorticate branches and lacks ascomata.

The Species

Stereocaulon sasakii Zahlbr., Feddes Repert. 33: 48 (1933).

Illustrations: Yoshimura (1974), figs. 77a & b; Pl. 33: fig. 329; Brodo et al. (2001), p. 668.

Thallus: fruticose, ± erect and caespitose, or (v. *tomentosoides*) subprostrate and dorsiventral, sometimes becoming congested; primary thallus: evanescent; **pseudopodetia:** 20-24 mm long, in lower part *c.* 1 mm wide, rather loosely to somewhat narrowly and firmly attached, at the base simple to weakly branched, in the upper part infrequently short, erect-curved branched, or more often well-branched; **surface:** white to gray-white, dull, dying below but not ferruginous nor blackened towards the base, not of ligneous appearance; tomentum: whitish or cream-colored, thin and felty (to thick and floccose or spongy in v. *tomentosoides*); soredia: absent; **phyllocladia:** usually numerous and crowded, lateral, granular (0.1-0.3 mm across, sometimes even less towards the base) to more often verrucose to flattened and crenate-squamulose, elongate-squamulose or digitate-squamulose [to 0.6 mm across according to Lamb, 1977], fully exposed, whitish or whitish gray, sometimes darker toward their bases; **cephalodia:** usually aeruginose-glaucescent, irregularly pulvinate, becoming subglobose, indistinctly tuberculate, not scabrid, formed as in *S. myriocarpum* Th. Fr. but often few or concealed in the tomentum, *c.* 0.2-0.3 mm across, containing *Nostoc*; **Apothecia:** usually frequent in upper part, mostly lateral, at the tips of short secondary branches, 0.3-0.5 (-1.0) mm diam., distinctly constricted at the base, rounded, not dividing into secondary discs; disc: plane to slightly convex, ± dark brown [black according to the protologue], when wet brown; margin: narrow, distinct at first, whitish to brown, entire, persistent; cortex: subchondroid, yellowish, 14-16 µm thick, plectenchymatous; exciple: dimidiate, in upper part around hymenium dark gray, in lower part hyaline and containing infrequent algae; hymenium: hyaline below to orangish brown or red-black and granular above, I+ blue, 40-45 µm high; paraphyses: filiform, dense, straight, loose to coherent, unbranched, non-septate (below apex), tips moderately clavate, thickened (2.5-3.5 µm wide in Sonoran material), brown; hypothecium: pale brown; **asci:** oblong-clavate, in Sonoran material *c.* 42 x 8-10 µm; **ascospores:** acicular-filiform with rounded ends, in Sonoran material rare and probably immature, 3-septate, *c.* 20 x 2.5 um (otherwise 23-25 x 2-2.5 µm); **Pycnidia:** not seen; **Spot tests:** phyllocladia K+ yellow, C-, KC+ violet, P- or + pale yellow; **Secondary metabolites:** atranorin and (usually) lobaric acid.

Substrate and ecology: on soil, humus, or among mosses, or (v. *tomentosoides*) on rock; **World distribution:** eastern (to south-central) Asia; North America (Alaska to the southwestern USA); **Sonoran distribution:** known from a few specimens from a single locality at 3,300 m in eastern Arizona.

Notes: This taxon is similar to *S. tomentosum* Fr., in the cephalodia (small, bluish, indistinctly corticate), phyllocladia (granular to squamulose, non-sorediate, without darker centers), pseudopodetia (± fragile, whitish, and tomentose), and apothecia (under 1 mm diam., mostly lat-

eral, with narrow spores). It differs from *S. tomentosum* mainly in chemistry (lobaric instead of stictic acid) and distributional pattern (restricted to E. Asia and W. North America, rather than occurring in circumboreal-Arctic areas and South America). Another similar species, *S. myriocarpum* Th. Fr. (known from Asia and North, Central, and South Americas), likewise contains stictic rather than lobaric acid, and further differs from *S. sasakii* in having an unpigmented hypothecium. While some authors (e.g., Goward, 1999) treat *S. sasakii* as a whole (along with *S. myriocarpum* Th. Fr., under a broad concept of *S. tomentosum*, a thorough study that includes material from areas outside the Sonoran Region is necessary to resolve the taxonomy of this complex. Although a few other species of *Stereocaulon* are known from northern California or from southern parts of Mexico, this is the only complex known to occur in areas with climates even approaching that of the Sonoran region.

The Arizona material reported by Nash et al. (1998) as var *simplex* (Riddle) Lamb [*Journ. Hattori Bot. Lab.* 43: 230 (1977)] actually seems to fit the protologue of *S. sasaki* (Zahlbruckner 1933) fairly well, in that the pseudopodetia are somewhat branched in the upper parts and ± richly covered with mostly granular phyllocladia; the various apparent differences in some apothecial characters in the description of our material are probably not significant. The var. tomentosoides Lamb [*Journ. Hattori Bot. Lab.* 43: 230 (1977)] differs from the typical variety in having prostrate-decumbent and crowded pseudopodetia forming dorsiventral mats, a thicker tomentum, and a different main distributional area (W. North America rather than E. Asia), and according to Lamb (1977) may eventually deserve species rank. The material reported by Nash et al. (1998) as v. *tomentosoides* seems to fit this variety, but the pseudopodetia are rather short and narrow (up to 15 mm long; often < 0.5 mm thick), the tomentum is not as thick as in *S. tomentosum*, and apothecia are lacking. This material also contrasts with the other Arizona collection (but fits within Lamb's concept of *S. sasakii* as a whole) in that the phyllocladia are mostly distinctly squamulose.

STRIGULA

by A. Aptroot

Strigula Fr., Syst, Myc. 2: 535 (1823).

Family: Strigulaceae; Type: *Strigula smaragdula* Fr.; No. species: *c.* 50 world-wide; Selected lit.: Harris (1995); Purvis et al. (1992).

Life habit: lichenized; **Thallus:** crustose, mostly immersed in the substrate; **photobiont:** primary one a trentepohlioid alga or *Phycopeltis*, secondary photobiont absent; **Ascomata:** perithecial, globose, in upper part conical; **involucrellum:** present in some species, blackish brown; true **exciple:** dark or pale brown or colorless; **ascomatal wall:** black, not continuous below the hamathecium; **hamathecium:** composed of branched pseudoparaphyses, anastomosing above the asci, amyloid; **asci:** bitunicate, cylindrical, with tholus, non-amyloid; **ascospores:** hyaline, ellipsoid, transversely 1-20-septate to muriform, with eusepta, 2-20 x 8-70 µm; walls: not ornamented; **Conidiomata:** pycnidial, globose or conical, at least partially immersed; **conidia:** hyaline, simple to transversely septate to muriform, always with gelatinous appendages, including both macro- (1 or more septate, oblong to fusiform) and microconidia (simple, ellipsoid or narrowly ellipsoid); **Secondary metabolites:** none detected; **Geography:** cosmopolitans, but most diverse in the tropics; **Substrate:** mostly foliicolous, but also on bark, calcareous or non-calcareous rocks.

Notes: The species of this genus occur commonly in the tropics as epiphylls. It is separated from *Anisomeridium* and *Arthopyrenia* by the appendaged conidia, the thin, anstomosing hamathecium filaments and the often multiseptate ascospores.

The Species

Strigula stigmatella (Ach.) R.C. Harris, in D. Hawksw., P. James & Coppins, Lichenologist 12: 107 (1980).

Basionym: *Lichen stigmatellus* Ach., Lichenogr. suec. prodr.: 15 (1798); Illustrations: Harris (1975), p. 257; Wirth (1995), p. 139.

Thallus*:* continuous, effuse, immersed in the substrate; **upper surface**: white to pale gray, smooth; **algae:** trentepohlioid; **Perithecia:** hemispherical, black, semi-immersed in the thallus, 0.3-0.5 mm diam.; **involucrellum:** closely clasping the exciple; **true exciple:** pale brown to colorless; **ascomatal wall:** black, absent below the hamathecium; **hamathecium:** composed of branched pseudoparaphyses, anastomosing above the asci, filaments *c.* 1 µm wide, not inspersed with oil droplets; **asci:** clavate to cylindrical, 70-80 x 12-15 µm, with 8, irregularly arranged ascospores; **ascospores:** hyaline, fusiform, (4-) 6-7 (9)-septate (starting with a median euseptum), 25-45 x 5-8 µm; walls: not ornamented, without a gelatinous sheath; **Pycnidia:** *c.* 100 µm diam.; conidia: **macroconidia:** 5-7 septate, 20-30 x 4-6 µm; microconidia: not seen; **Spot tests:** all negative, UV negative. **Secondary products:** none detected

Substrate and ecology: on bark of various woody plants; **World distribution:** temperate regions of the Northern Hemisphere; **Sonoran distribution:** only recorded from southern California.

STROMATELLA

by M. Schultz

Stromatella Henssen, Lichenologist 21: 111 (1989).

Family: Lichinaceae; Type: *Stromatella bermudana* (Riddle) Henssen; No. species: one world-wide; Selected lit.: Henssen (1989).

Life habit: lichenized; **Thallus:** crustose, squamulose-areolate, gelatinous when wet; **surface:** black, finely tessellate; **anatomy:** ecorticate, homoiomerous, paraplectenchymatous; **photobionts:** primary one a chroococcoid cyanobacterium, secondary photobiont absent; **Ascomata:** apothecial, laminal on thallus, orbicular, immersed to semi-immersed, margin indistinct to distinct, with crenate or nodulose thalloid rim; **ontogeny:** hemiangiocarpous, forming pycnoasco-carps from ascogonia beneath pycnidia; **anatomy:** exciple: hyaline or brownish-yellow; hypothecium: hyaline or brownish-yellow; epithecium: hyaline or brownish yellow; **asci:** prototunicate, wall thin, nonamyloid, 8-spored; **ascospores:** simple, ellipsoid to broadly ellipsoid, 12-26 x 8-11 µm; walls: thin, hyaline; **Conidiomata:** pycnidial, laminal, immersed; **conidia:** ellipsoid or bacilliform, *c.* 3 x 1 µm; **Secondary metabolites:** none detected; **Geography:** arid, semi-arid, coastal or inland habitats; **Substrate:** limestone and calcareous rock.

Notes: The diagnostic feature of the genus *Stromatella* is the development of ascomata in a stroma. But the genus also has pycnoascomata, where the ascomata develop beneath a pycnidium, and this is similar to *Porocyphus*. In terms of anatomy *Stromatella* is most similar to *Psorotichia* and *Porocyphus*.

The Species

Stromatella bermudana (Riddle) Henssen, Lichenologist 21: 112 (1989).

Basionym: *Psorotichia bermudana* Riddle, Bull. Torrey Bot. Club 43: 154 (1916); Illustrations: Henssen (1989), pp. 111 & 112; and Fig. 99 on next page

Thallus: crustose-areolate; **areoles:** 0.5-2 mm wide, up to 0.75 mm thick, ± angular, **surface:** black, tessellate due to

vertical growth of slender, elongated, densely aggregated lobules [50-75(-100) µm long]; **anatomy:** densely reticulate, almost paraplectenchymatous; **lower side:** attached to the substrate by thick bundles of rhizohyphae;

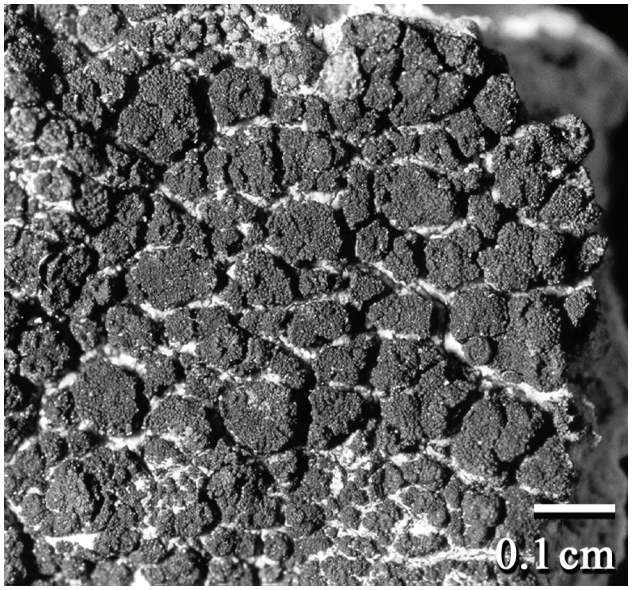
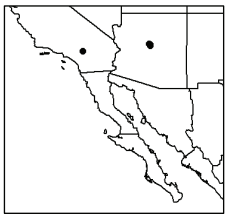


Fig. 99. *Stromatella bermudana*, photo by M. Schultz.

Apothecia: immersed to sessile, zeorine, 1-3 per areole, up to 0.75 mm wide; disc: dark reddish, flat, sometimes umbonate, thalline margin persisting, thin, often somewhat crenulate or nodulose; exciple: thin but distinct, up to 15 µm wide, faintly yellowish-brown colored; epihymenium: reddish-brown; hymenium: up to 125 µm high, hyaline, amyloid; paraphyses: distinctly septate, sparingly branched and anastomosing, apically often richly branched and cells distinctly moniliform, up to 5 µm wide and yellowish-brown colored; hypothecium: sometimes elongated as a stipe; **asci:** 8-spored; **ascospores:** simple, hyaline, broadly ellipsoid, (12.5-) 15-17.5 (-20) x 7.5 (-10) µm; walls: thin; **Pycnidia:** immersed, globose to broadly pyriform, 0.075-0.1 mm in diam.; **conidia:** cylindrical, 3 x 1 µm; **Spot tests:** all negative; **Secondary metabolites:** none detected.

Substrate and ecology: on limestone in sheltered, steep or exposed faces of boulders in rocky slopes in chaparral and woodlands; **World distribution:** SW North America and Bermuda; **Sonoran distribution:** limestone deposits in central Arizona and southern California.



Notes: The Sonoran material matches all features of *S. bermudana* except that stroma were not found. The species also resembles species of *Psorotichia* and *Porocyphus* from which it is distinguished by the tessellate surface of its areoles (best seen at a higher magnification, 40x) and the rather large size of its areoles. *Paulia gibbosa* has a similar tessellate surface and surface areoles of the same size, but differs in its loosely reticulate anatomy with larger photobiont cells (>10 µm), the larger, bulging, peltate squamules (4-6.5 mm wide), the smaller apothecia (up to 0.3 mm wide) and its type of ascoma development.

SYNALISSA

by M. Schultz

Synalissa Fries, Syst. Orb. Veget. pars 1: 297 (1825).

Family: Lichinaceae; Type: *Synalissa symphorea* (Ach.) Nyl.; No. species: *c.* five world-wide; Selected lit.: Moreno and Egea (1991).

Life habit: lichenized; **Thallus:** umbilicate, subfruticose, fruticose, gelatinous when wet; **surface:** black, dark brown-red, sometimes grayish pruinose, smooth or rough; **anatomy:** ecorticate, homoiomerous, loose network of hyphae surrounding photobiont cells, central hyphal strands often present in basal parts; **photobionts:** primary one a chroococcoid cyanobacterium, secondary photobi-

ont absent; **Ascomata:** apothecial, sometimes appearing perithecioid, terminal, orbicular, sessile to stipitate, margin distinct to prominent, with thick thalloid rim; **ontogeny:** hemiangiocarpous, formed from ascogonia free beneath the thallus surface; **anatomy:** exciple: absent or hardly developed, hyaline; epithecium: hyaline or brownish yellow; hypothecium: hyaline or pale brownish-yellow; **asci:** prototunicate, wall thin, non-amyloid, 8-32-spored; **ascospores:** simple, broad ellipsoid or globose; 7-12 x 6-9 µm; walls: thin, hyaline; **Conidiomata:** pycnidial, laminal, immersed; **conidia:** ellipsoid or bacilliform, *c.* 3 x 1 µm; **Secondary metabolites:** none detected; **Geography:** arid, semi-arid to warm temperate regions; **Substrate:** limestone, calcareous, or siliceous rocks.

Notes: Species of *Peccania* are similar; however, they have a distinct central strand, red patches in the hymenium and filiform conidia. Some *Lichinella* species are also similar; however, they have a fountain-like arrangement of the hyphae and thallinocarpous ascomata.

The Species

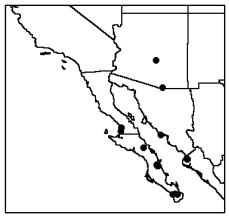
Synalissa matogrossensis (Malme) Henssen, Ber. Deutsch. Bot. Ges. 92: 486 (1979).

Basionym: *Peccania matogrossensis* Malme, Ark. f. Bot. 29A (6): 19 (1937); Illustrations: Henssen (1979), p. 505; and Fig. 100 below.

Fig. 100. *Synalissa matogrossensis*, photo by M. Schultz.

Thallus: small fruticose cushions (up to 5 mm wide and 3 mm high), lobules terete, (60-) 75-150 µm thick, irregularly to subdichotomously branched, usually not densely aggregated, apices often swollen; **surface:** blackish red with dark brown-red tinge (lighter when moist), smooth but often covered by numerous tiny, short side branches (50-75 µm thick) causing a rough appearance of the lobules; **substrate attachment:** by small holdfast; **Apothecia:** on swollen tips of lobules, lecanorine, small (up to 0.3 mm wide), with persisting thalline margin that is often warty or may support tiny side branches; disc: dark red-brown, punctiform, later open; exciple: lacking; hymenium: up to 100 µm high, hyaline, non-amyloid; paraphyses: distinctly septate, thin, sparingly branched and anastomosing, apical cells not thickened; **asci:** 8-spored; **ascospores:** simple, hyaline, ellipsoid, 10-15 x 5 µm; walls: thin; **Pycnidia:** immersed, at swollen lobe tips, globose, up to 0.075 mm in diam.; **conidia:** cylindrical, 3 x 1 µm; **Spot tests:** all negative; **Secondary metabolites:** none detected.

Substrate and ecology: on siliceous, volcanic, or calcareous rocks; lowland to montane; **World distribution:** SW North America and Neotropics; **Sonoran distribution:** Baja California and Baja California Sur, Sonora and Sinaloa; rarely in central and southern Arizona (probably overlooked).



Notes: At lower magnification (5-10x) the aggregated cushions seem to form a ± areolate crust. Similar "crusts" forms *Lichinella stipatula* that has lobules of the same size, but a very different ascocarp ontogeny. Closer examination will reveal the small fruticose growth habit of both species. *Lichinella stipatula* has photobiont cells with a thin (-2.5 µm) yellowish brown gelatinous sheath, a more compact anatomy with a fountain-like arrangement of the hyphae, polysporous asci with broad ellipsoid spores and a hymenium that is covered with portions of lichen tissue (thallinocarps). *Synalissa symphorea* has larger, thicker, club-shapes lobes and polysporous asci.

SYNCESIA

by A. Tehler

Syncesia Taylor, in Mackay, Fl. Hibern. II. 103 (1836).

Family: uncertain; Type: *Syncesia albida* Taylor, = *Syncesia myrticola* (Fée) Tehler; No. species: 17 world-wide; Selected lit.: Tehler (1996b).

Life habit: lichenized; **Thallus:** crustose, effuse rarely pulvinate, coherent rarely incoherent, usually tomentose rarely dense or byssoid, usually homoiomerous but rarely heteromerous; **surface:** white to creamy-white to white-brownish; smooth to slightly verrucose or rugose, epruinose or slightly pruinose; prothallus: usually brown when free-growing; soredia: absent; **cortex:** usually present but sometimes absent, 10-25 µm thick with hyphae interwoven; **medulla:** usually indistinct, rarely present and then white to dirty white; **photobionts**: primary one a *Trentepohlia*, secondary photobiont absent; **Ascomata:** stromatoid (pseudomonocarpocentral), synascomatal, but when young solitary and apothecioid, circular to elongated in outline, more or less elevated often with constricted base, (0.5-) 1-2 (-3) mm diam; usually with 5-15 discs within the ascomata; disc: circular to elongated, *c.* 0.1-0.5 mm diam., exposed, pruinose, tomentum often present; exciple: cortex rarely developed, algae often present; proper exciple: parathecial; epithecium: brown or brownish, branched or richly branched hyphae; hymenium: with paraphysoids parallel, sparsely branched, hyaline, 1 µm diam.; hypothecium: dark-brown (carbonaceous), usually extending down to substrate; **asci:** (55-) 70-90 (-100) x (10-) 15 (-23) µm; **ascospores:** fusiform, rarely linear fusiform, curved sometimes nearly straight, 3-septate, hyaline; **Conidiomata:** pycnidial, solitary, elevated or immersed, dark-brown; **conidia:** filiform, curved to semicircled, hyaline; **Secondary metabolites:** orcinol depsides, ß-orcinol depsides, aliphatic acids and dibenzofurans; **Geography:** predominately tropical and subtropical regions of Latin America, including the West Indies and adjacent Central America and northwestern South America and a second area in the Brazilian Highlands of Minas Gerais and São Paulo; **Substrate:** usually on bark (rarely within bark – endophloeodal), also rarely on rock.

The Species

Syncesia depressa (Tuck.) Tehler, Flora Neotropica 74: 40 (1997).

Basionym: *Chiodecton depressum* Fée, Essai crypt. écorc. 65 (1824); Synonym: *Chiodecton glaucoleucum* Nyl.; Illustrations: Tehler (1997), pp. 42 & 43.

Thallus: crustose, tomentose, non-rimose; **surface:** creamy to white, 0.01-0.06 mm thick, smooth, slightly pruinose, soredia absent; prothallus absent; **cortex:** not developed; **medulla:** indistinct; **Ascomata:** stromatoid (pseudomonocarpocentric), very rarely apothecioid, in synascomata, up to 1.6 mm in diam.; individual discs: flat or slightly convex, 0.05-0.3 mm diam, usually ± tomentose; thalline exciple: level with the disc, without cortex and algae; proper exciple: present, thin; epithecium: light brown to brown, 20-30 µm thick; hymenium: hyaline, 70-80 µm high; paraphysoids: hyaline, sparsely branched, parallel, *c.* 1 µm in diam.; **asci:** clavate, 60-70 x 10-15 µm, 8-spored; **ascospores:** fusiform, hyaline, 3-septate, 41-48 x 4 µm; **Pycnidia:** not seen; **Spot tests:** thallus K+ yellow-reddish (K- if norstictic in very low concentration), C-, KC-, P+ orange; UV+ cream-colored; **Secondary metabolites:** norstictic acid.

Substrate and ecology: in bark, growing on trees and shrubs; **World distribution:** known from a few localities in Curaçao, Colombia, Venezuela, and Florida, USA; **Sonoran distribution:** one locality in Sinaloa, near Mazatlán.

THELENELLA

by H. Mayrhofer

Thelenella Nyl., Mem. Soc. Sci. Nat. Cherbourg 3: 193 (1855).

Family: Thelenellaceae; Type: *Thelenella modesta* (Nyl.) Nyl.; No. species: *c.* 20 world-wide; Selected lit.: Mayrhofer and Poelt (1985), Mayrhofer (1987a), Mayrhofer and McCarthy (1991), and Harris (1995).

Life habit: lichenized; **Thallus:** crustose, superficial to partially immersed, attached by the whole lower surface; **upper surface:** membranous to rimose, rimose-areolate to uneven warted; soredia and isidia absent; **photobiont:** primary one a chlorococcoid alga, secondary photobiont absent; **Ascomata:** perithecial, ± immersed but appearing as prominent warts, pale to brownish, globose; exciple: colorless below, brownish above and around the ostiole; open involucrellum present in only a few species; hamathecium: composed of persistent paraphyses, richly branched and anastomosed; periphysoids towards the inner side of the ostiole; periphyses absent; **asci:** bitunicate, fissitunicate dehiscence, thick-walled, with non-amyloid tholus; apex: without an ocular chamber; 2 (-8)-spored; **ascospores:** submuriform to strongly muriform, colorless, rarely becoming pale yellow-brown, or brown, ellipsoid to narrowly ellipsoid or fusiform; **Conidiomata:** pycnidial, immersed, of the *Roccella*-type; **conidia:** filiform; **Secondary metabolites:** none detected; **Geography:** world-wide; **Substrate:** bark, non-calciferous rocks (often maritime or oceanic habitats).

Notes: It is characterized by its crustose thallus, very thick-walled asci without an ocular chamber, fissitunicate dehiscence, submuriform to strongly muriform ascospores, persistent, branched-anastomosed paraphyses and the presence of periphysoids. The related genus *Chromatochlamys* is distinguished by asci with an ocular chamber. The similar genus *Protothelenella* is distinguished by asci with an amyloid tholus and an amyloid hamathecium.

Key to the species of ***Thelenella*** from the Sonoran region:

1. Ascospores brown ..... ***T. hassei***
1. Ascospores colorless 2

2. Thallus on rocks 3
2. Thallus on bark 4

3. Involucrellum absent ..... ***T. inductula***
3. Involucrellum present ..... ***T. weberi***

4. Ascospores submuriform, 20-30 µm long, 7-11 µm wide ..... ***T. sychnogonioides***
4. Ascospores muriform, 25-42 µm long, 11-17 µm wide ..... ***T. modesta***

The Species

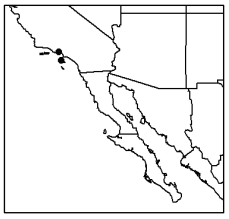
Thelenella hassei (Zahlbr.) H. Mayrhofer, Biblioth. Lichenol. 26: 37 (1987).

Basionym: *Microglaena hassei* Zahlbr., Beih. Bot. Centralbl. 13: 152 (1902); Illustration: Mayrhofer (1987a), p. 41.

Thallus: thin, superficial, membranous to rimose; **upper surface:** greenish to olive-gray, smooth; **prothallus:** absent; **Perithecia:** immersed, dispersed, 0.3 to 0.5 mm diam.; ostiole: dark brown; involucrellum: absent; exciple: colorless below, brownish above; hamathecium: composed of persistent paraphyses, richly branched and anastomosed; periphysoids towards the inner side of the ostiole; periphyses absent; **asci:** cylindrical, 4- to 8-spored; **ascospores:** brown, muriform, with 6-8 lateral and 2-3 longitudinal septa, ellipsoid to narrowly ellipsoid, 25-40 x 10-17 µm; **Pycnidia:** not seen; **Spot tests:** all negative; **Secondary metabolites:** none detected.

Substrate and ecology: on bark (*Juglans californica* and *Prunus ilicifolia*); **World distribution:** southern California and Mediterranean Europe; **Sonoran distribution:**

the Santa Monica Range and Catalina Island in southern California.



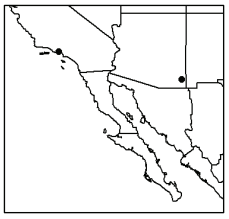
Notes: This species is characterized by its relatively thin thallus and brown ascospores. In contrast, *Thelenella modesta* has colorless ascospores.

Thelenella inductula (Nyl.) H. Mayrhofer, Biblioth. Lichenol. 26: 38 (1987).

Basionym: *Verrucaria inductula* Nyl. in Hasse, Bull. Torrey Bot. Club 24: 448 (1897); Synonym: *Thelenella sampaiana* (de Lesd.) H. Mayrhofer & Poelt; Illustrations: Mayrhofer and Poelt (1985), p. 67; Mayrhofer (1987a), p. 41.

Thallus: relatively thick, superficial, rimose-areolate to uneven warted; **upper surface:** ochre-brown to bright reddish brown; smooth to rough, dull; **prothallus** indistinct; **Perithecia:** dispersed to crowded, globose to slightly pear-shaped, 0.2 to 0.5 mm diam.; ostiole brown; involucrellum: absent; exciple: colorless below, brownish above; hamathecium: composed of persistent paraphyses, richly branched and anastomosed; periphysoids towards the inner side of the ostiole; periphyses absent; **asci:** cylindrical, 4- to 8-spored; **ascospores:** colorless, muriform, with 6-8 lateral and 2-3 longitudinal septa, narrowly ellipsoid, 24-36 x 9-13 µm; **Pycnidia:** immersed; **conidia:** filiform, colorless, 13-15 x 0.6-0.8 µm; **Spot tests:** all negative; **Secondary metabolites:** none detected.

Substrate and ecology: lava, granite, schist; dry and exposed slopes with low vegetation; **World distribution:** SW Europe, Macaronesia and SW North America; **Sonoran distribution:** Santa Monica Range in southern California and Chiricahua National Monument in Arizona.



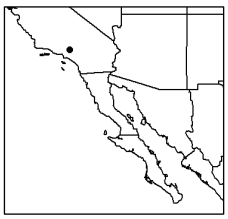
Notes: *Thelenella inductula* is characterized by its relatively thick, rimose- areolate, ochre brown to bright reddish brown thallus and colorless ascospores. The other saxicolous species in the area, *Thelenella weberi*, is distinguished by the presence of an open involucrellum and its larger ascospores.

Thelenella modesta (Nyl.) Nyl., Mém. Soc. Sci. Nat. Cherbourg 3: 193 (1855).

Basionym: *Verrucaria modesta* Nyl., Bot. Not.: 164 (1853); Synonym: *Microglaena subcorallina* Hasse; Illustrations: Mayrhofer and Poelt (1985), p. 67; Mayrhofer (1987a), pp. 54, 56-57 & 59.

Thallus: thin to thick, superficial, membranous, rimose to deeply cracked-areolate; **upper surface:** yellow-gray to pink or red-brown, fading to pale gray or gray in the herbarium; smooth to uneven-warted; **prothallus:** absent; **Perithecia:** dispersed; ostiole dark-brown; involucrellum: absent; exciple: colorless below, brownish above; hamathecium: composed of persistent paraphyses, richly branched and anastomosed; periphysoids towards the inner side of the ostiole; periphyses absent; **asci:** cylindrical, 4- to 8-spored; **ascospores:** colorless, rarely becoming pale yellow-brown when overmature, muriform, with 7-9 lateral and 2-3 longitudinal septa, ellipsoid to narrowly ellipsoid, 25-42 x 11-17 µm; **Pycnidia:** immersed; **conidia:** filiform, colorless, 11-14 x 0.6-0.8 µm; **Spot tests:** all negative; **Secondary metabolites:** none detected.

Substrate and ecology: bark (on smooth bark of *Quercus agrifolia* and *Juglans californica* in southern California); **World distribution:** temperate and mediterranean Europe, mediterranean northern Africa, North America and Australia; **Sonoran distribution:** San Gabriel Mountains and the Santa Monica Range in southern California.



Notes: This species is characterized by its rimose to deeply cracked-areolate, yellow-gray to pink or red-brown thallus and muriform colorless ascospores. *Thelenella hassei* is distinguished by its brown ascospores.

Thelenella sychnogonioides (Zahlbr.) R. C. Harris, More Florida Lichens: 167 (1995).

Basionym: *Microglaena sychnogonioides* Zahlbr., Beih. Bot. Centralbl. 13: 151 (1902); Synonym: *Thelenella harrisii* H. Mayrhofer; Illustration: Mayrhofer (1987a), p. 35.

Thallus: inconspicuous, superficial, partially indistinct, membranous to rimose; **upper surface:** pale brown to gray-brown, smooth; **prothallus:** absent; **Perithecia:** immersed but appearing as prominent warts, dispersed; ostiole pale brown; involucrellum: absent; exciple: colorless to pale brown; **hamathecium:** composed of persistent paraphyses, richly branched and anastomosed; periphysoids towards the inner side of the ostiole; periphyses absent; **asci:** cylindrical, 8-spored; **ascospores:** colorless, submuriform to rarely muriform, with 6-7 lateral septa and 1 (-2) longitudinal septa, narrowly ellipsoid, 20-30 x 7-11 µm; **Pycnidia:** not seen; **Spot tests:** all negative; **Secondary metabolites***:* none detected.

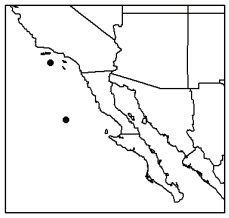
Substrate and ecology: bark, (on smooth bark of *Quercus agrifolia* and *Juglans californica* in southern California); **World distribution:** southern California and temperate Australia; **Sonoran distribution:** San Gabriel Mountains and the Santa Monica Range in southern California.

Notes: *Thelenella sychnogonioides* is characterized by its inconspicuous thallus, immersed perithecia appearing as prominent warts and submuriform ascospores. The arctic-alpine distributed *Thelenella pertusariella* is distinguished by its darker thallus and smaller ascospores.

Thelenella weberi H. Mayrhofer, Biblioth. Lichenol. 26: 65 (1987).

Illustration: Mayrhofer (1987a), p. 66.

Thallus: thick, superficial, rimose-areolate; **upper surface:** ochre to gray-brown, dull; **prothallus:** absent; **Perithecia:** immersed but appearing as prominent half-globose warts, dispersed; involucrellum: dark-brown, open, 20-40 µm wide**;** exciple: colorless below, pale brownish above; hamathecium: composed of persistent paraphyses, richly branched and anastomosed; periphysoids towards the inner side of the ostiole; periphyses absent; ostiole: dark-brown to blackish brown; **asci:** cylindrical, 8-spored; **ascospores:** colorless, muriform, with 7-11 lateral and 3 longitudinal septa, narrowly ellipsoid to subcylindrical, 35-47 x 14-19 µm; **Pycnidia:** immersed; **conidia:** filiform, colorless, 15-22 x 0.8-1 µm; **Spot tests:** all negative; **Secondary metabolites:** none detected.



Substrate and ecology: on sandstone and tuff in maritime influenced habitats; **World distribution:** SW North America; **Sonoran distribution:** southern California on San Nicolas Island and Baja California on Guadalupe Island.

Notes: This species is characterized by its perithecia appearing as prominent half-globose warts, an open involucrellum and large colorless muriform ascospores. The subantarctic distributed *Thelenella kerguelena* is distinguished by its smaller and cylindrical ascospores.

THELIDIUM

by O. Breuss

Thelidium A. Massal., Framm. lichenogr.: 15 (1855).

Family: Verrucariaceae; Type: *Thelidium amylaceum* A. Massal.; No. species: *c.* 80 world-wide; Selected lit.: Zschacke (1933) and Orange (1992).

Life habit: lichenized; **Thallus:** crustose, immersed or superficial, continuous or areolate, or nearly lacking, with or without a dark hypothallus; **upper surface:** pale grayish to blackish brown; **photobiont:** primary one a chlorococcoid alga, secondary photobiont absent; **Ascomata:** perithecial, immersed in thallus or in pits in limestone, or prominent to superficial, subglobose to pyriform; **involucrellum:** present or absent; exciple: pale or dark, formed of tangentially compressed cells; periphyses: simple to branched; interascal filaments absent; hymenial gel I+ orange-red, KI+ blue; **asci:** clavate, wall apically thickened, often with a small ocular chamber, non-amyloid, 8-spored; **ascospores:** biseriate, 1- to 3-septate, occasionally up to 5-septate or with 1-2 longitudinal septa, ellipsoidal to oblong-ellipsoid or ovate, colorless, smooth, non-halonate; **Conidiomata:** not observed; **Secondary metabolites:** none detected; **Geography:** world-wide, mainly temperate; **Substrate:** usually on rock (mostly limestone), rarely on other substrates, never maritime.

Notes: The genus is closely related to *Verrucaria* and *Polyblastia* and only separated by ascospore septation. The spores in *Thelidium* are mainly 2-celled.

The Species

Thelidium minimum (A.Massal. *ex* Nyl.) Arnold., Verh. zool.-bot. Ges. Wien 21: 1132 (1871).

Basionym: *Verrucaria minima* A.Massal. *ex* Nyl., Expos. Synop. Pyrenocarp.: 25 (1858).

Thallus: crustose, thin, dull, continuous to cracked or somewhat granulose; **upper surface:** gray to brownish; **Perithecia:** tiny (0.1 - 0.2 mm in diam.), almost globose, in hemispherical thalline warts; exciple: pale except for the apex; **involucrellum:** covering upper third or half of perithecium; **asci:** *c.* 40 x 15-20 µm; **ascospores:** ellipsoidal to ovate, 1-septate, 10-15 x 4-6 µm; **Conidiomata:** unknown; **Spot tests:** all negative; **Secondary metabolites:** none detected.

Substrate and ecology: on limestone on dry sites; **World distribution:** with certainty known only from central Europe (Harada 1992) and Mexico; **Sonoran distribution:** only known from one locality in Baja California Sur.

Notes: *Thelidium minimum* is characterized by an epilithic thallus, a well-developed involucrellum, and small ascospores. *Thelidium impressum* (Stizenb.) Zsch., which has spores of similar size, differs in its endolithic thallus. *Thelidium microsporum* Lynge is an arctic species that almost lacks a thallus and has even smaller spores.

THELOPSIS

by M. Tretiach, P. L. Nimis, and T. H. Nash III

Thelopsis Nyl., Mém. Soc. Imp. Sci. Nat. Cherboug 3: 194 (1855) (nomen cons.).

Family: uncertain, Stictidaceae?; Type: *Thelopsis rubella* Nyl.; No. species: nine world-wide; Selected lit.: Vězda (1968), and Harris (1979).

Life habit: lichenized; **Thallus:** crustose, superficial or immersed, thin, homiomerous, effuse; prothallus: absent; **upper surface:** various shades of gray or orange-red, smooth; **photobiont:** primary one a trentepohlioid alga, secondary photobiont absent; **Ascomata:** perithecial, globose, partially immersed to sessile, ± tough, pale reddish brown to black, not friable; **involucrellum:** absent; **true exciple:** hyaline to brownish black, 30-60 µm wide, upper and inner parts paraplectenchymatous; **asci:** cylindrical to oblong, thin walled, without conspicuous tholus, I-, 8-spored; **hamathecium:** paraphyses thread-like, unbranched, persistent; hymenium: hyaline, I+ blue changing to red-brown; **asci:** narrowly cylindrical, tapering apically,

unitunicate, thin-walled, without apical thickening or apparatus, multispored; **ascospores:** ellipsoid to shortly fusiform, hyaline, 1-3 septate to submuriform, 13-120 x 2-20 µm; **Conidiomata:** pycnidial, very rare, pale; **conidia:** thread-like, straight or slightly curved; **Secondary metabolites:** none detected; **Geography:** Mediterranean regions of Europe and southern North America; **Substrate:** species occurring on either bark, calcareous or acidic rocks, or detritus.

Notes: Among the perithecioid genera with trentepohlioid algae occurring in the Sonoran region, *Thelopsis* is most similar to *Topelia.* In *Thelopsis* and exciple is lacking and the spores are usually only transversely septate, rarely submuriform and always occur as more than 8 per ascus; whereas, in *Topelia* a well developed exciple is present and the spores are soon muriform and are 8 per ascus. The only other pyrenocarpous genus in the region with a large number of spores per ascus is *Trimmatothele*, but its spores are always simple and its photobiont is a chlorococcoid green alga.

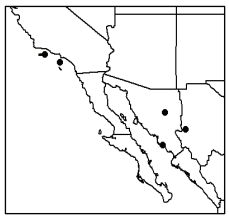
The Species

Thelopsis isiaca Stizenb., St. Gallisch naturw. Ges. (1893-1894): 262 (1895).

Synonyms: *Thelopsis subporinella* Nyl. *ex* Hasse, *Thelopsis subporinella* var. *grisella* de Lesd., *Thelopsis rubella* var. *uniseptata* Olivier; Illustration: Vězda (1968), fig. 47.

Thallus: crustose, endophloeodal, or rarely developing as thin to thick thallus over the substrate, when well developed becoming rimose to warty areolate (areoles up to 1 mm wide); **upper surface:** (if evident) light gray or pale lime colored, smooth to rugose; **Perithecia:** subglobose, somewhat flattened above, 0.4-0.5 mm wide, partially immersed; exciple: colorless, *c.* 30 µm wide; hymenium: hyaline or pale brown, I+ blue-green, rapidly changing to red-brown; periphyses: up to 25 µm long and *c.* 1 µm wide; paraphyses: slender, septa best seen in I, *c.* 280-300 x 1.5 µm, flexuose; **asci:** narrowly cylindrical, tapering apically, thin-walled, without apical thickening or apparatus, 200-250 x 10-12 µm, 100 to 150-spored; **ascospores:** ellipsoid, becoming 1-septate, colorless, halonate, 12-15 x 5-8 µm; **Pycnidia:** immersed; **conidia:** ellipsoid to ovoid, *c.* 3-5 x 1-1.5 µm; **Spot tests:** thallus K-, C-, KC-, P-; **Secondary metabolites:** none detected.

Substrate and ecology: on trees (*Umbellularia californica*) in open habitats and also on acidic rocks; **World distribution:** southern Europe, Egypt and southern California; **Sonoran distribution:** Santa Monica Mountains and the Channel Islands of southern California, and mountainous areas of Sonora and Chihuahua.



Notes: A careful comparison of Mediterranean and Sonoran material of the this species revealed that the Sonoran specimens fall well within the range of variation of the old world material with respect to pycnidial and thallus characters. Prof. E. Barreno reports one specimen from Spain with filiform conidia.

THROMBIUM

by O. Breuss

Thrombium Wallr., Flora Krypt. Germ. 3: 298 (1831).

Family: Thrombiaceae; Type: *Thrombium epigaeum* (Pers.) Wallr.; No. species: *c.* five world-wide; Selected lit.: Zschacke (1934), and Swinscow (1964).

Life habit: lichenized; **Thallus:** crustose, areolate, granular or film-like, or evanescent, or endolithic; **upper surface:** grayish green or yellowish green to brownish; **photobiont:** primary one a chlorococcoid alga (*Leptosira*),

secondary photobiont absent; algal layer: not well developed; **Ascomata:** perithecial, immersed or sessile; exciple: pale to medium brown or black, without an involucrellum, lacking ostiolar filaments; interascal filaments: present, persistent, not or sparsely branched; **asci:** cylindrical or narrowly clavate, thin-walled; apex: slightly thickened, I+ blue, with a narrow cylindrical axial mass; 8-spored; **ascospores:** hyaline, simple, ellipsoid, thin-walled, smooth, without halo; **Conidiomata:** not seen; **Secondary metabolites:** not detected; **Geography:** widespread but often overlooked; **Substrate:** soil, detritus, rock.

Notes: *"Thrombium" discordans* (Nyl. in Hasse) Zahlbr., found on bark of oak in the San Gabriel Range (Hasse 1903), does not belong to the genus. It has perithecioid apothecial ascocarps and non-amyloid asci.

Key to species of ***Thrombium*** from the Sonoran region:

1. Perithecial wall black throughout; paraphyses *c.* 2.5 µm thick; ascospores 18-26 x 6.5-9 µm ..... ***T. epigaeum***
1. Perithecial wall pale except for the apex; paraphyses *c.* 1.5 µm thick; ascospores 16-20 x 7-8 µm .. ***T. aoristum***

The Species

Thrombium aoristum (Nyl.) Arnold, Flora 53: 486 (1870).

Basionym: *Verrucaria aorista* Nyl., Flora 47: 355 (1864).

Thallus: crustose, thin and indistinct; **upper surface:** greenish, subgelatinous when wet; **Perithecia:** almost globose, up to 0.45 mm diam., fully immersed with only the ostioles showing as black dots; exciple: pale except for the apex, laterally 20-30 µm thick; periphyses: lacking; paraphyses: simple, few to many, *c.* 1.5 µm thick; **asci:** subcylindrical, 70-80 x 16-20 µm, 8-spored; **ascospores:** simple, (sub-) biseriate, ellipsoid, *c.* 16-20 x 7-8 µm; **Spot tests:** all negative; **Secondary metabolites:** none detected.

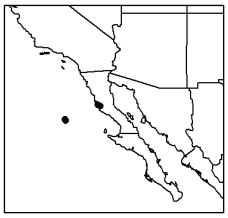
Substrate and ecology: on argillaceous or sandy soil in open habitats; **World distribution:** hitherto only known from France; **Sonoran distribution:** the Santa Monica Mountains in southern California.

Thrombium epigaeum (Pers.) Wallr., Flora Kryptog. Germ. 3: 294 (1831).

Basionym: *Sphaeria epigaea* Pers., Synops. Method. Fung. Add.: 27 (1801); Illustration: Thomson (1997), p. 610.

Thallus: crustose, effuse, film-like, smooth or slightly uneven, or evanescent; **upper surface:** grayish, greenish or yellowish green to brownish, subgelatinous when wet; **Perithecia:** almost globose, up to 0.45 mm in diam., fully immersed with only the ostioles showing as black dots; exciple: dark brown or black, laterally 20-30 µm thick, lacking periphyses; paraphyses: simple, few to many, *c.* 2.5 µm thick; **asci:** subcylindrical, 130-170 x 17-25 µm, 8-spored; **ascospores:** simple, (sub-)biseriate, narrowly ellipsoid, *c.* 18-26 x 7-10 µm; **Spot tests:** all negative; **Secondary metabolites:** none detected.

Substrate and ecology: on loamy or sandy soil, mosses or detritus, in sheltered places from lowlands to alpine regions; **World distribution:** widespread, often in holarctic regions of Eurasia, North and South America, and New Zealand; **Sonoran distribution:** NW Baja California and Guadalupe Island.



THYREA

by M. Schultz

Thyrea A. Massal., Sched. Critic.: 75 (1856).

Family: Lichinaceae; Type: *Thyrea plectopsora* A. Massal.; No. species: 12-15 world-wide; Selected lit.: Henssen and Jørgensen (1990), and Moreno and Egea (1992a).

Life habit: lichenized; **Thallus:** umbilicate, squamulose, subfruticose, foliose, gelatinous when wet; **surface:** black, sometimes grayish pruinose, smooth, granulose, papillose, sometimes isidiate; **anatomy:** ecorticate, heteromerous, with compact or loose central strand of periclinally arranged hyphae and reticulate anatomy at thallus periphery; **photobionts:** primary one a chroococcoid cyanobacterium, secondary photobiont absent; **Ascomata:** absent or present, apothecial, laminal on thallus or marginal, orbicular, immersed to semi-immersed, margin indistinct to distinct, with thalloid rim; **ontogeny:** hemiangiocarpous, forming pycnoascocarps from ascogonia beneath pycnidia; **anatomy:** exciple hyaline, hypothecium hyaline, epithecium pale brownish yellow; **asci:** prototunicate, wall thin, non-amyloid, 8-spored; **ascospores:** simple, ellipsoid, broadly ellipsoid or globose; 5-15 x 3-14 µm; walls: thin, occasionally thickened, hyaline; **Conidiomata:** absent or present, pycnidia laminal or marginal, immersed; **conidia:** ellipsoid or bacilliform, *c.* 3 x 1 µm; **Secondary metabolites:** none detected; **Geography:** cosmopolitan, in arid to semi-humid, tropical, subtropical and warm temperate regions; **Substrate:** limestone and calcareous rock, rarely siliceous rock.

Notes: *Thyrea* differs from *Digitothyrea* in having immersed to semi-immersed, small apothecia, in its sparsely or unbranched thalli and its type of ascoma ontogeny. Foliose species of *Lichinella* are similar in external appearance, but can be separated from *Thyrea* by their polysporous asci and thallinocarpous type of ascomata.

Key to species of ***Thyrea*** from the Sonoran region:

1. Thallus lobes erect, at least with ascending margins, bluish-gray pruinose, lobes 0.25-0.45 mm thick, often with small, globose isidia, surface otherwise smooth ..... ***T. confusa***
1. Thallus lobes adpressed, dull black with downcurved margins, lobes 0.5-1 mm thick, lacking globose isidia, upper surface distinctly papillose-warty ***T. pachyphylla***

The Species

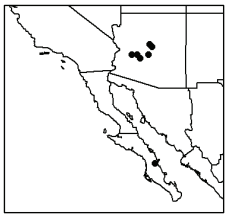
Thyrea confusa Henssen, Lichenologist 22: 146 (1990).

Synonyms: *Thyrea pulvinata* auct. non (Schaer.) A. Massal.; Illustrations: Wirth (1995), p. 907; Moreno and Egea (1992a), p. 64; Brodo et al. (2001), p. 682; and Fig. 101 below.

Fig. 101. *Thyrea confusa*, photo by M. Schultz.

Thallus: foliose, umbilicate, small cushions or rosettes up to 20 mm wide, lobes 2-5 mm wide or long, erect or if not at least margins ascending, irregularly branched, broadly rounded; **surface:** bluish-gray pruinose, partially also

black, often with small, globose isidia, otherwise smooth; **Apothecia:** not seen in Sonoran material, elsewhere rarely present, small, immersed to semi-immersed, zeorine; disc: slightly depressed, brownish, with persisting thalline margin; exciple: up to 10 µm wide, hyaline; hymenium: up to 150 µm high, hyaline, amyloid; paraphyses: distinctly septate, sparingly branched and anastomosing, apical cells slightly thickened up to 3 µm; **asci:** 8-spored; **ascospores:** simple, hyaline, globose to broadly ellipsoid, 7.5-10 x 5-7.5 µm; walls: thin; **Pycnidia:** immersed, globose, up to 0.1 mm wide; **conidia:** cylindrical, 3 x 1 µm; **Spot tests:** all negative; **Secondary metabolites:** none detected.



Substrate and ecology: on limestone on shaded, steep or vertical rock faces in chaparral or woodlands; **World distribution:** North America, Europe, Socotra Island, probably Asia and North Africa; **Sonoran distribution:** limestone deposits in central Arizona and Baja California Sur.

Notes: Older floras usually listed the species under the name *Thyrea pulvinata* auct., that may in fact represent *Thyrea confusa* but possibly also *Lichinella iodopulchra* (Henssen and Jørgensen 1990). *Lichinella iodopulchra* may also have pruinose lobes and deeply lobate thalli especially when old. However, it is distinguished by the absence of globose isidia, its usually down curved margins, its type of ascomata (thallinocarp), and the number of spores (>16). Also similar is *Lichinella nigritella*, which is usually deeply divided, with more slender and streched, erect lobules that are normaly not pruinose. The latter species also has larger globose to squamulose isidia; if it is fertile, then it is also distinguished by the type of ascomata (thallinocarp) and spore number (>16).

Thyrea pachyphylla (Müll. Arg.) Henssen, Lichenologist 22: 146 (1990).

Basionym: *Omphalaria pulvinata* var. *pachyphylla* Müll. Arg., Bull. Soc. Mur. Val. 10: 55 (1881); Synonyms: *Thyrea pulvinata* var. *pachyphylla* (Müll.Arg.) Zahlbr.; Illustrations: Moreno and Egea (1992a), p. 65 and (1992b), pp. 217 & 218; and Fig. 102 below.

Thallus: umbilicate, monophyllous or divided into 2-6 broadly rounded lobules (2-5 mm wide), up to 15 mm long, flat, margins downcurved; **surface:** dull black, distinctly warty-papillose and appearing reticulate, "papillae/warts" 0.1-0.2 mm wide, 0.1-0.15 mm high, epruinose, lacking isidia; lobules 0.5-1 mm thick; **Apothecia:** not seen in Sonoran material, elsewhere rarely developed, small, laminal, immersed, disc punctiform, with persisting thalline margin; exciple: probably thin, hyaline; **asci:** 8-spored; **ascospores:** simple, hyaline, globose or broadly ellipsoid, 8-12 x 6-8 µm; walls: thin; **Pycnidia:** laminal, immersed, globose, 0.1-0.15 mm wide; **conidia:** ellipsoid, 2-3 x 1-1.5 µm; **Spot tests:** all negative; **Secondary metabolites:** none detected.

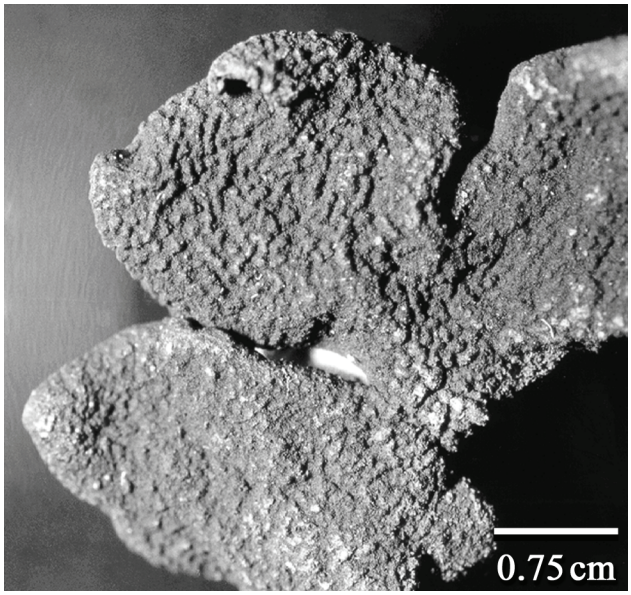


Fig. 102 *Thyrea pachyphylla*, photo by M. Schultz.

Substrate and ecology: on limestone on damp, vertical rock faces and along seepage tracks; montane; **World distribution:** SW Europe, NW Africa, SW North America; **Sonoran distribution:** Sonora.

Notes: Large thalli of *Lichinella iodopulchra* may be similar, however they lack the warty-papillose to reticulate upper surface texture.

TOMASELLIA

by A. Aptroot

Tomasellia A. Massal., Flora 39: 283 (1856).

Family: Xanthopyreniaceae; Type: *Tomasellia arthonIoides* (A. Massal.) A. Massal.; No. species: 10 worldwide; Selected lit.: Harris (1995), and Purvis et al. (1992).

Life habit: non-lichenized, saprophytic; **Thallus:** crustose, mostly immersed in the substrate, inconspicuous, causing a slight bleaching of the bark surface; **photobiont:** absent; **Ascomata:** perithecial, circular, ellipsoid or irregular in outline, usually aggregated in pseudostromata; **ascomatal wall:** black, not continuous below the hamathecium; **hamathecium:** composed of branched pseudoparaphyses, not anastomosing, non-amyloid; **asci:** bitunicate, pyriform to clavate, with tholus, non-amyloid, 8-spored; **ascospores:** hyaline or pale brown, clavate to ellipsoid, 1-3-septate with eusepta, 15-26 x 3-8 µm; walls: not ornamented; **Conidiomata:** pycnidial, black; **conidia:** bacilliform, simple, colorless; **Secondary metabolites:** absent; **Geography:** cosmopolitan, but most common in the tropics; **Substrate:** mostly on bark, but also on wood or palm roots.

Notes: Sonoran species of this genus have recently been classified in two different genera in two different families (Harris 1995), but the differences between species of *Tomasellia* are not very discrete and do not warrent a separation at the generic (let alone family) level. The genus is characterized by the usually aggregated perithecioid ascomata and large-celled, never anastomosing, pseudoparaphyses. It is often confused with *Arthonia*, which has apothecia with roundish asci that may somewhat resemble compound perithecia.

Key to the species of ***Tomasellia*** for the Sonoran region:

1. Ascospores 3-septate when mature 2
1. Ascospores remaining 1-septate ..... ***T. eschweileri***
2. Ascospores over 17 µm long ..... ***T. californica***
2. Ascospores up to 17 µm long ..... ***T. americana***

The Species

Tomasellia americana (Willey) R. C. Harris, in Tucker and R. C. Harris, Bryologist 83: 19 (1980).

Basionym: *Cyrtidula americana* Minks *ex* Willey, Enum. Lich. New Bedford: 33 (1892); Illustration: Harris (1975), p. 231 as *Cyrtidula americana*.

Thallus*:* continuous, smooth, immersed in the substrate, whitish; **photobiont:** absent; **Perithecia:** hemispherical, black, immersed in groups of 1-5 below clypeus, *c.* 0.1-0.2 mm diam.; **ascomatal wall:** black, absent below the hamathecium; **hamathecium:** composed of branched pseudoparaphyses, not anastomosing, filaments *c.* 2 µm wide, not inspersed with oil droplets; **asci:** pyriform, *c.* 50-70 x 15-20 µm, with 8, irregularly arranged ascospores; **ascospores:** hyaline, clavate, 3-septate (starting with a constricted, submedian euseptum), 15-17 x 3-4.5 µm; walls: not ornamented, without a gelatinous sheath; **Spot tests:** K-, C-, KC-, P-, UV negative; **Secondary metabolites:** none detected.

Substrate and ecology: on bark of *Platanus*; **World distribution:** very rare, apparently endemic in North America (California, Louisiana and Massachusetts); **Sonoran distribution:** only collected once in southern California.

Tomasellia californica (Zahlbr.) R. C. Harris, in Tucker & Jordan, Wasmann J. Biol. 36: 87 (1979) [nom. inval., validated herewith].

Basionym: *Mycoporellum californicum* Zahlbr., Ann. Mycol. 10: 363 (1912); Synonym: *Mycoporum californicum* (Zahlbr.) R. C. Harris; Illustration: Harris (1975), p. 231.

Thallus: continuous, smooth, immersed in the substrate, whitish; **photobiont:** absent; **Perithecia:** hemispherical, black, immersed in groups of 1-5 below clypeus, 0.3-0.7 mm diam.; **ascomatal wall:** black, absent below the hamathecium; **hamathecium:** pseudoparenchymatous, without filaments, inspersed with and dissolving into oil droplets; **asci:** pyriform, *c.* 60-75 x 15-25 µm, with 8, irregularly arranged ascospores; **ascospores:** hyaline, clavate, 3-septate (starting with a supramedian euseptum), 17-22 x 5-7 µm; walls: not ornamented, without a gelatinous sheath; **Spot tests:** K-, C-, KC-, P-, UV negative; **Secondary metabolites:** none detected.

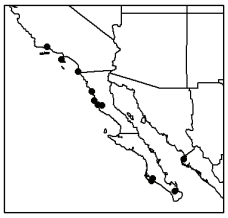
Substrate and ecology: on bark of various woody plants; **World distribution:** possibly endemic in western North America; **Sonoran distribution:** only found in southern California, including the Channel Islands.

Tomasellia eschweileri (Müll. Arg.) R. C. Harris, in Tucker and R. C. Harris, Bryologist 83: 19 (1980).

Basionym: *Mycoporellum eschweileri* Müll. Arg., Flora 71: 526 (1888); Synonyms: *Mycoporellum hassei* Zahlbr., *Mycoporum eschweileri* (Müll. Arg.) R. C. Harris, *Mycoporum lacteum* (Ach.) R. C. Harris, *Tomasellia lactea* (Ach.) R. C. Harris; Illustration: Harris (1975), p. 233.

Thallus: continuous, smooth, immersed in the substrate, whitish; **photobiont:** absent; **Perithecia:** hemispherical, black, immersed in groups of 1-10 below clypeus, *c.* 0.4-0.7 mm diam.; **ascomatal wall:** black, absent below the hamathecium; **hamathecium:** pseudoparenchymatous, without filaments, inspersed with and dissolving into oil droplets; **asci:** pyriform, *c.* 50-60 x 15-20 µm, with 8, irregularly arranged ascospores; **ascospores:** hyaline, clavate, 1-septate with a supramedian euseptum, 17-25 x 5-8 µm; walls: not ornamented, without a gelatinous sheath; **Spot tests:** K-, C-, KC-, P-, UV negative; **Secondary metabolites:** none detected.

Substrate and ecology: on bark of various woody plants, including *Eucalyptus, Machaerocereus, Nicotiana, Pachycereus, Pseudotsuga*; **World distribution:** pantropical and extending norhward into southern temperate areas; **Sonoran distribution:** one of the most common pyrenocarps on bark, with numerous records from southern California (including the Channel Islands), Baja California, Baja California Sur and Sinaloa.



Notes: A common, pantropical species, which is especially abundant in coastal regions (Harris 1975). It is accepted here in a broad sense, including *Tomasellia lactea* (Ach.) R.C. Harris, which is only characterized by larger, though overlapping ascospore dimensions. These two taxa were recently classified in *Mycoporum* (Harris 1995). The occurrence on cacti and barely woody plants like *Nicotiana* is remarkable.

TONINIA

by E. Timdal

Toninia A. Massal., Ric. auton. lich. crost.: 107 (1852), nom. cons.

Family: Bacidiaceae; Type: *Toninia cinereovirens* (Schaer.) A. Massal.; No. species: *c.* 50 world-wide; Selected lit.: Timdal (1991).

Life habit: lichenized or not, lichenicolous (especially when young) or not; **Thallus:** absent, endolithic, crustose, or squamulose, attached by the whole lower surface or basal end of squamule; **areoles/squamules:** dispersed, adjacent, imbricate, or ascending, 2-10 mm wide, rounded to

elongated or bullate, with entire, crenulate or lobed margin; **upper surface:** from white to dark gray, green, or brown, sometimes rose or pale yellow, dull to shiny, epruinose to densely white pruinose, smooth to deeply fissured; vegetative dispersal units lacking; **upper cortex:** varying from absent to 500 µm thick, containing remnants of algae (chlor-zinc-iodine!), usually consisting of an upper epinecral layer and a lower stainable layer, the latter composed of thick- to rather thin-walled, anticlinally oriented hyphae with shortly thread-like, angular, or rounded lumina, often containing crystals of calcium oxalate, rarely lichen substances; algal layer: 30-100 µm thick, horizontally continuous or rarely discontinuous; **photobiont:** primary one a chlorococcoid alga, secondary photobiont absent, algal cells 10-15 µm diam.; **medulla:** white, of intricately interwoven hyphae, I-, often containing lichen substances and/or calcium oxalate; **lower cortex:** poorly to well developed, composed of periclinally or anticlinally oriented hyphae, sometimes containing calcium oxalate; **lower surface:** white to brown; **Ascomata:** apothecial, laminal or marginal, sessile, with a constricted base, simple or rarely somewhat conglomerate, usually weakly concave to weakly convex and marginate when young, later often becoming more convex and immarginate, up to 5 (-10) mm diam., black, usually dull, epruinose or with white pruina of calcium oxalate; exciple: annular, composed of radiating, thick-walled, conglutinated hyphae with rounded to narrowly cylindrical lumina, varying from having a pale or colorless inner part and a darker gray, green, or brown rim, to being dark brown throughout; hypothecium: dark brown to colorless, composed of intricately interwoven hyphae, sometimes containing crystals of calcium oxalate, I-; epithecium: gray (K+ violet, N+ violet), green (K-, N+ violet or K+ violet/brown, N-), reddish brown (K+ red, N-), dull brown (K-, N-), or pale olivaceous brown to colorless (K-, N-) (pigments sometimes mixed), often containing crystals of calcium oxalate, rarely crystals of lichen substances; hymenium: hyaline, I+ blue, 50-80 µm high; paraphyses: straight, sparingly branched and anastomosing, not conglutinated, thin-walled, with an apical cell which is distinctly swollen and surrounded by a ± well developed gelatinous pigment cap or sometimes containing pigment in the cell wall; **asci:** clavate, surrounded by a gelatinous, amyloid sheet, with a well developed, amyloid tholus containing a deeper amyloid, conical zone around the axial mass and a well developed, conical, often pointed ocular chamber (*Bacidia*-type), 8-spored; **ascospores**: colorless, simple to 7 (-9) septate, broadly ellipsoid to acicular, smooth, without halo; **Conidiomata:** pycnidial, laminal, immersed or partly protruding, with colorless or pale brown to black ostiole, with short, sparingly branched conidiophores; **conidia:** acrogenous, filiform, curved; **Secondary metabolites:** usually none, but in some species terpenoids, depsides, usnic acid, or fatty acids; **Geography**: arctic to subtropical regions of the world, highest diversity in arid areas; **Substrate:** soil and rock, often calciferous.

Notes: Many species start their development on the thallus of other lichens. Some remain lichenicolous, but others become autonomous. The hosts referred to below may be visible only at an early stage, and may even be facultative in some species. Only a few secondary metabolites have been identified in *Toninia*. Most are terpenoids, and some species and subspecies show diagnostic patterns on the chromatograms (see Timdal [1991]).

Key to the species of ***Toninia*** in the Sonoran region:

1. Epithecium gray, K+ violet, N+ violet 2
1. Epithecium colorless, green, or brown, K- and/or N- . 7

2. Ascospores (1-) 3-septate, bacilliform to acicular .... ***T. submexicana***
2. Ascospores 1-septate, ellipsoid to fusiform 3

3. Ascospores ellipsoid, thallus crustose, areolate, epruinose ..... ***T. weberi***
3. Ascospores fusiform, thallus squamulose, pruinose or not 4

4. Upper surface ± entirely covered by white pruina; thallus rosulate or not 5
4. Upper surface at least partly epruinose; thallus not rosulate 6

5. Thallus rosulate, up to 40 mm diam.; pruina farinose; thallus lacking secondary metabolites ..... ***T. candida***
5. Thallus not rosulate, indeterminate; pruina granulose; thallus usually containing terpenoids .... ***T. subdiffracta***

6. Upper surface usually shiny, usually with regular, shallow fissures, usually epruinose; spores 10-16.5 x 3.5-4.5 µm; thallus usually containing terpenoids .... ***T. massata***
6. Upper surface dull or faintly shiny, smooth or sometimes with a few shallow fissures, usually partly pruinose; spores 12-24 x 3-5 µm; thallus not containing terpenoids ..... ***T. sedifolia***

7. Epithecium reddish brown, K+ red, N- 8
7. Epithecium colorless, green or medium brown, K-, N+ violet or N- 11

8. Upper surface reddish or olivaceous brown to dark brown, epruinose ..... ***T. ruginosa***
8. Upper surface grayish white to medium brown, usually pruinose 9

9. Ascospores 1-septate, squamules up to 2 mm diam. .... ***T. australis***
9. Ascospores (1-) 3-septate, squamules up to 3 (-5) mm diam. 10

10. Upper surface smooth ..... ***T. hosseusiana***
10. Upper surface with deep, regular fissures ***T. lutosa***

11. Epithecium colorless to pale olivaceous brown, N-, containing crystals dissolving in K; upper surface pale yellowish gray; thallus containing gyrophoric acid, usnic acid, and terpenoids ..... ***T. wetmorei***
11. Epithecium green or brown, not containing crystals dissolving in K; upper surface various; thallus containing terpenoids or no secondary substances 12

12. Upper surface with punctiform impressions or pores; squamules convex to bullate ..... ***T. tristis***
12. Upper surface lacking impressions and pores; squamules/areoles plane to moderately convex, or absent 13

13. Upper surface pale yellow, with deep, regular fissures ..... ***T. sculpturata***
13. Upper surface of different color, without regular fissures 14

14. Epithecium brown, N- ..... ***T. nashii***
14.Epithecium olivaceous green to pure green, N+ violet

15. Species not lichenized, growing in the thallus of *Lecania* ..... ***T. talparum***
15. Species lichenized, lichenicolous or not 16

16. Thallus crustose, rimose to areolate, yellowish to reddish brown ..... ***T. philippea***
16. Thallus squamulose, white to dark brown 17

17. Hypothecium and exciple dark reddish brown .... ***T. aromatica***
17. Hypothecium and inner part of exciple pale brown to colorless 18

18. Spores 1- to 3-septate, ellipsoid to bacilliform; squamules usually with a somewhat darker margin ..... ***T. cinereovirens***
18. Spores 3- to 7-septate, acicular; squamules with a concolorous margin ..... ***T. squalida***

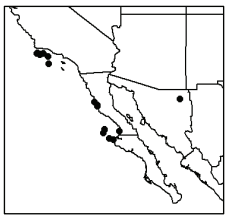
The Species

Toninia aromatica (Sm.) A. Massal., Framm. Lichenogr.: 24 (1855).

Basionym: *Lichen aromaticus* Sm., in Smith & Sowerby, Engl. bot. 25: Tab. 1777 (1807); Selected synonyms: *Toninia affinis* Vězda, *Toninia fusispora* (Körb.) Th. Fr., *Toninia pelophila* Poelt & Vězda; Illustration: Timdal (1991), p. 40.

Life habit: lichenized, lichenicolous or not; **Thallus:** squamulose; **squamules:** up to 4 mm diam., dispersed or adjacent, rounded or usually more irregular, weakly concave to weakly convex; **upper surface:** pale gray, olivaceous, or medium to dark brown, epruinose or partly to entirely pruinose, dull, smooth, lacking pores and pseudocyphellae, often with maculae in convex parts; **margin:** concolorous with upper surface; **upper cortex:** up to 90 µm high, lacking calcium oxalate; **Apothecia:** up to 1.5 mm diam., plane and marginate, sometimes becoming convex and immarginate, epruinose or faintly pruinose; exciple: dark reddish brown throughout; hypothecium: dark reddish brown; epithecium: bright to dark green (K-, N+ violet); **asci:** clavate, 8-spored; **ascospores:** ellipsoid to bacilliform, 1-3 septate, 12-22.5 x 4-5.5 µm; **Pycnidia:** laminal, immersed; **conidia:** filiform; **Spot tests:** all negative; **Secondary metabolites:** none detected.

Substrate and ecology: on soil and rock in open habitats, up to 1370 m; **Host:** crustose green algae-lichens or rarely cyanolichens; **World distribution:** widely distributed in the Northern Hemisphere, Australia, and New Zealand; **Sonoran distribution:** locally common on the coast, rare inland, in California, Baja California, Baja California Sur and Sonora.

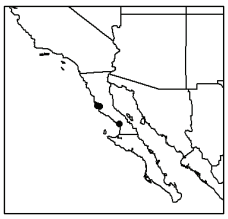


Toninia australis Timdal, Opera Bot. 110: 45 (1992).

Illustration: Timdal (1991), p. 46.

Life habit: lichenized, lichenicolous or not; **Thallus:** squamulose; **squamules:** up to 2 mm diam., scattered to adjacent, ± rounded, plane to moderately convex; **upper surface:** pale to dark gray or olivaceous to medium brown, epruinose or partly pruinose, dull or shiny, smooth or with shallow fissures, lacking pores and pseudocyphellae; **margin:** concolorous with upper surface; **upper cortex:** up to 100 µm high, lacking or containing calcium oxalate; **Apothecia:** up to 1.2 mm diam., plane and marginate when young, later often convex and immarginate, epruinose or faintly pruinose; exciple: dark reddish brown in the rim, paler in inner part; hypothecium: pale brown to colorless; epithecium: reddish brown (K+ red, N-); **asci:** clavate, 8-spored; **ascospores:** ellipsoid, 1-septate, 10-19.5 x 3-5 µm; **Pycnidia:** laminal, immersed; **conidia:** filiform; **Spot tests:** all negative; **Secondary metabolites:** none detected.

Substrate and ecology: on soil in open habitats near the coast, up to 380 m; **Host**: cyanolichens; **World distribution:** southern Africa, Australia, New Zealand, southernmost South America and Baja California; **Sonoran distribution:** rare in Baja California.



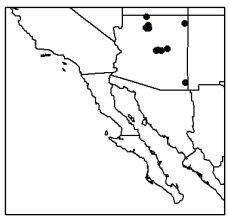
Notes: The species is morphologically quite similar to poorly developed specimens of *T. sedifolia*. The epithecial pigment and the spore shape are the main distinguishing characters. There are three other chemotypes of *Toninia australis* elsewhere.

Toninia candida (Weber) Th. Fr., K. svenska Vetensk.-Akad. Handl. 7, 2: 33 (1867).

Basionym: *Lichen candidus* Weber, Spicil. fl. goett.: 193 (1778); Illustration: Timdal (1991), p. 51.

Life habit: lichenized, lichenicolous at least when young; **Thallus:** squamulose, rosulate, up to 40 mm diam.; **squamules:** up to 5 mm diam., more less scattered and rounded when young, later adjacent or sometimes slightly imbricate, marginal squamules weakly concave to weakly convex, forming ± radiating lobes, central squamules more rounded and convex; **upper surface:** white, entirely covered by farinose pruina, dull, smooth, lacking pores and pseudocyphellae; **margin:** concolorous with upper surface; **upper cortex:** up to 60 µm high, containing calcium oxalate; **Apothecia:** up to 2 mm diam., remaining ± plane and marginate, densely pruinose; exciple: dark gray in the rim, reddish brown in inner part; hypothecium: reddish brown; epithecium: gray (K+ violet, N+ violet); **asci:** clavate, 8-spored; **ascospores:** fusiform, 1-septate, 15-24 x 3-4 µm; **Pycnidia:** not seen; **Spot tests:** all negative; **Secondary metabolites:** none detected.

Substrate and ecology: on calciferous rock on steep to overhanging rock walls, usually somewhat shady, in pinyon-juniper woodland and conifer forests at 1650-2130 m; **Host:** cyanolichens, especially *Collema*; **World distribution:** widely distributed in the temperate region of the Northern Hemisphere; **Sonoran distribution:** uncommon in Arizona.

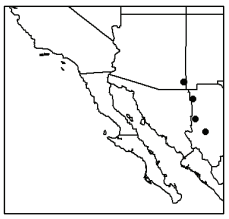


Toninia cinereovirens (Schaer.) A. Massal., Ric. auton. Lich. crost.: 107 (1852).

Basionym: *Lecidea cinereovirens* Schaer., Lich. helvet. Spicil. [fasc. 3]: 109 (1828); Selected synonyms: *Toninia olivaceoatra* H. Magn., *Toninia sbarbaronis* de Lesd.; Illustration: Timdal (1991), p. 53.

Life habit: lichenized, lichenicolous or not; **Thallus:** squamulose; **squamules:** up to 3 mm diam., scattered to adjacent or weakly proliferating, rounded to elongated, often lobed, weakly concave to weakly convex; **upper surface:** olivaceous brown to grayish brown or dark brown, epruinose, dull or slightly shiny, smooth or with shallow fissures, lacking pores and pseudocyphellae; **margin:** usually somewhat darker than the upper surface; **upper cortex:** up to 100 µm high, lacking calcium oxalate; **Apothecia:** up to 1 mm diam., plane and marginate or sometimes becoming convex and immarginate, epruinose or faintly pruinose; exciple: dark brown in the rim, pale brown to colorless in inner part; hypothecium: pale brown to colorless; epithecium: bright to dark green (K-, N+ violet); **asci:** clavate, 8-spored; **ascospores:** ellipsoid to bacilliform, 1-3 septate, 13.5-30.5 x 3-4.5 µm; **Pycnidia**: laminal, immersed or partly protruding; **conidia:** filiform; **Spot tests:** all negative; **Secondary metabolites:** none detected.

Substrate and ecology: on acidic rock in open habitats or in Madrean oak and pine forests, at 1600-1830 m; **Host:** cyanolichens; **World distribution:** widely distributed in the temperate region of the Northern Hemisphere, Kenya, Peru; **Sonoran distribution:** rare in southeastern Arizona and Chihuahua.



Toninia hosseusiana Gyeln., Ann. Hist.-Nat. Mus. Nat. Hung. 35, Bot.: 98 (1942).

Illustration: Timdal (1991), p. 67.

Life habit: lichenized, lichenicolous or not; **Thallus:** squamulose; **squamules:** up to 3 mm diam., scattered to adjacent, rounded or irregular to weakly elongated, plane to moderately convex; **upper surface:** white, entirely covered by farinose to granulose pruina, dull, smooth, lacking pores and pseudocyphellae; **margin:** concolorous with upper surface; **upper cortex:** up to 30 µm high, containing calcium oxalate; **Apothecia:** up to 2 mm diam., ± plane and marginate, sometimes becoming convex and immarginate, faintly to densely pruinose; exciple: dark reddish brown in the rim, paler in inner part; hypothecium: pale brown to colorless; epithecium: reddish brown (K+ red, N-); **asci:** clavate, 8-spored; **ascospores:** bacilliform to acicular, (1-) 3 septate, 29-37 x 2.5-3.5 µm; **Pycnidia:** laminal, immersed; **conidia:** filiform; **Spot tests:** all negative; **Secondary metabolites:** none detected.

Substrate and ecology: on acidic rock on steep to overhanging rock wall in Madrean oak-pine forest at 1800 m; **Host:** cyanolichens; **World distribution:** Mexico (Chihuahua and Oaxaca) and South America (Argentina, Peru, and Venezuela); **Sonoran distribution:** Chihuahua (single locality in Barranca del Cobre).

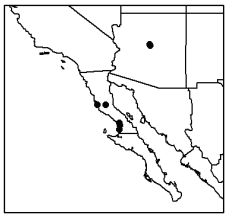
Notes: The spores are unusually long in the Chihuahuan specimen. Based on measurement of 65 spores in material from Oaxaca and South America, Timdal (1991) described the spores as narrowly ellipsoid to bacilliform, 16.5-26.5 x 3.5-5 µm. South American material sometimes contain terpenoids. The species is morphologically quite similar to *T. subdiffracta*; they differ mainly in the pigments in the apothecium, in spore shape, and in secondary chemistry.

Toninia lutosa (Ach.) Timdal, Opera Bot. 110: 69 (1992).

Basionym: *Lecidea lutosa* Ach., Lichenogr. univers.: 182 (1810); Synonyms: *Catillaria crystallifera* Kilias, *Toninia verrucosa* (A. Massal.) Flagey, *Toninia violacea* de Lesd.; Illustration: Timdal (1991), p. 69.

Life habit: lichenized, lichenicolous or not; **Thallus:** squamulose; **squamules:** up to 3 (-5) mm diam., scattered to adjacent, rounded, plane to moderately convex, sometimes with a central depression; **upper surface:** white to pale gray, partly to entirely covered by farinose pruina, dull, with deep, regular fissures, lacking pores and pseudocyphellae; **margin:** concolorous with upper surface or white; **upper cortex:** up to 220 µm high, containing calcium oxalate; **Apothecia:** up to 1.3 mm diam., ± plane and marginate, epruinose or faintly pruinose; exciple: dark reddish brown in the rim, paler in inner part; hypothecium: pale brown to colorless; epithecium: reddish brown (K+ red, N-); **asci:** clavate, 8-spored; **ascospores:** ellipsoid to bacilliform, 1-3 septate, 12-20 x 3-4.5 µm; **Pycnidia**: laminal, immersed; **conidia:** filiform; **Spot tests:** all negative; **Secondary metabolites:** none detected.

Substrate and ecology: on soil and calciferous rock in coastal scrub up to 1070 m and in interior pinyon-juniper woodland, up to 2200 m; **Host:** cyanolichens; **World distribution:** scattered in arid areas in the temperate region of the Northern Hemisphere, Namibia; **Sonoran distribution:** rare in Arizona and Baja California.

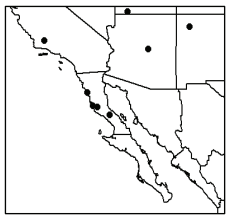


Toninia massata (Tuck.) Herre, Proc. Wash. Acad. Sci. 12: 103 (1910).

Basionym: *Lecidea massata* Tuck., Lich. Calif.: 25 (1866); Synonyms: *Toninia glaucomela* (Nyl.) Boistel, *Toninia kelleri* (Elenkin) H. Olivier; Illustration: Timdal (1991), p. 71.

Life habit: lichenized, lichenicolous or not; **Thallus:** squamulose; **squamules:** up to 2 mm diam., scattered to adjacent or rarely indistinctly imbricate, rounded or irregularly lobed, weakly convex to bullate; **upper surface:** olivaceous or grayish green to brown, epruinose or partly covered by farinose pruina, usually shiny, often with regular, shallow fissures, lacking pores and pseudocyphellae; **margin:** concolorous with upper surface; **upper cortex:** up to 80 µm high, lacking calcium oxalate; **Apothecia:** up to 1.5 (-2) mm diam., plane and marginate when young, later convex and immarginate, epruinose; exciple: dark gray in the rim, pale brown to medium brown in inner part; hypothecium: pale or reddish brown to colorless; epithecium: gray (K+ violet, N+ violet); **asci:** clavate, 8-spored; **ascospores:** fusiform, 1-septate, 10-16.5 x 3.5-4.5 µm; **Pycnidia:** not seen; **Spot tests:** all negative; **Secondary metabolites:** none or undetermined terpenoids (chemotype D).

Substrate and ecology: on soil in open habitats and in pinyon-juniper woodlands, up to 1530 m; **Host:** cyanolichens; **World distribution:** Mediterranean Europe, Macaronesia, Russia, western North America; **Sonoran distribution:** rare in Arizona and Baja California.



Notes: This rarely collected species resembles *T. sedifolia*, but differs in having more flattened squamules which never have a white margin, a more shiny and finely fissured upper cortex, shorter spores, and in usually containing terpenoids (chemotype D).

Toninia nashii Timdal, **sp. nov.**

Diagnosis: *Thallus crustaceus, brunneus, ecorticatus. Epithecium brunneum, K-, N-. Ascosporae bacilliformes, curvatae, (3-) 7-septatae, 24.5-34.5 x 3-4 µm.*

Type: U.S.A., California, Santa Barbara Co., San Miguel Island, secondary ridge crest on S side of Green Mountain, 34°01’55"N, 120°22’45"W, *c.* 180 m, slight dpression with bare soil, on sandstone, 1998, Nash 41464 (ASU, holotype; O, isotype).

Life habit: lichenized, not lichenicolous; **Thallus:** granular to areolate; **areoles:** up to 2 mm diam., irregular and often forming a ± continuous crust; **upper surface:** grayish brown, ecorticate, scurfy, epruinose, dull, lacking pores and pseudocyphellae; **margin:** concolorous with upper surface; **upper cortex:** lacking; **Apothecia:** up to 1

mm diam., remaining ± plane and marginate or plane and marginate when young, later convex and immarginate, epruinose; exciple: brownish black in the rim, reddish brown in inner part; hypothecium: reddish brown to dark brown; epithecium: medium brown, (K-, N-); **asci:** clavate, 8-spored; **ascospores:** bacilliform, slightly curved, (3-) 7-septate, 24.5-34.5 x 3-4 µm; **Pycnidia:** not seen; **Spot tests:** all negative; **Secondary metabolites:** none detected.

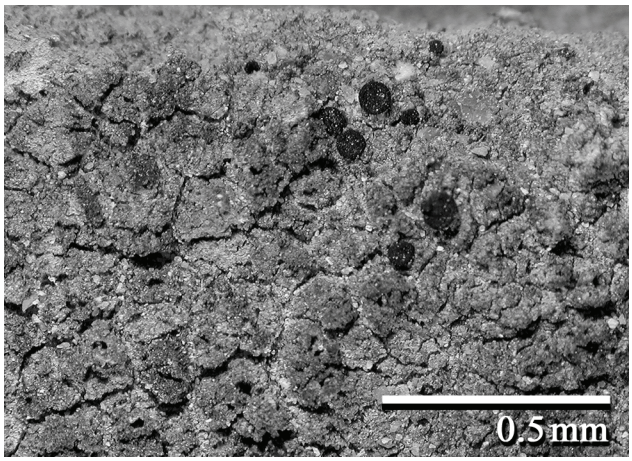


Fig. 103. *Toninia nashii*, photo by E. Timdal.

Substrate and ecology: on sandstone in open habitat at the coast, at *c.* 180 m; **Host:** none; **World and Sonoran distribution:** California (San Miguel Island, single locality).

Notes: *Toninia nashii* differs from the other crustose species of *Toninia* in having a medium brown, K-, N- epithecium and long, slightly curved, mainly 7-septate spores. *Toninia mesoidea* (Nyl.) Zahlbr. and *T. philippea* have a green, K-, N+ violet epithecium; the former more shortly bacilliform (13-17.5 x 5-6.5 µm), 3-septate spores, the latter ellipsoid, 1-septate spores. *Toninia pennina* (Schaer.) Gyelnik and *T. weberi* have a gray, K+ violet, N+ violet epithecium and ellipsoid, 1-septate spores. It is possible that the thallus described above belongs to a host lichen, not *T. nashii*. In that case, the most similar species would be *T. subfuscae* (Arnold) Timdal, which differs in having a greenish, K-, N+ violet epithecium and shorter (9.5-16 × 4-5.5 µm), 1- to 3-septate spores.

Toninia philippea (Mont.) Timdal, Opera Bot. 110: 79 (1992).

Basionym: *Lecidea philippea* Mont., Ann. Sci. nat., bot., Ser 3, 12: 291 (1849); Selected synonyms: *Catillaria kansuensis* H. Magn., *Catillaria philippea* (Mont.) A. Massal., *Catillaria riparia* (Müll. Arg.) Zahlbr.; Illustration: Timdal (1991), p. 80.

Life habit: lichenized, not lichenicolous; **Thallus:** rimose to granular or areolate; **areoles:** up to 0.8 (-1.2) mm diam., adjacent, angular, plane to moderately convex; **upper surface:** yellowish to reddish brown, epruinose, dull, smooth, lacking pores and pseudocyphellae; **margin:** concolorous with upper surface; **upper cortex:** up to 40 µm high, lacking calcium oxalate; **Apothecia:** up to 0.7 mm diam., remaining ± plane and marginate or plane and marginate when young, later convex and immarginate, epruinose or faintly pruinose; exciple: greenish brown to dark green in the rim, pale brown to reddish brown in inner part; hypothecium: dark reddish brown; epithecium: bright to dark green (K-, N+ violet); **asci:** clavate, 8-spored; **ascospores:** ellipsoid, 1-septate, 10-15.5 x 4.5-6 µm; **Pycnidia**: laminal, immersed or partly protruding; **conidia:** filiform; **Spot tests:** all negative; **Secondary metabolites:** none detected.

Substrate and ecology: on sandstone in pinyon-juniper woodland at 1890 m; **Host:** none; **World distribution:** widely distributed, but scattered, in the Northern Hemisphere; **Sonoran distribution:** northern Arizona (single locality).

Toninia ruginosa (Tuck.) Herre, Proc. Wash. Acad. Sci. 12: 103 (1910).

Basionym: *Lecidea ruginosa* Tuck., Lich. Calif.: 25 (1866); Illustration: Timdal (1991), p. 89.

Life habit: lichenized, lichenicolous or not; **Thallus:** squamulose; **squamules:** up to 5 mm diam., adjacent or sometimes forming a ± continuous crust, rounded or irregularly lobed, weakly convex to bullate; **upper surface:** reddish brown or olivaceous brown to dark brown, epru-

inose, dull or shiny, smooth or with shallow fissures, lacking pores and pseudocyphellae; **margin:** concolorous with upper surface; **upper cortex:** up to 100 µm high, lacking calcium oxalate; **Apothecia:** up to 1.5 mm diam., remaining ± plane and marginate or plane and marginate when young, later convex and immarginate, epruinose or faintly pruinose; exciple: dark reddish brown in the rim, paler in inner part; hypothecium: pale brown to colorless; epithecium: reddish brown (K+ red, N-); **asci:** clavate, 8-spored; **ascospores:** narrowly ellipsoid to acicular, 1-7 (9) septate, 12-42 x 3-4.5 µm; **Pycnidia:** laminal, immersed; **conidia:** filiform; **Spot tests:** all negative; **Secondary metabolites:** none detected.

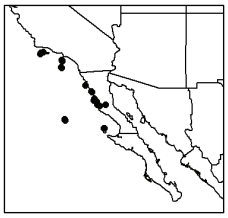
Substrate and ecology: on soil and rock in open habitats and woodlands, up to 2470 m; **Host**: cyanolichens; **World distribution:** widely distributed in temperate western North America, rare in western Europe, Greenland, and Tadzhikistan; **Sonoran distribution:** rather common in Arizona, California, Baja California, Baja California Sur and Chihuahua.

Note: Two subspecies were recognized by Timdal (1991), one widely distributed and one restricted to coastal California and Baja California. Intermediate specimens occur in the area of overlap.

Ssp. *pacifica* Timdal, Opera Bot. 110: 90 (1992).

Illustration: Timdal (1991), p. 89.

Squamules: up to 5 mm diam., dispersed to adjacent, bullate; **upper surface:** medium brown to reddish brown; **ascospores:** narrowly ellipsoid to bacilliform, 1- to 3 (-4) septate, 12-31 x 3-4.5 µm.

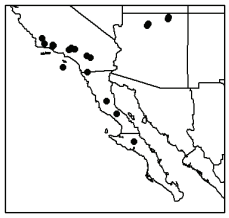


Substrate and ecology: on soil and rock in Californian coastal scrub and Vizcaino subdivision of Sonoran Desert, up to 800 m; **Host:** cyanolichens; **World and Sonoran distribution:** rather common in coastal California (extending north of the Sonoran area) and Baja California.

Ssp. *ruginosa*

Illustration: Timdal (1991), p. 89.

Squamules: up to 3 mm diam., adjacent or forming a ± continuous crust, weakly to moderately convex; **upper surface:** dark olivaceous brown; **ascospores:** bacilliform to acicular, 3- to 7 (-9) septate, 20-42 x 3-4 µm.



Substrate and ecology: on soil and rock, mainly among mosses or in rock fissures, in open habitats and woodlands, up to 2470 m; **Host:** cyanolichens; **World distribution:** see species; **Sonoran distribution:** rather common in Arizona, California, Baja California and Baja California Sur.

Toninia sculpturata (H. Magn.) Timdal, Opera Bot. 110: 92 (1992).

Basionym: *Catillaria sculpturata* H. Magn., Lich. Central Asia: 66 (1940); Synonym: *Toninia flavida* Tomin; Illustration: Timdal (1991), p. 92.

Life habit: lichenized, lichenicolous; **Thallus:** squamulose; **squamules:** up to 1.5 (-3) mm diam., scattered to adjacent, rounded, weakly to strongly convex; **upper surface:** pale yellow, epruinose or partly covered by farinose pruina, dull, with deep, regular fissures, lacking pores and pseudocyphellae; **margin:** concolorous with upper surface; **upper cortex:** up to 300 µm high, lacking calcium oxalate; **Apothecia:** up to 1 mm diam., plane and marginate when young, later convex and immarginate, faintly pruinose or densely pruinose; exciple: medium brown in the rim, pale brown to colorless in inner part**;** hypothecium: pale brown to colorless; epithecium: medium brown (K-, N-); **asci:** clavate, 8-spored; **ascospores:** ellipsoid to bacilliform, 1-septate, 10.5-17.5 x 5-6 µm; **Pyc-**

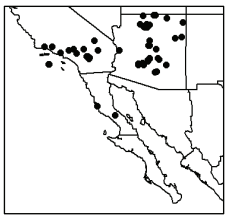
nidia: laminal, immersed; **conidia:** filiform; **Spot tests:** all negative; **Secondary metabolites:** none detected.

Substrate and ecology: on calciferous rock, on boulder in open pinyon-juniper woodland at 1950 m; **Host**: cyanolichens. 1950 m; **World distribution:** scattered in arid areas in the temperate region of the Northern Hemisphere; **Sonoran distribution:** northern Arizona (single locality).

Toninia sedifolia (Scop.) Timdal, Opera Bot. 110: 93 (1992).

Basionym: *Lichen sedifolius* Scop., Fl. carniol., Ed. 2, 2.: 395 (1772); Selected synonym: *Toninia caeruleonigricans* auct.; Illustrations: Timdal (1991), p. 94; Brodo et al. (2001), p. 684.

Life habit: lichenized, lichenicolous or not; **Thallus:** squamulose; **squamules:** up to 3 mm diam., scattered to adjacent or irregularly imbricate, rounded or elongated, weakly convex to bullate; **upper surface:** olivaceous green to grayish green or olivaceous brown to grayish brown, epruinose to partly (rarely entirely) covered by farinose pruina, dull or faintly shiny, smooth or sometimes with a few shallow fissures, lacking pores and pseudocyphellae; **margin:** concolorous with upper surface or white; **upper cortex:** up to 60 µm high, containing calcium oxalate; **Apothecia:** up to 3 mm diam., plane and marginate when young, later convex and immarginate, epruinose or faintly pruinose or densely pruinose; exciple: dark gray in the rim, medium brown to dark reddish brown in inner part; hypothecium: reddish brown; epithecium: gray (K+ violet, N+ violet); **asci:** clavate, 8-spored; **ascospores:** fusiform, 1-septate, 12-24 x 3-5 µm; **Pycnidia:** not seen; **Spot tests:** all negative; **Secondary metabolites:** none detected in Sonoran material but some terpenoids found elsewhere.

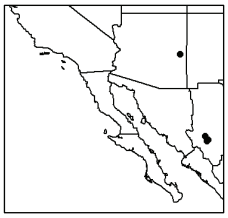


Substrate and ecology: on soil and in fissures of often calciferous rock in open habitats and woodlands, up to 2380 m; **Host:** cyanolichens; **World distribution:** widely distributed throughout the Northern Hemisphere, more scattered in the Southern Hemisphere; **Sonoran distribution:** rather common in Arizona and California, rare in Baja California.

Toninia squalida (Ach.) A. Massal., Ric. auton. lich. crost.: 108 (1852).

Basionym: *Lecidea squalida* Ach., Lichenogr. univers.: 169 (1810); Selected synonyms: *Toninia havaasii* H. Magn., *Toninia multiseptata* Anzi, *Toninia squarrosa* (Ach.) Th. Fr., *Toninia verruculosa* (Th. Fr.) Vain.; Illustration: Timdal (1991), p. 98.

Life habit: lichenized, lichenicolous or not; **Thallus:** squamulose; **squamules:** up to 3 mm diam., adjacent or forming a continuous crust, irregularly lobed, weakly concave to weakly convex; **upper surface:** medium brown to dark brown, epruinose, dull, often with shallow, irregular fissures, lacking pores and pseudocyphellae; **margin:** concolorous with upper surface; **upper cortex:** up to 100 µm high, lacking calcium oxalate; **Apothecia:** up to 1.5 mm diam., plane and marginate when young, later convex and immarginate, epruinose; exciple: dark brown to dark green in the rim, pale brown to colorless in inner part; hypothecium: pale brown to colorless; epithecium: bright to dark green (K-, N+ violet); **asci:** clavate, 8-spored; **ascospores:** acicular, 3-7-septate, 23-41.5 x 2.5-4.5 µm; **Pycnidia:** laminal, immersed; **conidia:** filiform; **Spot tests:** all negative; **Secondary metabolites:** none detected.

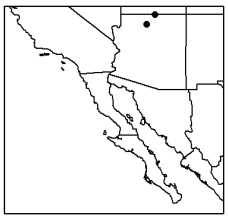


Substrate and ecology: on soil and rock in confer woodlands and forests, at 2150-2950 m; **Host:** cyanolichens; **World distribution:** widely distributed in the temperate and arctic regions of Northern Hemisphere; **Sonoran distribution:** rare in Arizona and Chihuahua.

Toninia subdiffracta Timdal, Opera Bot. 110: 100 (1992).

Illustration: Timdal (1991), p. 100.

Life habit: lichenized, lichenicolous or not; **Thallus:** squamulose; **squamules:** up to 4 mm diam., scattered when young, later ± adjacent, rounded or becoming slightly elongated, weakly to moderately convex; **upper surface:** white to pale gray, often with a green tinge, ± entirely covered by granular pruina, dull, with shallow fissures, lacking pores and pseudocyphellae; **margin:** concolorous with upper surface; **upper cortex:** up to 50 µm high, containing calcium oxalate; **Apothecia:** up to 1.5 (-2.5) mm diam., remaining ± plane and marginate, faintly pruinose or densely pruinose; exciple: dark gray in the rim, reddish brown in inner part; hypothecium: reddish brown; epithecium: gray (K+ violet, N+ violet); **asci:** clavate, 8-spored; **ascospores:** fusiform, 1-septate, 14.5-21 x 3.5-5 µm; **Pycnidia:** not seen; **Spot tests:** all negative; **Secondary metabolites:** none or undetermined terpenoids (chemotype D).



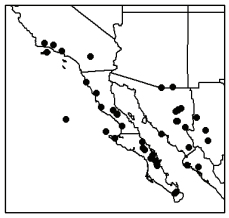
Substrate and ecology: on soil and rock, mainly on steep to overhanging rock walls, usually somewhat shady, at 1620-1920 m; **Host:** cyanolichens; **World distribution:** rare in Arizona, Colorado, New Mexico, and Utah; **Sonoran distribution:** northern Arizona.

Toninia submexicana de Lesd., Lich. Mexique: 25 (1914).

Illustration: Timdal (1991), p. 102.

Life habit: lichenized, lichenicolous or not; **Thallus:** squamulose; **squamules:** up to 3 mm diam., scattered to adjacent or irregularly imbricate, rounded to elongated, often lobed, weakly concave to weakly convex; **upper surface:** dark olive-brown, epruinose, shiny, smooth, lacking pores and pseudocyphellae; **margin:** concolorous with upper surface; **upper cortex:** up to 70 µm high, lacking calcium oxalate; **Apothecia:** up to 1 mm diam., remaining ± plane and marginate, epruinose; exciple: dark gray in the rim, pale to colorless in inner part; hypothecium: pale brown to colorless; epithecium: gray (K+ violet, N+ violet); **asci:** clavate, 8-spored; **ascospores:** bacilliform to acicular, (1-) 3-septate, 17-42.5 x 3.5-5 µm; **Pycnidia:** laminal, immersed; **conidia:** filiform; **Spot tests:** all negative; **Secondary metabolites:** none detected.

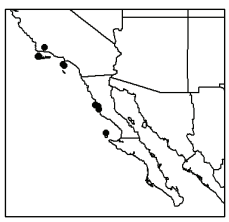
Substrate and ecology: on soil and rock in ± open habitats, up to 1250 m; **Host:** cyanolichens; **World distribution:** southwestern North America and South America; **Sonoran distribution:** rather common in southern Arizona, coastal California, Baja California, Baja California Sur, Chihuahua, Sinaloa, and Sonora.



Toninia talparum Timdal, Opera Bot. 110: 103 (1992).

Illustration: Timdal (1991), p. 104.

Life habit: not lichenized, lichenicolous; **Thallus:** absent; **Apothecia:** up to 1 mm diam., remaining ± plane and marginate or plane and marginate when young, later convex and immarginate, epruinose; exciple: greenish brown in rim, usually paler in inner part; hypothecium: pale brown to colorless; epithecium: bright to dark green (K-, N+ violet); **asci:** clavate, 8-spored; **ascospores:** ellipsoid, 1-septate, 10-14.5 x 4-5.5 µm; **Pycnidia:** not seen; **Secondary metabolites:** none detected.



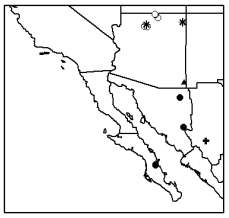
Substrate and ecology: on crustose lichens over soil and rock in open habitats, up to 1280 m; **Host:** *Lecania*; **World** and **Sonoran distribution:** locally rather common in California (extending north of the Sonoran area) and Baja California.

Toninia tristis (Th. Fr.) Th. Fr., Lichenogr. scand. 2: 341 (1874).

Basionym: *Psora tabacina* var. *tristis* Th. Fr., Bot. Notiser 1865: 38 (1865); Synonym: *Toninia tabacina* auct.; Illustrations: Timdal (1991), p. 111; Brodo et al. (2001), p. 685.

Life habit: lichenized, lichenicolous or not; **Thallus:** squamulose; **squamules:** up to 4 (-8) mm diam., scattered to adjacent, rounded, weakly convex to bullate; **upper surface:** castaneous brown to dark brown, epruinose, dull or shiny, smooth or with shallow fissures, with scattered punctiform impressions developing into pores, lacking pseudocyphellae; **margin:** concolorous with upper surface; **upper cortex:** up to 160 µm high, lacking calcium oxalate; **Apothecia:** up to 1.5 (-4) mm diam., remaining ± plane and marginate or plane and marginate when young, later convex and immarginate, epruinose; exciple: medium brown to dark brown (sometimes with a green tinge) in the rim, usually paler inner part; hypothecium: colorless to pale brown or reddish brown; epithecium: bright to dark green (K-, N+ violet) or medium brown (K-, N-); **asci:** clavate, 8-spored; **ascospores:** ellipsoid to fusiform, simple or 1-septate, 8-24 x 3-5.5 µm; **Pycnidia:** laminal, immersed, often below pores; **conidia:** filiform; **Spot tests:** all negative; **Secondary metabolites:** various terpenoid patterns (chemotype 1, 4, or 6 of Timdal 1992, plus undescribed chemotypes 8 and 9).

Substrate and ecology: on soil and rock, at 400-1950 m; **Host:** cyanolichens; **World distribution:** widely distributed in the Northern Hemisphere, Peru; **Sonoran distribution:** Arizona, Baja California Sur, Chihuahua and Sonora.



Notes: Nine subspecies were recognized by Timdal (1991) and two additional ones are described here. They are distinguished mainly by anatomical (spore septation, spore size, pigments), chemical (terpenoid patterns), ecological (soil and/or rock), and phytogeographical features. The subspecies are well separated, and intermediate specimens are not known. Five subspecies occur in the Sonoran area.

Key to the subspecies of ***Toninia tristis*** in the Sonoran region:

1. Spores exclusively simple 2
1. Spores at least partly 1-septate 3

2. Orange pigment (K+ red) present in upper part of the hypothecium and in the lumina of many paraphyses, asci and spores; squamules up to 6 (-8) mm diam.; chemotype 6 ..... **ssp. *arizonica***
2. Orange pigment absent; squamules up to 3 (-4) mm diam.; chemotype 8 ..... **ssp. *chihuahuana***

3. Orange pigment (K+ red) present in upper part of the hypothecium and in the lumina of many paraphyses, asci and spores; chemotype 4 ..... **ssp. *asiae-centralis***
3. Orange pigment absent; chemotypes different 4

4. Squamules up to 4 (-6) mm diam.; epithecium ±green; chemotype 9 ..... **ssp. *gigantea***
4. Squamules up to 2 (-3) mm diam.; epithecium ±brown; chemotype 1 ..... **ssp. *tristis***

Ssp. *arizonica* Timdal, Opera Bot. 110: 112 (1992).

Illustration: Timdal (1991), p. 111.

Squamules: up to 6 (-8) mm diam.; epithecium brown, partly with a green tinge; **ascospores:** narrowly ellipsoid to fusiform, simple, 11.5-17 x 4-5.5 µm; **orange pigment:** (K+ red) present in the upper part of the hypothecium and inside the lumina of many paraphyses, asci, and spores; **Secondary metabolites:** terpenoids (chemotype 6).

Substrate and ecology: on soil over limestone, rock wall in small canyon; **Host:** *Heppia*; **World and Sonoran distribution:** southeastern Arizona (single locality), at 1750 m (triangle).

Ssp. *asiae-centralis* (H. Magn.) Timdal, Opera Bot. 110: 112 (1992).

Basionym: *Lecidea asiae-centralis* H. Magn.; Illustration: Timdal (1991), p. 111.

Squamules: up to 2 (-3) mm diam.; epithecium brown, sometimes with a faintly green tinge; **ascospores:** narrowly ellipsoid to fusiform, mainly 1-septate, 12.5-19 x 3.5-5.5 µm; **orange pigment:** (K+ red) present in the upper part of the hypothecium and inside the lumina of many paraphyses, asci, and spores; **Secondary metabolites:** terpenoids (chemotype 4).

Substrate and ecology: on soil and sandstone at 1650-2160 m; **Host:** cyanolichens; **World distribution:** widely distributed in arid areas in the arctic and temperate regions of the Northern Hemisphere, Peru; **Sonoran distribution:** rare in northern Arizona (open circle).

Ssp. *chihuahuana* Timdal, **ssp. nov.**

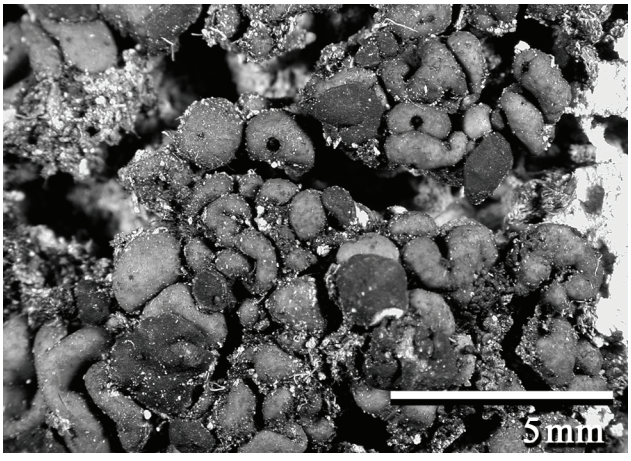


Fig. 104. *Toninia tristis ssp. chihuahuana*, photo by E. Timdal.

Diagnosis: *Squamae ad 3 (-4) mm diam.; epithecium fuscum vel olivaceum; ascosporae simplices; hypothecium et hymenium pigmentum aureum non continentes; thallus substantiae terpenoideae continens.*

Type: MEXICO, Chihuahua, Barranca del Cobre, small, broad secondary valley within the canyon, with pines (*Pinus chihuahuana*, *Pinus* spp.), some oaks (*Quercus crassifolia* and *Quercus* spp.) and cypress (*Cupressus arizonica*), 27°26.3'N, 107°29.3'W, 1800 m, 1994, Timdal SON 68/31 (O, holotype).

Squamules: up to 3 (-4) mm diam.; epithecium brown with a green tinge; **ascospores:** broadly to narrowly ellipsoid, simple, 10.5-17 x 5-5.5 µm; **orange pigment:** absent; **Secondary metabolites:** undescribed chemotype 8 (series of undetermined terpenoids).

Substrate and ecology: on soil in oak-pine-cypress forest at 1800 m; **Host:** cyanolichens; **World and Sonoran distribution:** Chihuahua (single locality) (cross).

Notes: The subspecies is mainly recognized by its unique chemotype. In addition, ssp. *arizonica* differs in containing an orange pigment (K+ red) in the hypothecium and inside the lumina of many paraphyses, asci, and spores; ssp. *gigantea* in having partly 1-septate, longer spores and a more green epithecium. The three other most similar subspecies, ssp. *fujikawae* (Satô) Timdal (Japan), ssp. *pseudotabacina* Timdal (Europe, North Africa, Macaronesia), and ssp. *thalloedaemiformis* (Szatala) Timdal (eastern Mediterranean Europe), all have a green epithecium.

Additional specimen examined: MEXICO, Chihuahua, small secondary valley within Barranca del Cobre (Copper Canyon), 27°26'20"N, 107°29'20"W, 1800 m, on soil among mosses, oak-pine-cypress forest, 1994, Nash 36927 (ASU).

Ssp. *gigantea* Timdal **ssp. nov.**

Diagnosis: *Squamae ad 4 (-6) mm diam.; epithecium viride vel olivaceum; ascosporae simplices vel 1-septatae; hypothecium et hymenium pigmentum aureum non continentes; thallus substantiae terpenoideae continens.*

Type: MEXICO, Baja California Sur, Sierra de la Giganta, Route 1 at 70 km post, 25°33'N, 111°20'W, 410-470

m, on steep rock wall, 1993, Timdal SON25/4 (O, holotype).

Squamules: up to 4 (-6) mm diam.; epithecium pure or olivaceous green; **ascospores:** narrowly ellipsoid to fusiform or bacilliform, simple or 1-septate, 14-22.5 x 4-5.5 µm; **orange pigment:** absent; **Secondary metabolites:** undescribed chemotype 9 (series of undetermined terpenoids).

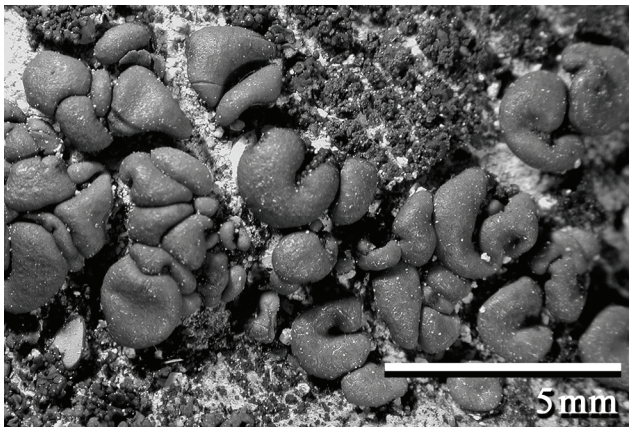


Fig. 105 *Toninia tristis ssp. gigantea*, photo by E. Timdal.

Substrate and ecology: on rock, mainly on steep, shady rock walls in thorn forest vegetation, at 400-1090 m; **Host:** cyanolichens; **World and Sonoran distribution:** rare in Baja California Sur and Sonora (filled dot).

Notes: The subspecies is mainly recognized by its unique chemotype. In addition, ssp. *asiae-centralis*, ssp. *coahuilae* Timdal (Coahuila), and ssp. *tristis*, which also have partly 1-septate spores, differ in having smaller squamules and a brown epithecium. Ssp. *asiae-centralis* also contains an orange pigment (K+ red) in the hypothecium and inside the lumina of many paraphyses, asci and spores. Most similar is perhaps ssp. *canadensis* Timdal (Alaska and Canadian Rocky Mountains), which differs merely in the size of the squamules and in the chemotype.

Additional specimens examined: MEXICO, Baja California Sur, along Rte 1, 68 km NE of Ciudad Insurgentes in pass through Sierra de la Giganta, 25°36'N, 111°20'W, 400 m, hillside and rock ledges in thorn forest with *Acacia*, *Lycium*, *Prosopis*, 1988, Wetmore 63938 (MIN); Sonora, 17 km E of Esqueda, 30°39'30"N, 109°27'30"W, 1090 m, on north facing rocks along desert wash with scattered mesquite, 1992, Wetmore 69902 (MIN); - along Route 16, 6.8 km W of turnoff to San Nicolas (and E of Tepoca), 28°25.9'N, 109°13.8'W, 700 m, thorn forest vegetation dominated by *Acacia cymbispina*, 1994, Timdal SON82/7 (O).

Ssp. *tristis*

Illustration: Timdal (1991), p. 111.

Squamules: up to 2 (-3) mm diam.; epithecium brown, sometimes with a faintly green tinge; **ascospores:** narrowly ellipsoid to fusiform, mainly 1-septate, 13.5-20.5 x 3.5-5.5 µm; **orange pigment:** absent; **Secondary metabolites:** terpenoids (chemotype 1).

Substrate and ecology: on soil and in fissures of calciferous rock in pinyon-juniper woodland, at 1460-1950 m; **Host:** cyanolichens; **World distribution:** northern and central Europe, western North America; **Sonoran distribution:** rare in northern Arizona (star).

Toninia weberi Timdal, Opera Bot. 110: 118 (1992).

Basionym: *Thalloidima granulosum* Szatala, Ann. Hist.-Nat. Mus. Natl. Hung., n. ser. 5: 132 (1954) [non *Toninia granulosa* (Michx.) Vain.]; Illustration: Timdal (1991), p. 118.

Life habit: lichenized, not lichenicolous; **Thallus:** areolate; **areoles:** up to 1 mm diam., adjacent, rounded to angular, plane to moderately convex; **upper surface:** dark brown, often with a gray tinge, epruinose, dull or somewhat shiny, smooth or with shallow, irregular fissures, lacking pores and pseudocyphellae; **margin:** concolorous with upper surface; **upper cortex:** up to 50 µm high, lacking or containing calcium oxalate; **Apothecia:** up to 0.8 mm diam., plane and marginate when young, becoming convex and immarginate, epruinose; exciple: dark gray in the rim, reddish brown in inner part; hypothecium: red-

dish brown; epithecium: gray (K+ violet, N+ violet); **asci:** clavate, 8-spored; **ascospores:** ellipsoid, 1-septate, 10-14 x 4.5-6.5 µm; **Pycnidia:** laminal, immersed; **conidia:** filiform; **Spot tests:** all negative; **Secondary metabolites:** none detected.

Substrate and ecology: on sandstone at 1680 m; **Host:** none; **World distribution:** scattered in arid areas of Asia (China and Iran) and North America (Arizona, Colorado and New Mexico); **Sonoran distribution:** northern Arizona (single locality).

Toninia wetmorei Timdal, **sp. nov.**

Diagnosis: *Thallus squamulosus. Squamae ad 3 mm diam., rotundatae vel irregulares, pallide flavocinereae, epruinosae. Epithecium pallide olivaceobrunneum vel hyalineum, K-, N-. Ascosporae simpliciae vel 1-septatae, 12-15.5 x 3.5-4.5 µm. Thallus acidum gyrophoricum, acidum usnicum, et substantiae terpenoideae continens.*

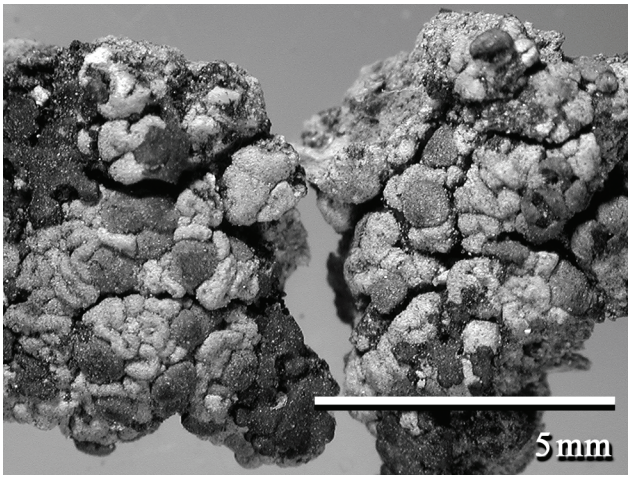


Fig. 106. *Toninia wetmorei*, photo by E. Timdal.

Type: MEXICO, Baja California Sur, Sierra Laguna, along ridge leading to the crest after turnoff to Rancho La Victoria, 23°36’28"N, 109°55’18"W, 1400 m, open oak forest (*Quercus tuberculata*) with shrubs, 1998, Wetmore 79680 (MIN, holotype).

Life Habit: lichenized, probably lichenicolous; **Thallus:** squamulose; **squamules:** up to 3 mm diam., adjacent, rounded to irregular, moderately convex; **upper surface:** pale yellowish gray, epruinose, dull, smooth, lacking pores and pseudocyphellae; **margin:** concolorous with upper surface; **upper cortex:** up to 20 µm high, containing crystals dissolving in K, lacking calcium oxalate; **Apothecia:** up to 1 mm diam., plane to weakly convex, with a narrow, indistinct margin, faintly pruinose; exciple: dark brown in the rim, paler in inner part; hypothecium: olivaceous brown in upper part, dark brown in lower part; epithecium: pale olivaceous brown (K-, N-) to colorless, containing crystals dissolving in K; **asci:** clavate, 8-spored; **ascospores:** narrowly ellipsoid, simple or 1-septate, 12-15.5 x 3.5-4.5 µm; **Pycnidia:** not seen; **Secondary metabolites:** gyrophoric acid, usnic acid, undetermined terpenoids.

Substrate and ecology: on rock in open oak forest at 1400 m; **Host:** probably cyanolichens; **World** and **Sonoran distribution:** Baja California Sur (single locality).

Notes: Within *Toninia*, the species shows several unique characters: a pale olivaceous brown (K-, N-) to colorless epithecium, presence of crystals dissolving in K in the epithecium, and presence of gyrophoric acid and usnic acid in the thallus. There are no apparently closely related species, and it is difficult to place it in any of the informal subgroups of *Toninia* proposed by Timdal (1991). In the two other yellow species of *Toninia*, *T. gobica* Golubk. (Mongolia) and *T. sculpturata*, the pigment is a cell wall pigment which is insolvable in acetone.

TOPELIA

by T. H. Nash III and P. L. Nimis

Topelia P. M. Jørg. & Vězda, Beih. Nova Hedwig. 79: 502 (1984).

Family: Gyalectaceae?; Type: *Topelia rosea* (Servít) P. M. Jørg. & Vězda; No. species: five world-wide; Selected lit.: Jørgensen and Vězda (1984), and Tretiach and Vězda (1992).

Life habit: lichenized; **Thallus:** crustose, superficial or immersed, often inconspicuous and poorly developed; **upper surface:** various shades of white, gray, green, or orange to pink; occasionally with isidia or schizidia; **photobiont:** primary one a trentepohlioid alga, secondary photobiont absent; **Ascomata:** perithecioid but in some species expanding an appearing apothecioid, immersed to subimmersed in the thallus; **involucrellum:** absent; true **exciple:** hyaline to brownish black, 30-60 µm wide, upper and inner parts paraplectenchymatous; **asci:** narrowly cylindrical, without conspicuous tholus but with a tiny refractive ring, non-amyloid, 8-spored; **hamathecium:** composed of short-celled, stiff periphyses (up to 45 x 2 µm); hymenium: hyaline or pale brown, I+ blue-green, rapidly changing to red-brown; paraphyses: slender, *c.* 200 x 1.5-2 µm, flexuose, not branched and without apical thickening; **asci:** narrowly cylindrical, 100-180 x 12-18 µm, tapering apically, unitunicate, thin-walled, without apical thickening or apparatus, 8-spored; **ascospores:** broadly ellipsoid to ovoid, hyaline, muriform with eusepta, 2-20 x 13-120 µm; **Conidiomata:** pycnidial, ± sessile; **conidia:** bacilliform, macro- and micro- may be present; **Secondary metabolites:** none detected; **Geography:** Mediterranean regions of Europe and across southern USA and the Caribbean; **Substrate:** species occurring on either bark or rocks, especially calcareous ones.

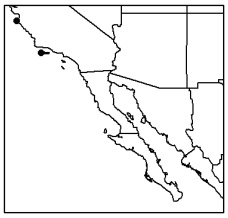
Notes: Among the perithecioid genera occurring in the Sonoran region, *Topelia* is most similar to *Thelenella* and *Thelopsis*. *Thelenella* differs by lacking periphyses, having an I- hymenium and richly branched, anastomosing paraphyses and having thick-walled asci. In contrast, the ascocarps, hymenium and asci of *Thelopsis* are very similar to *Topelia*, but the exciple and spores are different. In *Thelopsis* and exciple is lacking and the spores are usually only transversely septate, rarely submuriform and always occur as more than 8 per ascus; whereas, in *Topelia* a well developed exciple is present and the spores are soon muriform and are 8 per ascus.

The Species

Topelia californica P. M. Jørg. & Vězda, Beih. Nova Hedwig. 79: 504 (1984).

Illustration: Jørgensen and Vězda (1984), p. 511.

Thallus: crustose, thin; **upper surface:** gray to pinkish, smooth to minutely warty; **Ascomata:** initially perithecioid but expanding and appearing to be apothecioid, ochraceous, often aggregated, immersed to subimmersed, up to 0.5 mm diam.; "margin": thalline, appearing as a white rim; "disc": flat, dull, epruinose; exciple: brown to dark brown peripherally, 30-60 µm wide hymenium: hyaline or pale brown, I+ blue-green, rapidly changing to red-brown; paraphyses: slender, *c.* 200 x 1.5-2 µm, flexuose, not branched and without apical thickening; **asci:** narrowly cylindrical, tapering apically, thin-walled, without apical thickening or apparatus, 8-spored; **ascospores:** ellipsoid, muriform, colorless, (20-) 23-28 (-32) x 9-12 µm; **Pycnidia:** immersed; **conidia:** cylindrical, 3-4 (-6) x 1-1.3 µm; **Spot tests:** cortex and medulla K-, C-, KC-, P-; **Secondary metabolites:** cortex with an unknown rusty red pigment.



Substrate and ecology: on trees (*Quercus agrifolia*) in open habitats; **World distribution:** central and southern California; **Sonoran distribution:** Channel Islands of southern California.

TORNABEA

by P. M. Nimis and M. Tretiach

Tornabea Østh., Taxon 29: 688 (1980).

Family: Physciaceae; Type: *Tornabea scutellifera* (With.) J. R. Laundon; No. species: one world-wide; Selected lit.: Nimis and Tretiach (1997).

Notes: Because the genus is now regarded as monotypic, a generic description would simply recapitulate the specific description given below. Two other genera have been proposed: *Tornabenia* Trevis. and *Tornabeniopsis* Follmann, but the former is a *nom. illegit* and the latter is *nom. inval.* (Nimis and Tretiach 1997).

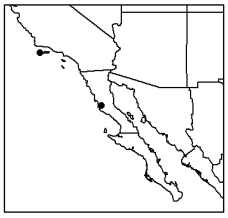
The Species

Tornabea scutellifera (With.) J. R. Laundon, Lichenologist 16: 211. (1984).

Basionym: *Lichen scutelliferus* Withering, Bot. Arrange. Veg. nat. growing Great Britain. 728 (1776); Synonym: *Tornabea atlantica* and see Laundon (1984) and Nimis and Tretiach (1997); Illustrations: Nimis and Tretiach (1997), pp. 219 & 221; Laundon (1984), p. 226.

Life habit: lichenized; **Thallus:** fruticose, 2-3 cm tall, erect to spreading, ± dichotomously branched, sometimes entangled, often flattened but terminal branches sometimes terete, branches up to 3 mm thick; **lobe surface:** light gray brown to gray to reddish brown, smooth to densely tomentose; isidia absent; usually with blastidia; **cortex:** prosoplectenchymatous, 60-100 (-200) µm thick, with conglutinated, thick-walled, mostly longitudinally oriented hyphae, sometimes covered with a colorless layer; **medulla:** white, lax, sometimes with compact, hyphal strands, often rudimentary; **photobiont:** primary one a trebouxioid alga, secondary photobiont absent; **attachment:** by a holdfast; **Apothecia:** present or absent, often numerous, laminal on branches, sessile with constricted base, up to 1.5 cm diam., with a persistent, lecanorine margin, gray; disc: black-brown, convex; hymenium: colorless; **asci:** elongate-clavate, *Physcia*-type, 8-spored; **ascospores:** ellipsoid to broadly ellipsoid, brown, 1-septate (very rarely 2-septate), polarilocular, varying from the *Physconia*- to *Orcularia*-type 20-30 x 10-15 µm, septum 5.3-7.7 µm wide; **Pycnidia:** immersed, upper part brown; conidiophores type VII (Vobis 1980); **conidia:** bacilliform to fusiform, 3.5-4.5 (-5) x 1 µm; **Spot tests:** cortex and medulla K-, C-, KC-, P-; **Secondary metabolites:** none detected.

Substrate and ecology: often growing near the ocean on boulders and branches in open habitats; **World distribution:** west coast of South America, SW coast of North America, Macaronesia, western Europe, especially the Mediterranean region eastwards to Pakistan; **Sonoran distribution:** Channel Islands of southern California and coastal region of NW Baja California.



Notes: Originally the species was treated in *Anaptychia*, but the lobes of *Tornabea* are entirely corticated and they lack the dorsiventral orientation of foliose taxa and do not have cilia South American populations have been considered to be a second species (*T. ephebea* (Ach.) Kurok., but Nimis and Tretiach (1997) reduced it to synonymy.

TRIMMATOTHELE

by T. H. Nash III

Trimmatothele Norman ex Zahlbr., in Blombg. et Forss. Enum. Plat. Scand. (1880).

Family: Verrucariaceae; Type: *Trimmatothele perquista*; No. of species: three world-wide; Selected lit.: Fink (1935), Herre (1912), Zschacke (1934).

Life habit: lichenized; **Thallus:** crustose, superficial or immersed, thin, becoming warty or areolate when well developed, homiomerious, effuse; prothallus: absent; **upper surface:** pale lime to dark gray or brown-black, smooth; **photobiont:** chlorococcoid green alga; **Ascomata:** perithecioid, hemispherical to spherical, brown to black, ± immersed, 0.1-0.4 mm wide; ostiole: minute, inconspicuous; **involucrellum:** absent; **true exciple:** brown to black, 20-30 µm wide; **asci:** clavate, thin walled, non-amyloid, over 100-spored; **hamathecium:** periphyses: present; hymenial gel I- or I+ yellowish,K/I+ blue; paraphyses: absent or disappearing; hymenium: hyaline, hypothecium: hyaline to pale brown; **asci:** *Verrucaria*-like, narrowly cylindrical, tapering apically, thin-walled, up to ca. 180 µm long, multispored; **ascospores:** ellipsoid, hyaline, simple, 2.5-4.5 x 2-3 µm; **Conidiomata:** not observed; **Secondary metabolites:** none detected; **Geography:** oceanic influenced parts of Europe and California, USA; **Substrate:** species occurring on either on bark or rocks, including limestone and marl.

Notes: The only other pyrenocarpous genus in the region with a large number of spores per ascus is *Thelopsis*, but its spores become one-septate and its photobiont is a trentepoid yellow-green alga. The genus has not been revised recently, in part due to lack of adequate collections. A fourth species (*T. versipellis* Zahlbr.) was originally attributed to the genus, but was transferred to *Trimmatothelopsis* in the Dermatocarpaceae (Zschacke 1934) due to the presence of paraphyses. As far as we know the latter genus does not occur in North America.

The Species

Trimmatothele umbellulariae Herre, Bryologist 15: 82 (1912).

Thallus: crustose, endophloeodal, very thin and obscure, partially immersed, **upper surface:** (if evident) dusky gray or pale lime colored, smooth to rugose; **Perithecia:** superficially semispherical to conical, 0.1-0.3 mm wide, partially immersed, black, wall dimidiate; hymenium: hyaline or pale brown; hypothecium: hyaline; **asci:** narrowly cylindrical, tapering apically, thin-walled, 100 to 150-spored; **ascospores:** ovoid to short ellipsoid, colorless, yellowish in I, 2.5-3 x 2-2.5 µm; **Spot tests:** thallus K-, C-, KC-, P-; **Secondary metabolites:** none detected.

Substrate and ecology: on trees (*Umbellularia californica*) in open habitats; **World distribution:** central, coastal California; **Sonoran distribution:** not yet known.

Note: Originally the species is described from Berkeley, Califonia and has not yet been reported from the Sonoran region. It is included for comparative purposes with *Thelopsis* and because its substrate (*Umbellularia californa*) is a common tree in southern California. Thus, it should be found.

VULPICIDA

by B. D. Ryan

Vulpicida Mattsson & M. J. Lai, Mycotaxon 49: 427 (1993).

Family: Parmeliaceae; Type: *Vulpicida juniperinus* (L.) Mattsson & M. J. Lai; No. species: six world-wide; Selected lit.: Mattsson (1993) and Mattsson and Lai (1993).

Life habit: lichenized; **Thallus:** foliose and rosette-forming, or subfruticose and caespitose, loosely adnate to loosely attached; **lobes:** somewhat elongate, averaging to 2-7 (-10) mm wide, moderately thick, usually dorsiventral with raised tips (or terete in one Eurasian species), flat and canaliculate or terete, adnate or raised; marginal projections: present or absent; cilia absent; **upper surface:** bright to dark yellow, greenish yellow, or almost grayish green, often wrinkled or ± folded, continuous; with or without soredia; isidia and pseudocyphellae absent; **upper cortex:** paraplectenchymatous, with 3-5 layers of pachydermatous cells; uppermost cells: isodiametric, 3-5 µm diam.; cells of the two lower layers: usually elongated, 5-6 x 2-3 µm, sometimes isodiametric; parts of upper cortex exposed to the sun with usnic acid crystals; epicortex: usually non-pored, smooth and thin, *c.* 1 µm, brown in some non-Sonoran species; **medulla** bright yellow, 20-30 µm thick; hyphae 3-5 µm thick, surface smooth; cell walls: containing *Cetraria*-type lichenan, I+ blue; **photobiont:** primary one a trebouxioid alga, secondary photobiont absent; spherical, 3-15 µm diam., in a layer 10-30 µm thick; algae more abundant in young and more exposed parts of the thallus; **lower cortex:** ± similar to upper one but often less inspersed; **lower surface** pale yellow to whitish, central parts black in some species, rhizinate; rhizines: laminal, pale to black, rather sparse, rarely close to the margin, simple or irregularly branched; **Apothecia:** submarginal or laminal, sessile, roundish; disc: brown, imperforate; thalline margin: prominent, often crenulate; exciple: gray, hyaline, or yellow; hymenium: hyaline below and brown above, with blue IKI reaction in lower part (0.3% iodine solution); paraphyses: not (or scarcely) branched and anastomosing; hypothecium: hyaline; **asci:** *Lecanora*-type s.l. (*Melanelia*-type), broadly to very broadly clavate, 30-40 x 10-15 µm; tholus: well-developed, *c.* 10 µm high, with moderate to very strong IKI reaction (0.03% iodine solution), with wide ocular chamber and large (4 x 2 µm) axial body; 8-spored; **ascospores:** simple, hyaline, spherical to subspherical or broadly ellipsoid, *c.* 4-6 (-7) x (3-) 4-5 (-6) µm, obtuse at the poles, without distinct endospore thickening, not amyloid; **Pycnidia:** often abundant (but rare or absent in some species), usually on marginal or occasionally laminal projections, 80-170 x 70-120 µm, immersed or emergent and sessile or stalked, generally conspicuous, wall at least partly with black pigment; **conidia:** formed acrogenously, sublageniform, 6-8 x 1-2 µm or citriform, 3-4 x 1-2 µm; **Secondary metabolites:** usnic acid, pulvinic acid derivatives, terpenoids or fatty acids; **Geography:** arctic to boreal or temperate, Northern Hemisphere; **Substrate:** on bark, wood, soil, detritus, or rock (calciferous or not).

Notes: *Vulpicida* is a segregate from *Cetraria* and is distinguished by the distinctly yellow color of the thallus caused by pulvinic acid derivatives in the medulla and usnic acid in the cortex, smooth medullary hyphae, ± globose ascospores, and the absence of cilia and pseudocyphellae. The other yellowish species formerly placed in *Cetraria* or its segregate *Tuckermannopsis* but now placed in other genera have usnic acid but lack pulvinic acid derivatives. Other characters used to distinguish *Vulpicida* from similar genera are the moderately sized asci with often very strong amyloid reaction in the tholus, the strongly gelatinized lower layer of the exciple, the small cortical cells, and the lageniform to citriform conidia. Morphologically the genus is most similar to *Tuckermannopsis*, but differs in the shape of the asci and conidia. Some of the information presented below on external morphological characters in the individual species (especially colors and dimensions) is based primarily on observations of material from the Sonoran region.

Key to the species of ***Vulpicida*** in the Sonoran region:

1. Thallus sorediate; medulla and soredia deep lemon yellow (vulpinic and pinastric acids), rest of upper surface usually duller and more greenish or grayish tinged .... ***V. pinastri***
1. Thallus not sorediate (except in rare specimens); medulla yellow (vulpinic acid), usually the entire thallus (at least the upper surface) appearing bright yellow. .... ***V. canadensis***

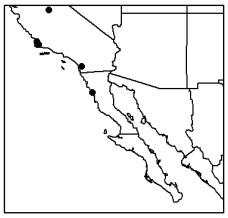
The Species

Vulpicida canadensis (Räsänen) Mattsson & M. J. Lai, Mycotaxon 49: 427 (1993).

Basionym: *Cetraria juniperina* var. *canadensis* Räsänen, Ann. Miss. Bot. Gard. 20: 12 (1933); Synonyms: *Cetraria canadensis* (Räsänen) Räsänen; *Tuckermannopsis canadensis* (Räsänen) Hale; Illustrations: Hale and Cole (1988), pl. 1c; Mattsson (1993), figs. 1F, 3B, 4B; Brodo et al. (2001), p. 730; McCune and Geiser (1997), p. 310.

Thallus: foliose, loosely attached, adnate to suberect, forming almost orbicular rosettes 1.5-4.5 (-6) cm broad, sometimes with long, narrow or broad, often erect lobes that give a fruticose impression; **lobes:** short, 2-4 (-10) mm wide; dorsiventral, flat or occasionally slightly canaliculate, generally ascending, with raised lobe tips; branches: usually short; margins: becoming dissected; projections: not seen; **upper surface:** intensely bright and deep yellow; foveolate, ridged and wrinkled (hand lens); soredia or isidia absent; **upper cortex:** 15-40 (-50) µm thick with uppermost cells isiodiametric and 3-5 µm diam.; cells of the lower two layers: usually elongated, 3-7 x 3-5 µm; **medulla:** yellow, hyphae 3-6 µm thick; **photobiont:** cells (7-) 11-19 µm diam., in layer 10-22 µm thick; **lower cortex:** similar to upper one; **lower surface:** concolorous with upper one, wrinkled, strongly ridged; rhizines very sparse or absent; **Apothecia:** common, 1-4 mm diam., laminal (to submarginal); thalline margin: crenulate; disc: dark brown; **asci:** broadly clavate, 27-40 x 10-15 µm; tholus: with moderate amyloid reaction; 8-spored; **ascospores:** subspherical, 5-6 x 4-5 µm; **Pycnidia:** almost spherical, (90-) 110-120) x 100-110 (-120) µm, immersed, black, laminal, wall 10-20 µm, with *c.* three layers of isodiametric cells 2-3 µm diam., the uppermost parts black, closely connected to the cortex, lower parts with pale brown pigmentation; **conidia:** citriform, 3-4 x 2 µm; **Spot tests:** cortex K-, C-, KC+ yellowish, P-; medulla K+ yellowish, C-, KC-, P-; **Secondary metabolites:** cortex with usnic acid; medulla with pinastric and vulpinic acids, rarely traces of other aromatic substances; sometimes also an unknown fatty acid.

Substrate and ecology: in the Pacific NW common on bark and wood of conifers, especially on twigs; occasional on hardwood trees or shrubs; in open, moderately xeric to mesic forests, in areas with high insolation and occasionally high humidity; **World distribution:** western North America (northern Rocky Mountains and on the east side of the Cascades; British Columbia to Baja California); **Sonoran distribution:** rare, low elevations in southern California and Baja California.



Notes: It is characterized by the bright greenish yellow foliose thallus without soredia and having laminal, immersed pycnidia. Because pulvinic acid derivatives are reported as being restricted to the medulla, the reason why the surface is bright yellow, rather than yellow green as in most species having usnic acid in the cortex, needs to be clarified.

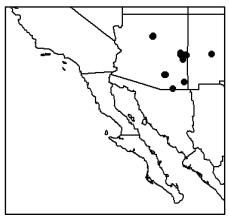
Vulpicida pinastri (Scop.) Mattsson & M. J. Lai, Mycotaxon 49: 428 (1993).

Basionym: *Lichen pinastri* Scop., Flora Carn. 2: 382 (1772); Synonyms: *Cetraria pinastri* (Scop.) S. Gray, *C. juniperina* v. *pinastri* (Scop.) Ach., *C. caperata* Vain., *Tuckermannopsis pinastri* (Scop) Hale; Illustrations: Mattsson (1993), figs 21; Goward et al. (1994), p. 134, McCune and Geiser (1997), p. 311; Brodo et al. (2001), p. 731.

Thallus: foliose, mostly < 3 cm diam., forming adnate rosettes with short lobes, especially when on rock, or with elongated and more erect lobes when growing on thin

branches; **lobes:** radiating or irregularly arranged, slightly scattered or overlapping, dorsiventral, adnate to ascending, (0.5-) 1-2 (-3) mm wide, ascending, rounded, flat or slightly canaliculate with short branches; margins: crisped (undulate and ± ascending), crenate to crenate-incised, ultimate segments mostly short and 0.2-1.0 (-1.5) mm wide; **upper surface:** yellowish green or mainly greenish yellow, or almost grayish green in more shaded habitats (gradually turning yellowish brown in the herbarium), smooth, dull, without maculae; **soredia:** bright greenish yellow, finely granular, in marginal, roundish to crescent-shaped soralia (or occasionally partly laminal); **upper cortex:** paraplectenchymatous, 22-30 µm thick, the cells heavily pigmented with yellow granular inclusions; uppermost cells isodiametric, 2-3 µm diam., cells of lower layers elongated, 3-6 x 2-3 µm; epicortex: hyaline, 1 (-2) µm thick; **medulla:** yellow; very loose, much incrusted with yellow pigment granules, hyphae 3-6 µm thick; **photobiont** cells 5-15 µm diam., layer 20-45 µm thick; **lower cortex:** paraplectenchymatous, clearer than the upper cortex, with few granular inclusions, 25-50 µm thick; **lower surface:** concolorous with upper surface or pale yellow to brownish yellow with scattered whitish rhizines; **Apothecia:** very rare, submarginal towards tips of lobes, *c.* 1-2.5 mm broad; disc: rather pale red-brown, flat, epruinose; thalline margin: confluent with upper side of thallus, even, sorediate; hymenium: 70 µm tall; **asci:** broadly clavate, 25-35 x 10-12 µm; tholus: with strong amyloid reaction; 8-spored; **ascospores:** almost spherical, *c.* 5-6 µm diam.; **Pycnidia:** rare, on projections, pyriform to almost spherical, 80-120 x 70-100 µm, wall 20-30 µm with *c.* 3 layers of isodiametric cells 2-3 µm, black in upper parts, dark brown in lower; **conidia:** sublageniform, 6-8 x 2 µm; **Spot tests:** cortex K-, C-, KC- or + yellow, P-; medulla K-, C-, KC-, P-; **Secondary metabolites:** cortex with usnic acid; medulla with pinastric and vulpinic acids (majors), zeorin and unknown aromatic substances (accessory).

Substrate and ecology: on bark or wood, most frequent in open, continental mountain forests, generally at medium to high elevations, often in cold sites and tolerant of snow burial; **World distribution:** circumboreal, low arctic and lower alpine regions to the south; North America, Europe and Asia; **Sonoran distribution:** Arizona, 2500-3660 m, in mixed conifer forests and into the alpine.



Notes: Usually it is easily recognized by the characteristic bright yellow color of the primarily marginal soralia, which contrast with the duller, more grayish or greenish yellow of the rest of the upper surface. The width, arrangement, and especially the adnation, of the lobes are somewhat variable; morphs with very narrow, crowded and appressed lobes can occasionally (especially if heavily sorediate) be confused with coarse forms of *Candelaria concolor*, but in that species (which is more common at lower elevations and in rather dry sites), the upper surface has virtually the same bright yellow color as the soredia.

WAYNEA

by R. Moberg

Waynea Moberg, Lichenologist 22: 249 (1990).

Family: Bacidiaceae; Type: *Waynea californica* Moberg; No. species: three world-wide; Selected lit.: Moberg (19 90a).

Life habit: lichenized; **Thallus:** squamulose, heteromerous, without a prothallus; **squamules:** scattered, raised on one edge; **upper surface:** olive-green to brown-green; soredia present or absent; isidia absent; **upper cortex:** paraplectenchymatous; **medulla:** white, I-; **photobiont:** primary one a chlorococcoid alga, secondary photobiont absent; **lower cortex:** absent; **Ascomata:** apothecial, stipitate with short stalks, margin pale, biatorine; paraphyses: simple or rarely branched, slightly swollen at apices; **asci:** cylindrical-clavate, with amyloid tholus and fuzzy coat, 8-

spored; **ascospores:** 3-septate, hyaline and non-halonate; **Secondary metabolites:** none detected; **Geography:** Mediteranean region of Europe and western North America; **Substrate:** on bark.

Notes: Originally *Waynea* was described as a monotypic genus. Subsequently two additional species have been placed in the genus based on careful morphological and anatomical comparisons (Roux et al. 1995), but neither of the other species have yet been found fruiting. Thus, their proper placement requires further confirmation.

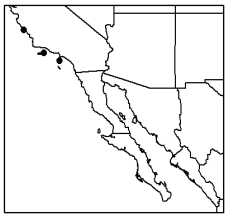
The Species

Waynea californica Moberg, Lichenologist 22: 249 (1990).

Illustrations: Moberg (1990a), pp. 250 & 251.

Thallus: squamulose, heteromerous, irregular, consisting of small thalli (up to 0.5 mm wide) joining to form larger patches within which at least some convex squamules are raised on one edge; **upper surface:** olive-green to brown-green, ± glossy, paler spots develop into globular knob-like outgrowths that later form soredia in cup-like soralia; **upper cortex:** paraplectenchymatous, 20-30 µm thick, with thick-walled cells *c.* 5 µm diam.; **medulla:** white, composed of loosely interwoven hyphae particularly in lower part, hyphae with crenulate wall, I-; **photobiont:** a green alga, *Myrmecia*-type; cells: globose, 5-10 µm diam.; **lower surface:** black centrally and paler towards the margin; erhizinate or with sparsely developed, simple rhizines; **Apothecia:** up to 0.5 mm diam., short stalked, bluish gray, biatorine, margin slightly paler; exciple: distinct, cells anticlinal and elongated, 3-4 µm wide and thick walled (lumina 1-2 µm in water); epihymenium: colorless, K- or faintly K+ violet, N-; hymenium: hyaline, up to 80 µm tall, more or less conglutinated; paraphyses: simple or rarely branched, colorless, 1.5-3 µm thick, with slightly swollen apices; hypothecium: colorless, indistinctly delimited; **asci:** cylindrical-clavate, with an amyloid fuzzy coat and a thick I+ blue apical dome in young apothecia, 8-spored; **ascospores:** hyaline, fusiform or slightly thicker on one side, 3-septate, thick walled; **Pycnidia:** not seen; **Spot tests:** cortex and medulla K-, C-, KC- and P-; **Secondary metabolites:** none detected.

Substrate and ecology: on bark of oaks, especially *Quercus agrifolia* in maritime habitats; **World** and **Sonoran distribution:** coastal California from Monterey County to the Channel Islands.



Previously Reported but Currently Excluded Species from the Greater Sonoran Desert Region

by T. H. Nash III

[**Note:** A more complete compilation will be provided in Vol. II.]

Alectoria jubata (L.) Ach. from Arizona (Darrow 1950) and southern California (Hasse 1913) and ***Alectoria jubata*** var. ***implexa*** (Hoffm.) Ach. from Baja California (Howe 1911) were based on various *Bryoria* spp.

Arthopyrenia spaeroides (Wallr.) Zahlbr. [=*Acrocordia cavata* (Ach.) R. C. Harris] – erroneously reported in Harris (1973) according to Harris in Aptroot (1997).

Bryoria capillaris (Ach.) Brodo & D. Hawksw. – Brodo and Hawksworth show a tentative record from San Diego County but indicate that the specimen could not be verified as not all specimens are determinable. To our knowledge no authentic specimen has been collected since then, and consequently the species has not been treated.

Bryoria vrangiana (Gyeln.) Brodo & D. Hawksw. from North America (including Arizona) are based on confusion over the type and misidentifications of a coarse and spinulose morph of *B. fuscescens* and possibly some corticolous material of *B. chalybeiformis* (L.) Brodo & D. Hawksw. (Brodo, personal communication). The taxonomy of *B. vrangiana* was discussed by Krog (1979).

Cetrelia cetrarioides (Del. *ex* Duby) W. Culb. & C. Culb. reported as *Parmelia cetrarioides* Del. *ex* Duby by Herre (1944) for Sonora proved to be *Flavopunctelia praesignis* (Nyl.) Hale.

Diploschistes ocellatus (Vill.) Norman was recorded from the area, but is not present in North America.

Hassea bacillcosa Zahlbr. – was described by Zahlbruckner as a crustose cyanolichen with perithecia occurring on bark, but upon reassessment it has proved to be a parasite and will be handled in volume II (Breuss and Harris, personal communication).

Hypogymnia apinnata Goward & McCune - occurs from Santa Cruz, California northward in the coastal states.

Hypogymnia enteromorpha (Ach.) Nyl. - This name was applied in a broad sense to many esorediate *Hypogymnia* species. In the strict sense, it occurs from Monterey, California northward in the coastal states.

Hypogymnia metaphysodes (Asah.) Rass. – incorrectly reported from Arizona (Nash et al. 1997). It occurs from northern California north to Alaska and north of about 44° in the Rocky Mountains.

Mycoporum compositum (A. Massal.) R. C. Harris – erroneously reported in Fink (1935) according to Harris in Aptroot (1997).

Parmelia enteromorpha Ach. – In the old literature this name was applied in a broad sense to many esorediate *Hypogymnia* species. In the strict sense, *H. enteromorpha* (Ach.) Nyl. occurs from Monterey, California northward in the coastal states.

Pertusaria granulata (Ach.) Müll. Arg. – reported by Darrow (1950) was a misidentification of *Pertusaria wulfenoides* de Lesd.

Pertusaria multipuncta (Turner) Nyl. – reported by Darrow (1950) but that was a misidentification of *Pertusaria amara* (Nyl.) Ach.

Physcia albinea (Ach.) Nyl. – a name widely used named based on Thomson (1963), but all the Sonoran material originally determined as this species has been reannotated as other species.

Physcia callosa Nyl. – a name widely used name based on Thomson (1963), but it is now treated as a synonym of *Physcia tribacia* (Ach.) Nyl. (Moberg 1997).

Physcia cascadensis H. Magn. – now treated as a synonym of *Physcia phaea* (Tuck.) J. W. Thomson, see Moberg (1997), p. 177.

Physcia mexicana de Lesd. – apparently occurs farther south than the Sonoran region; material identified as such from the Sonoran region proved to be *Physcia biziana* (A. Massal.) Zahlbr.

Physcia semipinnata (J. F. Gmel.) Moberg – a name used for some coastal material from southern California; most specimens have been redetermined as *Physcia villosula* Moberg.

Physcia subtilis Degel. – an eastern U.S. species thought previously to occur in the West, but most material has been annotated as *Physcia halei* J. W. Thomson.

Thelidium circumspersellum (Nyl.) Zschacke – material determined by Hasse is annotated by O. Breuss as *Porina linearis* (Leight.) Zahlbr. (= *Trichothelium lineare* (Leight.) R. C. Harris. The North American

checklist places authentic material of the species in *Verrucaria*.

Thelidium microbola (Tuck.) Hasse – material determined by Hasse is now annotated by O. Breuss as *Verrucaria* sp.

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INDEX TO THE TERMINOLOGY

This index quickly refers the reader to the terminology explained in the introduction. Terms which are only mentioned in footnotes are printed in small font.

Previously Reported but Currently Excluded Species from the Greater Sonoran Desert Region

by T. H. Nash III

[**Note:** A more complete compilation will be provided in Vol. II.]

Alectoria jubata (L.) Ach. from Arizona (Darrow 1950) and southern California (Hasse 1913) and ***Alectoria jubata*** var. ***implexa*** (Hoffm.) Ach. from Baja California (Howe 1911) were based on various *Bryoria* spp.

Arthopyrenia spaeroides (Wallr.) Zahlbr. [=*Acrocordia cavata* (Ach.) R. C. Harris] – erroneously reported in Harris (1973) according to Harris in Aptroot (1997).

Bryoria capillaris (Ach.) Brodo & D. Hawksw. – Brodo and Hawksworth show a tentative record from San Diego County but indicate that the specimen could not be verified as not all specimens are determinable. To our knowledge no authentic specimen has been collected since then, and consequently the species has not been treated.

Bryoria vrangiana (Gyeln.) Brodo & D. Hawksw. from North America (including Arizona) are based on confusion over the type and misidentifications of a coarse and spinulose morph of *B. fuscescens* and possibly some corticolous material of *B. chalybeiformis* (L.) Brodo & D. Hawksw. (Brodo, personal communication). The taxonomy of *B. vrangiana* was discussed by Krog (1979).

Cetrelia cetrarioides (Del. *ex* Duby) W. Culb. & C. Culb. reported as *Parmelia cetrarioides* Del. *ex* Duby by Herre (1944) for Sonora proved to be *Flavopunctelia praesignis* (Nyl.) Hale.

Diploschistes ocellatus (Vill.) Norman was recorded from the area, but is not present in North America.

Hassea bacillcosa Zahlbr. – was described by Zahlbruckner as a crustose cyanolichen with perithecia occurring on bark, but upon reassessment it has proved to be a parasite and will be handled in volume II (Breuss and Harris, personal communication).

Hypogymnia apinnata Goward & McCune - occurs from Santa Cruz, California northward in the coastal states.

Hypogymnia enteromorpha (Ach.) Nyl. - This name was applied in a broad sense to many esorediate *Hypogymnia* species. In the strict sense, it occurs from Monterey, California northward in the coastal states.

Hypogymnia metaphysodes (Asah.) Rass. – incorrectly reported from Arizona (Nash et al. 1997). It occurs from northern California north to Alaska and north of about 44° in the Rocky Mountains.

Mycoporum compositum (A. Massal.) R. C. Harris – erroneously reported in Fink (1935) according to Harris in Aptroot (1997).

Parmelia enteromorpha Ach. – In the old literature this name was applied in a broad sense to many esorediate *Hypogymnia* species. In the strict sense, *H. enteromorpha* (Ach.) Nyl. occurs from Monterey, California northward in the coastal states.

Pertusaria granulata (Ach.) Müll. Arg. – reported by Darrow (1950) was a misidentification of *Pertusaria wulfenoides* de Lesd.

Pertusaria multipuncta (Turner) Nyl. – reported by Darrow (1950) but that was a misidentification of *Pertusaria amara* (Nyl.) Ach.

Physcia albinea (Ach.) Nyl. – a name widely used named based on Thomson (1963), but all the Sonoran material originally determined as this species has been reannotated as other species.

Physcia callosa Nyl. – a name widely used name based on Thomson (1963), but it is now treated as a synonym of *Physcia tribacia* (Ach.) Nyl. (Moberg 1997).

Physcia cascadensis H. Magn. – now treated as a synonym of *Physcia phaea* (Tuck.) J. W. Thomson, see Moberg (1997), p. 177.

Physcia mexicana de Lesd. – apparently occurs farther south than the Sonoran region; material identified as such from the Sonoran region proved to be *Physcia biziana* (A. Massal.) Zahlbr.

Physcia semipinnata (J. F. Gmel.) Moberg – a name used for some coastal material from southern California; most specimens have been redetermined as *Physcia villosula* Moberg.

Physcia subtilis Degel. – an eastern U.S. species thought previously to occur in the West, but most material has been annotated as *Physcia halei* J. W. Thomson.

Thelidium circumspersellum (Nyl.) Zschacke – material determined by Hasse is annotated by O. Breuss as *Porina linearis* (Leight.) Zahlbr. (= *Trichothelium lineare* (Leight.) R. C. Harris. The North American

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INDEX TO THE TERMINOLOGY

This index quickly refers the reader to the terminology explained in the introduction. Terms which are only mentioned in footnotes are printed in small font.

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INDEX OF NEWLY DESCRIBED TAXA IN THIS FLORA

Lichen Flora of the Greater Sonoran Desert Region

Volume 1 (including most of the pyrenolichens, squamulose lichens and macrolichens)

edited by **ThomasH. Nash III, Bruce D. Ryan Corinna Gries** and **Frank Bungartz**

The senior editor has collected lichens extensively throughout the greater Sonoran Desert region over the past 30 years. In 1989 he and Dr. Gries lead a scientific, lichen expedition for over 30 participants from the International Association of Lichenology through Arizona and Baja California. At the conclusion of this trip a Sonoran flora (an identifycation manual) was planned based on thorough revisions and first hand knowledge of the region's lichen flora.

With financial support from the U.S. National Science Foundation14 major expeditions were mounted to regions of Arizona, California, Baja California, Baja California Sur, Chihuahua, Sonora and Sinaloa, a region covering over 500,000 km^2.

Altogether over 70 scientists from 15 countries have participated. Because the region is topographically diverse, ranging from sea level to over 3,600 m, where alpine communities can be found, the lichen flora is also diverse. In fact, over 40% of the lichens known to North America occur in the region.

This initial volume covers almost 600 species in over 140 genera, and includes most of the pyrenocarpous lichens, the squamulose lichens, the Lichinales and most of the macrolichens. Following an introduction to the region's climate, geology, geomorphology and vascular plant communities found in the region, an extensive introduction to characters important in lichen identification is provided. This includes anatomy, morphology, sexual and asexual reproductive strategies and chemistry. Practical hints on how to make observations and recipes for standard solutions are provided as well. Thereafter keys to genera are given and these are followed by individual generic treatments (genus description, key to species within the genus and species descriptions) arranged in alphabetical order. Distribution maps are included as well as photographs for many of the more obscure species.

The Lichen Flora of the Greater Sonoran Desert Region is the first attempt to provide a complete lichen flora for a major geographical region of North America outside of the Arctic. Although macrolichen guides are available for other regions, such species constitute only a minority of the lichens. Although many of the small, crustose lichen genera will be covered in volume II, this initial volume also includes many of the smaller-sized genera. For many of the groups the synthesis provided herein has not previously been available from other sources. These volumes should prove to be invaluable for both the professional lichenologist and the person just becoming acquainted with lichens. It will also provide a wealth of information for the ecologist and land manager, for whom lichens are important indicators of environmental quality.

Thomas H. Nash III is Professor of Plant Biology at Arizona State University, teaching ecology, lichenology, and statistics. He is director of the lichen herbarium at the university, a major collection which holds over 90,000 specimens. He has conducted wide ranging research in the taxonomy, ecology and physiology of lichens and published two previous books dealing with lichens. As senior editor he has coordinated all contributions to this flora.

Bruce D. Ryan is associate curator for the lichen herbarium and has published extensively in lichen systematics with an emphasis on *Lecanora*. He is a well-known expert in North American lichenology and has contributed especially to the introduction and the key to the genera treated in this flora.

Corinna Gries is a research professor in the Deptartment of Plant Biology and the Center for Environmental Studies at Arizona State University and has been a co-Principal Investigator with Dr. Nash on many research grants including several grants which have made this flora possible. As data manager and formatting expert for the flora her contribution has been invaluable.

After being involved with lichenological research in central Europe for several years, Frank Bungartz entered the Ph.D. program in Plant Biology and is now working on a systematic revision of saxicolous species of *Buellia*, a large crustose lichen genus. He edited the photographs in this flora and wrote various chapters of the introduction.

Cover Design: F. Bungartz
Cover Photographs:
Front - *Roccella peruensis* Kremp. (Photo by T. H. Nash III)
Back - *Candelina submexicana* (de Lesd.) Poelt (Photo by F. Bungartz)

The Lichen Flora of the Greater Sonoran Desert Region is the first comprehensive account of all species known from the North American Southwest including large parts of northwest Mexico. Volume 1 treats almost 600 species in more than 140 genera, most macrolichens, the pyrenolichens, several squamulose and some crustose genera. Identification keys and descriptions are provided for each species treated. Maps show our current knowledge about species distribution for the area. A detailed introduction discusses lichen morphology, anatomy, and secondary chemistry and thus helps the reader to understand the scientific terminology used in this book.

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