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THE LICHEN FLORA OF COLORADO: 2. PANNARIACEAE^{1,2}

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This paper discusses a small group of foliose or squamulose lichens in which, with one exception in our flora, the algal symbiont (phycobiont) is the blue-green genus *Nostoc*. The single species with green algae (*Dactylococcus fide* Gyelnik 1940) is related to the others by its fungal anatomy.

Students unfamiliar with this group should orient themselves by using the key to genera and species of fruticose and foliose lichens in Hale, *Lichen Handbook*, p. 106 *et seq.* While some of the western American species are not treated there, Hale's key is useful in the absence of a general key to the lichen genera.

Although the classification of the lichenized fungi is based upon the fungus alone and not on the combination of fungus and alga, it is nevertheless convenient to speak of certain groups of lichens whose taxa, with some few exceptions, contain blue-green phycobionts, as the *cyanophilic* lichens. Thus, while certain genera such as *Leptogium* and *Collema* are constant in this

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feature, others, such as *Peltigera*, *Sticta*, and *Nephroma* contain one or more taxa which have a green phycobiont.

In *Leptogium* and *Collema* the phycobiont contributes a great deal to the mass of the lichen, especially by the gelatinous matrix in which the cells are imbedded. When wetted, these lichens swell noticeably. In *Pannaria*, the *Nostoc* colonies form glomerules in the medullary region of the thallus, and a well-developed fungal cortex and medulla are formed. These lichens are light-colored, in contrast to the deep gray or olive-black of the Collemaceae, and they do not swell greatly when wet. Whereas one can correctly infer the presence of blue-green algae in the Collemaceae by macroscopic observation, the presence of blue-green algae in *Pannaria* is only evident by sectioning or bruising the thallus.

Pannaria, our only genus in the family as circumscribed here, has a small-foliose or squamulose thallus. The lobes range from 0.2 to 3 mm. wide, are appressed or ascending, bare, tomentose, or rhizinose on the lower side, ashy or mineral-gray, yellowish-brown, or brown. The exposed medulla is white. The phycobionts are distributed through the upper portion of the medulla.

The paraplectenchymatous cortex consists of from two to five rows of thin- to thick-walled isodiametric cells with large lumina. This layer is extremely thin in the cortical covering of the isidioid lobules which are very densely packed with algae. The medulla is a loosely packed prosenchyma enclosing discrete glomerules of *Nostoc*. The *Nostoc* may or may not show definite chains of cells. The lower edge of the medulla often consists of a loose horizontal mesh of black hyphae or may terminate in organized broom-like black rhizinae. There is no lower cortex. Isidia or isidia-like lobules are often formed on the thallus margins; these sometimes have a slightly powdery appearance and have been referred to by some authors as soredia.

The apothecia develop in the "normal" fashion for Ascomycetes (gymnocarpous) on the surface of the thallus. The disks are usually reddish-brown or darker, plane or convex, with or without a smooth or usually crenate thalline margin. They are closely sessile on the thallus except in *P. hypnorum* where the sides of the apothecia are free and the apothecia, when young, are goblet-shaped with the margin curving inward to hide much of the disk. When the thalline margin is absent, the proper exciple, which is present in all species, is visible as a paler rim of the same color and texture as the disk. In section the proper exciple appears as a tissue of rectangular cells of a paraplectenchyma extending under the hymenium as a narrow zone and broadening out to form an inversely conical zone on the apothecial margin. In apothecia lacking a thalline margin, or having one which is soon excluded by growth of the disk, the edge of the proper exciple sometimes grows out and down toward the

thallus by the extension of discrete pointed pale or black hyphae. At times this may be observed with only the dissecting microscope.

The hymenium is hyaline, usually with a yellowish gelatinous layer on the upper surface. The paraphyses are simple, adherent, and septate above with the terminal cell or cells enlarged. The spores are produced 8 per ascus and are hyaline, ellipsoid-fusiform, with a slightly thickened episporium, in some species mamillate or lumpy-thickened on the surface. The spores usually range in size around $11-30 \times 4-12 \mu$ and do not appear to present size differences especially useful in classification.

Since the internal anatomy is similar in all the species, the species descriptions will emphasize external morphology which, in the Colorado species, is sufficient for identification.

In Colorado the Pannariaceae comprise five species which are usually placed in three genera. In the present treatment all of these are considered to belong to the single genus *Pannaria*, for the following reasons. All agree in their basic internal anatomy, both vegetative and reproductive, and differ principally only in gross morphology. The species *Psoroma hypnorum* has been separated by most authors on the basis of the green phycobiont, a practice inconsistent with the current philosophy of lichen classification. The species with a thalline margin have been placed in *Pannaria*; those lacking it have been placed in *Parmeliella*. In some species this is purely a developmental phenomenon (*P. microphylla*). In those species in which the character appears to be constant, the separation into different genera goes counter to other combinations of morphological characters. In other words, each genus then contains series of species which are more obviously related to species in the other genus than to those in the same genus (e.g. *Parmeliella pannosa* Muell.-Arg. and *Pannaria mariana* Muell.-Arg.). It appears to be taxonomically more valid to include these in a single genus because of their community of characters than to separate them on the basis of a single character.

The five species of *Pannaria* in Colorado demonstrate a morphological reduction series in which the largest and most conspicuous species, *P. pityrea*, is clearly foliose and possesses well-developed rhizinae. The other species are variously reduced in size and lobation through squamulose forms until in *P. lepidiota* the thallus is almost crustose.

KEY TO THE SPECIES

- 1a. Phycobiont a green alga; thallus distinctly green when wet, except for patches of smaller squamules (cephalodia) containing *Nostoc*; apothecia often very large, deeply concave at first, the thalline margin bearing numerous irregular flat thalline lobules.....1. *P. hypnorum*

- lb. Phycobiont *Nostoc*; thallus blue-gray or darker when wet; cephalodia absent; apothecia margins not conspicuously flat-lobulate (2)
- 2a. Thallus distinctly foliose, with marginal lobes up to 3 mm. wide; lower surface of marginal lobes with stiff black rhizinae; margins of lobes with isidioid lobules, these becoming so crowded in the thallus center as to obscure the thallus surface; on moss over rocks.....2. *P. pityrea*
- 2b. Thallus squamulose or apparently crustose; rhizinae absent; isidia present or absent (3)
- 3a. Squamules forming a closely organized more or less uniform crust..... (4)
- 3b. Squamules elevated from the substrate (usually rock), brittle and easily broken away separately or in groups, smooth, lacking isidia, dark brown in color and usually with convex, dark brown apothecia; thalline margin present in young apothecia, usually disappearing with age 3. *P. microphylla*
- 4a. Apothecia abundant, often crowded and covering the thallus; thalline margin conspicuous and persistent; thallus without erect isidioid lobules 4. *P. pezizoides*
- 4b. Apothecia usually rare or absent; thalline margin usually lacking; thallus crust-like, with the marginal lobules rarely visible; thallus covered with erect, knobby isidioid lobules, bluish-gray at the tips and giving the thallus a bluish cast 5. *P. lepidiota*

PANNARIA

1. PANNARIA HYPNORUM (Vahl) Koerb., Syst. Lich. German. 108. 1855. *Lichen hypnorum* Vahl, Icon. Pl. Dan. 6 (16):8, tab. 956. 1787; *Psoroma hypnorum* S. Gray, A Natural Arrangement of British Plants 1: 445. 1821; Fink, Lich. Fl. U.S. 177. 1935.

Pannaria hypnorum has all the characters of the fungus *Pannaria* but instead of *Nostoc* it contains a green algal phycobiont. The thallus is minutely squamulose, tan, brownish or greenish, the green color showing up especially well when the thallus is wet. The apothecia are large, up to 2 mm. diam. or more, the thalloid exciple usually provided with crowds of rather large thalline lobules. Young apothecia are often goblet-shaped with high sides, later becoming more open and plane or concave. The thallus is a crowded or scattered mass of ascending lobules or squamules, simple or usually somewhat flabellately lobulate, without a distinct marginal area of radiating lobes. Although indistinguishable in the dry condition, clusters of smaller thallus squamules contrast, when wet, with the normal vegetative ones by taking on the blue-green color of the cyanophilic thallus type. These squamules contain *Nostoc* and represent cephalodia.

This is an abundant species on forest floor detritus such as needle duff,

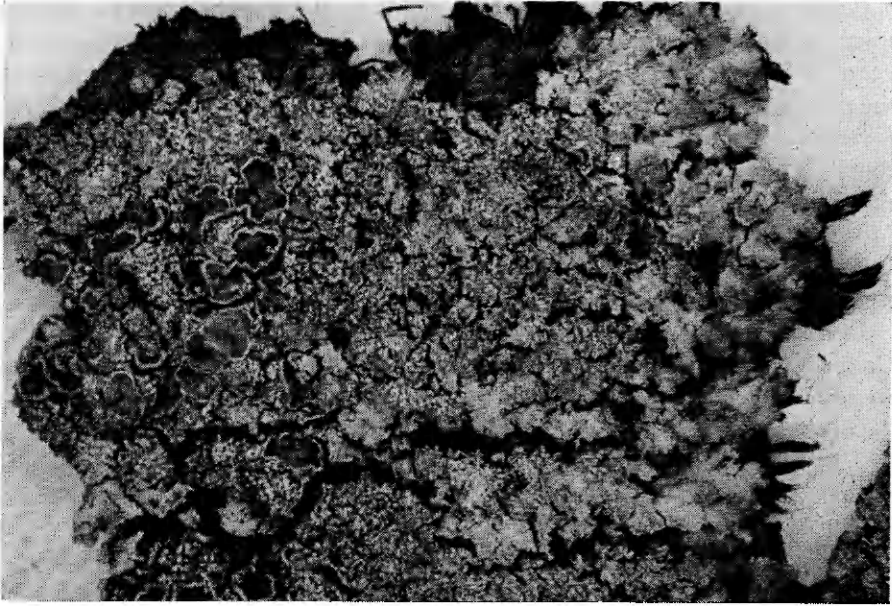


FIGURE 1. *Pannaria pityrea*, thallus overgrowing moss. Note the prominent thalline margin of the apothecia, left center, and distinctly lobed margins (x 3.5).

rotting twigs, moss, and other lichens. It cannot be confused with any other *Pannaria* since its green color is unique in the genus. The herbarium contains material from Colorado, Wyoming, and Montana, but the species certainly occurs in all the forested areas of western North America.

COLORADO.⁴ Boulder: 538, 1816, 3899, 9133, 30009, 30189; Clear Creek: 13236; Custer: 172; Douglas: 589, 1060, 20726; Garfield: 14213; Grand: 1465, 1669, 24765, 24809, 30711, 30734; Gunnison: 2819, 6005, 13455; Huerfano: 5852, 5933, 24888; Jackson: 8401, 5343, Crypt. Vind. Exsicc. 4142; Larimer: 4343, 30344, 34001, 34067, 34380, 34867; Mineral: 663; Park: 2946, 5525; Routt: 322; San Juan: 6309; Summit: 2634; Teller: 2113, 10901.

2. PANNARIA PITYREA (DC.) Degel., Bot. Notiser 104. 1929. *Imbricaria pityrea* DC. in Lam. and DC., Flore Franç. ed. 3, 2: 391. 1805; *Pannaria conoplea* (Pers.) E. Fr., Lich. Europ. Reform. 88. 1831; *Pannaria rubiginosa* var. *lanuginosa* A. Zahlbr., Cat. Lich. Univ. 3: 258. 1925; Fink, Lich. Fl. U.S. 177. 1935.

⁴Documentation of specimens is by county, followed by record numbers of specimens in the University of Colorado herbarium (COLO).

Pannaria pityrea is easily recognized by its distinct marginal lobes and conspicuous black rhizinae. Small round lobulae appear on the margins, and toward the center of the mature thallus these become so crowded as to obscure the nature of the thallus. These lobules are densely packed with *Nostoc*, have a very thin cortex, and function as isidia. Degelius (1935) considered this species to be a lichen of an "oceanic" distribution pattern. However, its relatively high moisture requirements are met well enough in the Rocky Mountains where it occurs over mosses on boulders and cliff faces (siliceous rocks) in the foothills areas. In more mesic environments on the Pacific Coast it occurs just as commonly on trees.

In the West the species is represented in the herbarium from South Dakota, Colorado, Arizona, Texas, and New Mexico, and probably occurs in all the western states.

COLORADO. Boulder: 425, 1390, 1703, 2224, 2680, 5322, 17910, 17964, 529, 20432; Grand: 30735, 34597; Gunnison: 6072; Hinsdale: 38411; Huerfano: 5949; Larimer: 34982, 30223, 34377, 24510; Montrose: 29995; Park: 5709.

3. *PANNARIA MICROPHYLLA* (Sw.) Mass., Ricerch. Auton. Lich. 112. 1852. *Lichen microphyllus* Sw., Vetensk.-Akad. Handl. 301. 1791; *Parmeliella microphylla* Muell.-Arg., Flora 72: 507. 1889; Fink, Lich. Fl. U.S. 174. 1935.

Pannaria microphylla grows exclusively on siliceous rock, particularly cliffs over which water seeps from time to time. This species forms densely packed masses of ascending, minutely lobed squamules which tend to overlap each other and form a solid colony. However, these colonies become cracked, possibly through freezing and thawing of the water over them, into small blocks of thalli. Old thallus masses become several millimeters deep and the older parts underneath become black and brittle. The plants are easy to scrape from the rock but they are so brittle that good specimens are difficult to make without careful chiseling.

Apothecia are usually present. Young ones show a thalloid rim which disappears as the apothecia approach maturity. The mature apothecia are about 1 mm. diam., highly convex, and dark brown to almost black. There is no tendency toward the production of isidioid lobules, and the thallus color is brown (varying with exposure) with no tendency to pruinosity.

The herbarium contains western United States specimens from Colorado, Arizona, and New Mexico.

COLORADO. Boulder: 35106; Fremont: 14868; Hinsdale: 38421, 38434; Jefferson: 36345; Larimer: 35286, 35344; Montrose: 31327.

4. *PANNARIA PEZIZOIDES* (Web.) Trev., Lichenotheca Veneta no. 98. 1869. *Lichen pezizoides* Web., Spicil. Flor. Goettingens. 200. 1778.

Pannaria pezizoides is one of the common lichens on moist, compacted soils

in the mountains. It occurs in forested areas and above timberline. The thallus is inconspicuous, composed of tiny spreading flabellately-lobed squamules usually less than half a millimeter in diameter. The thallus is usually covered by very conspicuous red-brown apothecia reaching up to 2 mm. diam., often crowded and almost covering the thallus area. The red disks are set off by prominent, crenate-lobulate, gray, thalline rims. Depending on exposure, the thallus ranges from pale gray to brown, and the apothecia, while usually bright reddish-brown, may become almost black. The squamules of the thallus are usually flattened against the substrate and show no tendency to produce erect isidiose lobulae such as occur in *P. lepidiota*. The spores are thick-walled, with a lumpy or mamilliose episprium.

The herbarium contains material of this species from most of the western states, including Wyoming, Colorado, New Mexico, Alaska, and the western Canadian provinces.

COLORADO. Boulder: 588, 1304, 3880, 3892, 9132, 30459, 30473; Clear Creek: 2702, 5636; Fremont: 14868; Grand: 30662, 30763; Gunnison: 6280, 6239, 6006, 2813; Huerfano: 5870; Jackson: 8402; La Plata: 33465; Larimer: 30838, 34032, 34093, 34452, 34866; San Juan: 6076; Summit: 2638, 2660.

5. *PANNARIA LEPIDIOTA* (Sommerf.) Th. Fr., Nova Acta Reg. Soc. Scient. Upsal., ser. 3, 3: 174. 1861. *Lecidea carnos*a var. *lepidiota* Sommerf., Suppl. Fl. Lapon. 174. 1826; *Parmeliella lepidiota* Vainio, Természetr. Füzetek 22: 308. 1899; Fink, Lich. Fl. U.S. 173. 1935; *P. cyanolepra* (Tuck.) Herre, Proc. Wash. Acad. Sci. 12: 151. 1910.

Pannaria lepidiota is probably the most difficult of the *Pannaria* species to learn to recognize. It usually occurs as a sterile crust and might not remind one of any lichen group in particular. However, as one learns to recognize the other species, *P. lepidiota* falls into place. It is the most highly reduced or depauperate of the species, consisting of a tight mass of minute squamules, most of which are provided with erect lobules variously referred to in the manuals as isidia, isidioid soredia, or soredia. The cortex of these lobules is extremely thin, and what appears to be a fine pruinose weft covers the tips and gives them a bluish-white appearance. A colony of this species often is simply a mass of these minute, plump, erect lobules. Neither *P. microphylla* nor *P. pezizoides*, which may grow in similar sites, produces these structures. The apothecia, when present, are reddish-brown, convex, less than 1 mm. diam., and embedded in the general mass of lobules. The lobules are often so small as to be invisible except with a hand lens. *Pannaria lepidiota* occurs on moist ground and on moist cliff faces from the foothills to the alpine tundra.

The herbarium contains western American material from South Dakota, Colorado, and Alaska.

COLORADO. Boulder: 1692, 25784, 30137, 30493; Clear Creek: 4698, 2921; Douglas: 1054, 20746; El Paso: 10860; Grand: 24811, 25789, 34620; Gunnison: 6004; Larimer: 2451, 2989, 30343; Park: 8267.

OTHER WESTERN SPECIES

The species of *Pannaria* discussed above are all that are likely to be encountered in western United States with the exception of one Pacific slope species and one species of moist Alpine-Arctic affinities occurring in Alaska.

PANNARIA ARCTOPHILA Th. Fr., Bot. Notiser 8. 1863. *Parmeliella arctophila* Malme, Svensk Bot. Tidskrift. 121. 1915. This species is added to the North American flora by a recent discovery in Alaska: Mount McKinley National Park. Moist tundra, on ground under willows near river, base of Mount Eielson (Copper Mt.), 25 July 1956, *Weber & Viereck 7138* (verified by R. Santesson and an exact match for Malme, Exsicc. No. 415). *Pannaria arctophila* has a thallus consisting of minute, thinly-corticated, purplish-brown granules usually less than 0.2 mm. diam. The thallus is almost invisible without a lens. The apothecia are pale reddish-brown, up to 1 mm. diam., with paler proper margin. The thallus thinly covers small bits of detritus such as dead herbaceous stems, twigs, and mosses. It is likely that the species will be found in the alpine or subalpine areas of Colorado. *Pannaria arctophila* was previously known from Norway, Sweden, and the European Arctic.

PANNARIA SAUBINETII (Mont.) Nyl., Mem. Soc. Scienc. Nat. Cherbourg 2: 324. 1854. *Parmelia saubinetii* Mont., Ann. Sci. Nat. Bot. ser. 2, 6: 331. 1836; *Parmeliella saubinetii* A. Zahlbr., Österr. Bot. Zeitschr. 59: 498. 1909. *Pannaria saubinetii* is common on trees on the west coast in California, Oregon, and Washington. It occasionally occurs on rocks. The thallus consists of minute flat or ascending blue-gray flabellately-lobed squamules. The apothecia are light reddish-brown and from the earliest stages of development they lack a thalline exciple. The disk shows a prominent, paler, proper excipular rim. This species has not been reported previously from America. Washington: Olympic Hot Springs, *A. H. Smith 1997*; Oregon: On *Thuja*, Foley Springs, *Sipe 14*; Douglas Co., Calapooia Creek, *Weber 1123*; California: San Mateo, Del Norte, several collections.

DOUBTFUL TAXA

PARMELIELLA RUDERATULA (Nyl. ex Hasse) Hasse, Contr. U.S. Nat. Herb. 17:79. 1913; *Pannularia ruderatula* Nyl. ex Hasse, Lichens, Southern Calif. ed. 2, 10. 1898. I have examined four packets, one containing extensive hand-specimens appear to be identical with *Placynthium microphyllizum* (Nyl. ex written notes by the author, representing isotypes in Farlow Herbarium. The



FIGURE 2. *Pannaria saubinetii*, detail of apothecia. Note absence of thalline margin, and paler rim of proper exciple (x 20).

Hasse) Hasse (= *Massalongia microphylliza* [Nyl. ex Hasse] A. Henssen, 1963). Two- and three-celled spores were found, contrary to Hasse's diagnosis, in *P. ruderatula*, thus eliminating the single character separating it from *M. microphylliza*.

PARMELIELLA CHEIROLOBA Muell.-Arg., Hedwigia 34: 140. 1895, is based on Eckfeldt 78, Columbia Falls, Montana, December 21, 1894 (G). This is a pale specimen of *Pannaria microphylla*. The substrate, not noted on the label, was very likely rock, as witness a few specimens intermixed of the saxicolous mosses *Encalypta* and *Mnium cf. orthorhynchum*. Mueller's statement "squamae 1½-5 mm. longae" is somewhat misleading. In a few thalli the horizontal range is up to perhaps 3 mm., but the ultimate lobes are still very small and always within the range of *P. microphylla*.

EXCLUDED GENERA

Fink (1935) listed several genera in the Pannariaceae which are not included here but which occur in this region. These were *Coccocarpia*, *Massalongia*, and *Placynthium*. In recent revisions, Henssen (1963) excluded *Coccocarpia* and placed it in the family Coccocarpiaceae. *Coccocarpia* has not yet been found in Colorado but occurs in Arizona, Texas, and New Mexico. *Massalongia* and *Placynthium* were transferred to the Peltigeraceae because of a special developmental feature of the apothecia, the so-called hemiangiocarpous type in which the apothecia develop under a covering subcortical layer which eventually ruptures. The apothecia must be examined at a very early age in order to see this distinction in ontogeny.

In Colorado, the only one of these groups which might be confused with *Pannaria* is *Massalongia carnosa* (Dicks.) Koerb. *Massalongia* grows in tufts of mosses, particularly *Grimmia*, on boulders from the foothills to the alpine zone. The thallus is dark chocolate-brown, the underside whitish to brown, with brown rhizinae. The margins are often lobulate or isidiate. The apothecia, when present, are brown, but these are usually absent in our region. Henssen says:

In sterile condition *M. carnosa* and *Parmeliella* [= *Pannaria*] *lepidiota* can be easily mistaken for each other, since both have a rosette-shaped brown thallus, a very similar anatomical structure, and often grow together. The thallus of *P. lepidiota*, however, becomes sorediose. So long as soredia are not yet developed, the two species can be distinguished by the upper cortex. The cells in *M. carnosa* are roundish with thin walls; in *P. lepidiota* they are angular and have strongly gelatinous walls and connecting pores. Such confusion of the species may account too for the statement that "*M. carnosa* should have a *sorediose* thallus."

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While this work was in press, Dr. Vernon Ahmadjian, Clark University, Worcester, Massachusetts, examined the phycobiont of *Pannaria hypnorum* and reports it to be *Myrmecia biatorellae* (Tschermak-Woess *et* Plessl) Petersen. The author is grateful to Dr. Ahmadjian for his diagnosis.