

Pannaria Delise ex Bory
(PANNARIACEAE)

After Jorgensen (1978), and many others

Rev. 5/94

Thallus foliose to squamulose and dorsiventral, or crustose (\pm areolate or granular), heteromerous, orbicular to spreading, loosely to closely attached; lobes (when present) broad and rounded to lacinate, or microphylline and \pm lobulate; upper surface dark blue-green, blue-gray to brownish, smooth or wrinkled-plicate, matt, glossy, or \pm scabrid or pubescent, with or without isidia and soredia; maculae and pseudocyphellae absent; upper cortex of anticlinal hyphae forming paraplectenchyma; attached to substrate by a well developed blue to black hypothallus or by a tomentum of "rhizines" (rhizoids?); rhizines felted, blue-black to whitish, often projecting beyond lobe margins as a byssoid prothallus; lower surface ecorticate, of loosely woven hyphae; medulla at least in part wooly.

Apothecia at first immersed, soon or eventually sessile to substipitate, laminal; disk circular, red-brown to black; thalloid exciple usually persistent but sometimes soon disappearing or even lacking from the start, concolorous with thallus, outer part pseudoparenchymatous, inner loosely organized with densely packed photobiont cells; true exciple thin, pale, \pm pseudoparenchymatous; hypothecium hyaline or pale; paraphyses unbranched or branched; asci clavate, unitunicate, I+; tholus I+; apical apparatus variable, a thin internal or external cap present in some species, or staining not apparent; spores 8, \pm uniseriate, oblong to ellipsoid or fusiform, or apiculate at one or both ends, simple, hyaline, epispore or perispore sometimes thick, sometimes warty.

Pycnidia immersed in thalline warts; fulcrum endobasidial; pycnospores bacilliform. Pannarin, atranorin, triterpenoids, or no substances. Photobiont Nostoc, Scytonema. On rock, soil or bark, often mossy, in moist, sheltered areas, primarily tropical, but some species extending to temperate, boreal, and arctic-alpine.

According to Jorgensen (1992, pers. comm.), the genus as presently delimited is heterogeneous, and several species will need to be transferred to new genera.

Key to Pannaria s. lato (including Parmeliella and Psoroma)

Pannaria and Parmeliella are often very difficult to distinguish from each other, and the differences between them are not clear to me at present (the presence or absence of a thalline apothecial margin is no longer considered a good character above the species level; both genera can have one); neither genus is homogeneous, and some of the species are also difficult to distinguish from various other cyanolichens. Although the European species have been monographed fairly recently, many of the N. American ones are rather poorly known, and many of the species are difficult to identify, especially when sterile. There are quite a few Pannaria-like taxa from California to Washington that do not seem to key out. The whole group needs to be thoroughly revised for N. America.

The crystal-forming "steroids" mentioned in one treatment are presumably the same as the

terpenoids mentioned in other treatments.

**I. Thallus without isidia or soralia; often fertile;
With well developed, enlarged, radiating lobes,
usually squamulose-foliose.**

1. Thallus usually placodioid-monophyllous. Upper surface with prominent longitudinal ridges as well as concentric lateral crescent-shaped ridges towards the circumference (giving an appearance somewhat resembling the shells of a Pecten mollusc). Apothecia with proper margin only, less than 1 mm diam. On trees or rock, usually in shaded, moist habitats, Maine to Labrador and Newfoundland, rare.Degelia plumbea

1. Thallus forming rosettes, more divided. Upper surface smooth or scabrid, never ridged. Apothecia with a thalline margin, more than 1 mm diam. Medulla rarely more than 100 μ m, of lax, randomly arranged hyphae.2

2. Apothecial disc black (wet or dry), rarely dark brown. Apothecia 1-2 mm diam., abundant, often \pm contiguous and angular by compression; disc roughened, matt, flat, conspicuous, irregularly crenulate; thalline margin usually white- to pale blue-gray; epithecium green-black, opaque; hymenium 100-200 μ m, I+ blue, hyaline or in part \pm red-brown; spores 11-15(-19) x (5-)8-11 μ m, ellipsoid to globular; walls smooth, without a perispore. Thallus verrucose crustose in center, in part minutely lobulate, forming closely adpressed, \pm incomplete rosettes, to 2-3 cm diam.; lobate at margins, lobes to 2 mm wide, 3 mm long, contiguous, convex, turgid, becoming fan-like, wider and elongate towards margins and verrucose-gnarled and fragmented towards center; upper surface pale gray or gray-brown striated-maculated white (lens), never bluish; hypothallus thin, but often visible between the squamules. Thallus P+ orange or P-, containing pannarin, but only in small amounts. Predominantly on basic mica-schists or epidiorite, or overgrowing associated mosses (on acid rocks according to Thomson), often in temporary seepage tracks, arctic-alpine, NE Canada to Iceland; also Alaska according to Jorgensen. May be mistaken for a placodioid Lecanora.Pannaria hookeri

2. Apothecial disc brown. 3

3. Thallus rosette-formed.4

3. Thallus squamulose-foliose, the marginal lobes rarely more than 3 mm long, brown, Pd-. Margin white felted-tomentose. Hymenium I+ blue-green, rapidly turning red-brown.(see Pannaria leucosticta and P. leucostictoides; if sorediate see P. pulveracea)

4. Apothecia without thalline margin.5

4. Apothecia with thalline margin.6

5. Thallus composed of minute to small, lead-colored, linear and flattened lobes, many-cleft and radiant at the circumference and becoming densely imbricated toward center; white below and bearing whitish rhizoids. Apothecia sessile, 0.2-0.6 mm diam., flat to convex, red-brown; the exciple thin, reddish brown, bearing minute white rhizoids below, often disappearing; spores ellipsoid, 5-10 x 3-4.5 μ m. On bark, southeastern U.S., to FloridaParmeliella stellata

5. Thallus foliose, brown-gray, becoming minutely lobulate on lobe margins; on thick prothallus, closely adnate, 4-8 cm broad; P- (no substances). Apothecia rare. Rather rare, on bark of deciduous trees or on rock, in hummocks and pastures, mostly subtropical, SE coastal plain, N. Carolina to Florida, west to Louisiana.Parmeliella pannosa

6. Lobes usually more than 2 mm broad, blue-gray to brown. Spore walls uneven or with otherwise conspicuous epispore. Usually on bark. Mostly mediterranean-atlantic climates.7

6. Lobes narrow, crowded and overlapping; upper side green-brown to pale yellow-brown or greenish gray to yellowish or bluish gray, distinctly wrinkled and powdery; the lobes irregular, imbricate, the margins wavy or shallowly crenate or dissected; underside pale, with dense pale to darkening tomentum. Thallus P+ orange-red (pannarin). Apothecia 0.8-2.5 mm diam., adnate, flat to convex, red-brown to brown-black, the exciple thin, colored like the thallus, wrinkled to crenate; hypothecium hyaline to slightly brownish; spores ellipsoid to ellipsoid-pointed, 13-18 x 7-10 μ m. On bark of oaks and junipers in exposed woods, near cliffs, or at the base of trees along roadsides, or sometimes on rock, throughout \pm southeastern U.S., to Florida, rather infrequent.Pannaria lurida

7. Spores ellipsoid, 15-19 x 9-10 μ m (20-24 x 10-12 including perispore). Thallus closely adnate, 2-3(-5) cm broad, foliose, \pm forming rosettes; becoming short lobulate; marginal lobes expanded, 7-8 mm long, 3-4 mm wide, deeply indented, mostly concave, with thick, pale, ascending margins; upper side smooth, \pm faintly scabrid or occasionally (often according to Hale) thinly white pruinose, whitish gray blue to light brownish gray, fawn, brown or olive; hypothallus fibrous, well developed, obscure or sometimes extending as a blue-black zone surrounding the thallus. Thallus Pd+ orange-red, with pannarin (P-, with no substances, according to Hale, but that strain is rare). Lower surface variable, dark brown or lighter; tomentum not projecting conspicuously at the margin. Apothecia common, 0.5-1.5 mm diam.; disc red-brown; thalline margin prominent, persistent, often crenulate, not white felted-tomentose. Hymenium I+ persistently deep blue. Perispore uneven, acuminate at one or both ends. Medulla P+ orange (pannarin). On mossy trees (usually at base), and rarely rocks, in humid, sheltered mature forests. Great Lakes region to New England and New Brunswick, S to southern Appalachians; British Columbia to New Mexico.Pannaria rubiginosa

7. Spores ovoid-ellipsoid, 16-25 x 7-10 μ m. Thallus rather thin and smooth; rosette-forming, radiating, orbicular, 2-6 cm wide, on a thick, felted, cottony, brown-black prothallus projecting 2-6 mm beyond lobe apices, closely appressed to substratum. Lobes narrow, 0.5-1.2 mm wide, flat to slightly convex, many-cleft, discrete at margins, or contiguous from margins to center and crowded and often \pm confluent without visible division between them, to minutely lobulate-imbricate centrally; margins of lobes entire (crenate to variously cut according to Fink), thickened, occasionally somewhat ascendent; upper surface blotched (x10 lens), smooth, occasionally striate, when dry pale gray-fawn to pinkish brown (or bright green-gray to ashy according to Fink), when wet leaden gray; margins of lobes sometimes white-frosted. Apothecia common, aggregated towards center, 0.4-1.2(-1.5) mm diam.; disc flat, red to brown-red; thalline margin thick, persistent, smooth to delicately crenulate, concolorous with thallus. Usually without substances, rarely with ursolic acid. On bark, mostly subtropical (southeastern U.S., to Florida) Parmeliella mariana (Fr.) P. M. Jorg. & D. J. Galloway (syn. Pannaria mariana)

ADD [I need to study my material of this to decide whether it is actually new and what it's distinguishing characteristics are, but it is the only clearly foliose-lobed, non-sorediate, non-isidiate, species I know of in western N. America, unless it's possibly P leucosticta or a related species that I'm treating under squamulose species but that can be somewhat lobed at the margins, e.g., P. laceratula or P. leucostictoides]:

Thallus small, closely appressed; lobes rather narrow, clearly radiating; upper surface flat, smooth. Apothecia with thalline margin. On bark of alder in old-growth forest in western Oregon. Pannaria "siletii" Ryan ined. (?)

II-A. Thallus without soredia or isidia.

**Thallus normally without enlarged, radiating lobes,
squamulose-crustose or granulose.**

On bark or wood (or over mosses on bark or wood).

(If photobiont green, see Psoroma).

1. Upper surface somewhat roughened/scabrid, especially toward lobe margins; marginal lobes usually radiating, flattened to concave, usually broader than central lobes; apothecial rim thalline, "warty", often covered below in minute white hairs. 2

1. Upper surface smooth throughout; marginal lobes not radiating, similar in cise to central lobes; apothecial rim thalline or not, never warty or hairy. 3

2. Marginal lobes averaging to less than 1.2 mm wide; medulla P- (without pannarin). Epispore smooth, without apiculi. Upper surface dark gray to gray or gray-blue, with lobes apically blackened and squamules \pm browning to buff; nodules lighter colored; margins and young lobes white scabrid to felted-tomentose; overall appearance blue-gray. Thallus squamulose-foliose, orbicular, effigurate or not, 1.0-1.6(-2.4) cm broad, under 200 μ m thick, centrally composed of small squamules with nodules; often broken up into areoles; margins of squamules \pm raised; marginal lobes (usually present) 1.5-3.0 mm long, 0.5-1.0 mm wide, slightly ascending; lower surface pale. Hypothallus black, extending beyond lobes, conspicuous, thick, often appearing almost rhizinate. Apothecia common, often crowded towards middle, 0.3-1(-1.6) mm diam.; thalline margin conspicuous, whitened, crenulate; disc concave, becoming plane or sometimes convex, shiny, red brown to darkening; hymenium 110-125 μ m, I+ bluegreen then red-brown or orange in thinner sections; paraphyses simple, coherent at tips; epithecium (gold) brown. Spores 8/ascus, uniseriate, subglobose to ellipsoid, often apically pointed, 14-18(20) x 7-10 μ m. Containing atranorin, various unknown fatty acids, and terpenoids. Also reported to contain "steroids" (the same as in P. leucosticta), developing crystals on the margins in the herbarium. On bark of deciduous trees, primarily oak, sometimes overgrowing other lichens, mainly inland. Alaska to California; rare in moist forests in northern Idaho. (If lobes not white-scabrid to pruinose, and epispore epiculate, see P. leucosticta). P. leucostictoides

2. Marginal lobes usually averaging to more than 1.5 mm wide; medulla P+ orange or yellow (pannarin), rarely P-. (P. rubiginosa)

3. Epispore conspicuously warted. Hymenium I+ persistently deep blue.(P. pezizoides)

3. Epispore smooth or lacking. Hymenium I+ blue-green rapidly turning red-brown, or I+ pale blue, fading. 4

4. Spores 13-17(-20?) x 5-7.5 μ m. Eastern and western. Usually isidiate. (P. tryptophylla)

4. Spores over 17 μ m long and 7.5 μ m wide. (?--need to check on P. leucosticta) 5

5. Margins of lobes white pruinose. Growing in Eastern U.S., and in Canada. Epispore with

broadly acuminate apiculi. Upper surface gray to chestnut-brown; overall appearance brownish to grayish, but without bluish tinges. Thallus thin, to 200 μm . Apothecia frequent, always with a thalline margin. Spores usually containing many oil droplets. Thallus 3-6 cm broad, distinctly squamulose, composed of numerous confluent squamules; margins with raised finger-like projections; lower surface rather dark, tomentose. Apothecia common, with \pm flat, brown disc and persistent, conspicuous white felted-tomentose thalline margin. Containing "steroids", developing crystals on the margins in the herbarium. On deciduous trees, rarely on rocks, in mature forests. (If discs brown-black and epispore lacking, see P. leucophaea). Pannaria leucosticta

5. Margins of lobes \pm concolorous, never strongly whitened. Growing in Western areas. (Also see P. maritima, which may possibly occur on Douglas fir, and has a bluish appearing felt on the tips or margins of the lobes and nodules). 6

6. Upper surface of lobes distinctly dull, strongly convex; apothecial margin usually not thalline. No substances. Squamules deeply crenate-digitate; margins concolorous with rest of lobe. Usually on bark. Thallus squamulose, 2.5-7.0 cm wide; squamules 0.5-1.0 mm wide, slightly to deeply incised, at first appressed, becoming ascending and imbricate; hypothallus absent. Apothecia common, usually abundant, adnate, 0.5-1(-2.0) mm diam.; proper margin conspicuously lighter colored than disc, becoming excluded; disc plane becoming convex, light orange, sometimes darkening to reddish orange. Hymenium 110-130 μm high, I+ blue-green then quickly reddish yellow in parts; paraphyses coherent; epithecium golden-brown. Spores 8, uniseriate, ellipsoid, \pm tapered at ends, 15-17 x 5-6 μm (according to Jorgensen, 1978; epispore thin, sometimes indistinct. Usually on bark, especially on loose bark at base of Arbutus, but also abundant on conifer twigs; occasionally on rock. Maritime and inland. British Columbia to California, with rare disjuncts in northern Idaho. According to Goward, et al. (1994), material from British Columbia has spores 18-21 x 7.5-10 μm , and may be a distinct taxon. (If discs brown-black, see P. leucophaea). Pannaria "saubinetii"

6. Upper surface of lobes somewhat shiny, predominantly plane; apothecial rim often thalline. Containing atranorin and various unknown fatty acids and terpenoids. Lobes averaging to less than 0.6 mm wide; lobe margins never strongly white-felted. Thallus K-, C-, P-. Hymenium I+ pale blue, gradually fading. Spores 18-20 x 10 μm Pannaria laceratula Hue

II-B. Thallus without soredia or isidia.
Thallus normally without enlarged, radiating lobes,
squamulose-crustose or granulose.
On soil or rock (or over mosses on soil or rock).

1. Squamules finely dissected, nearly cylindrical, dichotomously much-branched.

Apothecia without thalline margin. On rock. Vermont to Alabama, west to Illinois. Thallus composed of small, imbricated, marginally ascending squamules, passing centrally into a subsquamulose or granulose, warty crust; lead gray above, blackening toward center below; apothecia immersed to partly superficial, 0.5-1 mm diam., flat to convex, pale to dark red-brown, the exciple thin, concolorous with disc, soon disappearing; hypothecium hyaline; spores 17-23 x 6-10 μ m. A poorly known species (description from Fink, which is inadequate).Parmeliella crossophylla

1. Squamules weakly to finely dissected, \pm flattened, dichotomously much-branched or not. Apothecia with or without thalline margin. On soil, moss, or rock; distribution various. 2

2. Spores under 17 μ m long and 7.5 μ m wide. 3

2. Spores mostly over 17 μ m long and 7.5 μ m wide (?--check P. leucosticta), or apothecia absent. Thallus not isidiate. 4

3. Apothecia without thalline margin. Hymenium I+ persistent deep blue. Spores 13-17(-20?) x 5-7.5 μ m. Thallus usually isidiate. On mosses and soil in the arctic, mainly on trees in open woods further south. Arctic to temperate, south to South Carolina and Louisiana in the east, to Washington state in the west. (Parmeliella tryptophylla)

3. Apothecia with thalline margin present but often indistinct or only partial. Hymenium I+ blue-green then yellow or red-brown. Spores 15-17 x 5-6 μ m. Squamules (and lobes?) indented, incised or unevenly crenulate (scarcely branched). Upper surface of thallus gray, gray-brown, or nearly black (greenish gray to ashy or ashy brown according to Fink). Apothecia adnate to sessile (according to Fink); disc brown-black, rarely brownish in shade. Thallus of \pm rounded, adpressed, turgid squamules, to 2 mm diam., forming a rather thick, \pm cracked-areolate crust; hypothallus usually obvious, blue-black; squamules discrete at margin, often becoming \pm imbricate at center, not enlarged at margins. Apothecia to 1 mm diam., frequent, often clustered, \pm convex; thalline exciple often indistinct, sometimes unevenly developed on one side of an apothecium. Spores with outer surface smooth, without perispore; inner side of spore wall uneven. No substances. On sheltered, \pm basic moist rocks, more rarely on bases of trees in sheltered coastal sites or lake-sides (on siliceous rock especially in seepage areas on cliffs according to Weber). Widespread through much of boreal to temperate N. America, from New Brunswick to British Columbia and southward at least in the west (to Arizona and New Mexico according to Weber); western populations still present some taxonomic difficulties.Pannaria leucophaea

4. Thallus usually forming a tight crust; apothecia abundant; disc generally plane or at most weakly convex, rimmed by distinct thalline margin. Epispore conspicuously warted. Hymenium I+ persistently deep blue. 5

4. Thallus looser; lobes to some extent overlapping; apothecia sparse or abundant;

disc plane or hemispherical, with or without thalline margin. Epispore smooth or lacking. Hymenium I+ blue-green, rapidly turning red-brown.6

5. Thallus blue-gray to dark brown (never ochraceous); phycobiont blue-green. Apothecial margin regular, granulose-crenulate, persistent. Hypothallus usually weakly developed, black to blue-black; thallus of small squamules less than 1 mm broad, toward the center forming a granular thallus; upper side pale brown; underside white. Apothecia sessile, to 2 mm broad; disc light reddish brown, smooth, epruinose, slightly convex. Spores ovate, somewhat pointed, 26.5-30.5 x 9.5-12 μ m. No lichen substances. On moist compacted soils or soil over rock, damp mosses on rocks, walls, trees and the ground, seldom on old wood. Usually in sheltered, undisturbed sites. Arctic-alpine to boreal, south to Washington state and several places in eastern U.S. (south to Colorado and New Mexico according to Weber; S to California according to Goward, et al., 1994). [An undetermined species from the west slope of the Cascades, Washington, also seems to key out here; it has smaller apothecia and a different overall appearance than *P. pezizoides*].*Pannaria pezizoides*

5. Thallus ochre-brown to brown, fresh material greener when wet and with a golden luster; phycobiont green (*Myrmecia*), but blue-green algae in cephalodia. On mosses and soil, occasionally on bases of woody plants, usually on much humus, rarely on barks higher up, common, boreal-arctic, southward in the west to Oregon and the central Rocky Mountains. (*Psoroma*)

6. Tips or margins and squamules nodules covered by a white pruinose felt giving the thallus a bluish tinge, otherwise upper surface fuscous, dark olive brown. Apothecia without thalline margin. On drip surfaces especially in crevices or shaded sites in the supralittoral zone of the seashore, occasionally inland. Thallus squamulose, to 6 cm broad; squamules to 1 mm wide, dentate, occasionally marginally lobate and centrally areolate-cracked, developing erect nodules or papillae; squamules \pm crowded; hypothallus absent. Apothecia occasional, often hidden among squamules, adnate to sessile, 0.7-1.3(-2.0) mm diam.; proper margin concolorous with disc, usually distinct; disc plane to slightly convex, shiny, dark reddish brown. Hymenium 100 μ m high, I+ blue-green; paraphyses coherent; epithecium light brown; spores not abundantly developed, 8 per ascus, ellipsoid with apices slightly pointed, 17-20 x 8-10 μ m; epispore thin but distinct. Containing atranorin and unknown fatty acids. Similar to *P. leucostictoides*, but thallus brown to grayish, shiny, non-pruinose, and usually with marginal squamules not elongated. Primarily saxicolous. Washington and British Columbia. *Pannaria maritima*

6. Tips or margins white-felted or not (not appearing blue-felted, except sometimes in *P. praetermissa*); upper surface pale or dark. Apothecia usually at least partly with thalline margin (sometimes indistinct; usually lacking in *P. saubinetii*) Habitat and distribution various, sometimes maritime, but usually not in the supralittoral zone. 7

7. Growing in California. On rocks. Spores 15-25 x 6-9 μ m. Squamules not much branched, usually thickish, rough. Apothecia to 1.5 mm across. Poorly known, possibly a distinct species. "*Pannaria leucophaea* f. *californica*"

7. Growing in northern or eastern areas, or if growing in California (*P. praetermissa*), then

on soil or moss. Spores broader relative to length. 8

8. Apothecia common; thalline margin persistent, conspicuous. Spores usually containing many small oil droplets. Epispore with broadly acuminate apiculi.

Usually on bark, rarely on rock. Eastern or boreal-arctic. (*Pannaria leucosticta*)

8. Apothecia common or not; thalline margin often inconspicuous or absent. Spores various. 9

9. Peripheral lobes averaging to more than 0.8 mm wide; upper surface convex; lobe margins often white felted-tomentose. Apothecia common, with thick thalline margin, or rare, with thalline margin poorly developed or entirely lacking. Apothecia rare; thalline margin poorly developed, sometimes entirely absent. Spores containing 1 or few large oil droplets. Epispore conspicuous, broad, even, rounded. On soil and moss. Widely distributed, including southwestern and eastern N. America. Squamules and lobes \pm irregularly and weakly branched; upper surface brown to reddish brown or almost black when dry, with bluish pruina (bluish gray when wet), the margins often white felted-tomentose. Thallus thick, to 300 μ m, squamulose; squamules 1-3 mm long, 0.75-1.5 mm broad, or \pm rounded and 1-3 mm diam., smaller towards center, often growing densely compacted or imbricate, forming a continuous crust over the substrate, centrally thickly beset with \pm erect, finger-like, usually whitish pruinose, accessory lobules, which have been variously called soredia, isidia, or isidioid soredia, and which do produce bluish-gray soredia; lobules also present on margins. Hypothallus not apparent. Underside pale to white, without rhizines. Apothecia disc reddish brown to brownish black, usually convex. Spores 13-23 x 8-11.5 μ m, often containing a single, large oil droplet. Hypothecium hyaline; hymenium I+ blue turning red. Containing terpenoids and unknown fatty acids. On moist, \pm calcareous ground, arctic-alpine to boreal, south to Colorado and California in the west, south to Great Lakes region and Quebec in the east. [Also see "*Parmeliella lepidiota* v. *coralliphora*"] [If squamules ca. twice as long as wide, ca. 150 μ m thick, without "steroids", and spores 1-septate, 28-38 x 5-6 μ m, see *Massalongia carnosula*]. *Pannaria praetermissa*

9. Peripheral lobes averaging to less than 0.6 mm wide; upper surface plane or convex; lobe margins never strongly white felted-tomentose. Apothecia common; thalline margin well developed or not. Spores without epispore (?--check *P. laceratula*). Mostly northwestern, to Alaska. [if lobes 0.5-1 mm wide and apothecia with flesh-colored disc and soon disappearing thalline margin, see *P. saubinetii*, which usually grows on bark]. [also see "*Pannaria rudematula*"]. 10

10. (Usually?) growing directly on rock, in inland areas. Upper surface of squamules convex. No substances. Spores 16-22 x 8-11 μ m. Squamules and lobes dichotomously much-branched. Upper surface of thallus dark yellowish brown (according to Fink's key; greenish gray to straw-colored, becoming brownish gray to darker, according to his description). Apothecia immersed to adnate; disk flesh-colored to chestnut-brown and darker. Thallus closely adnate throughout or marginally ascending, irregularly lobed, the lobes smooth to minutely wrinkled, passing into a thick, closely adnate, granulose to warty, crust; lobes to 1.5(-3) mm long (to 5 mm long according to the protologue, but Weber found only occasional lobes to 3 mm long). Apothecia 0.5-1 mm diam., partly immersed to adnate, the disk flat to convex, the exciple

very thin, colored like the disk, soon disappearing; hypothecium hyaline to pale brownish; spores ovoid-ellipsoid. On soil [according to Fink; probably on rock, according to Weber, based on mixture with saxicolous mosses], Montana (incorrectly indicated by Ohlsson, under Pannaria leucostictoides, as being from British Columbia); directly on rock, British Columbia to Alaska (according to Goward, et al., 1994, who state that B.C. material is very similar to some forms of P. praetermissa and may possibly be conspecific). According to Weber, who examined the type of P. cheiroloba, this is a pale form of "Pannaria microphylla" [= P. leucophaea]; however, according to Jorgensen, P. cheiroloba is in need of further study; based on possible anatomical characters that Weber may not have noted, it may not even belong in this part of the key!).
"Parmeliella" cheiroloba

10. Growing on mosses over rock in hypermaritime areas. Upper surface predominantly plane. Containing atranorin and various unknown fatty acids and terpenoids. Spores 18-20 x 10 um. Alaska to British Columbia. Pannaria laceratula

III. Thallus with Soredia or Isidia, or Thallus Granulose; Foliose or Squamulose

1. Thallus with isidia. Thallus forming rosettes, divided. Upper surface smooth or scabrid, not ridged. Medulla rarely more than 100 μ m thick, of lax, randomly arranged hyphae.2

1. Thallus with soralia or soralia-like protuberances, or entirely granulose.
5

2. Thallus foliose, Pd+ orange-red; upper surface whitish blue to blue-gray, brown-gray or pale brown (fawn). Marginal lobes distinctly enlarged, to 7-8 mm long, 3-4 mm broad. Thallus \pm forming rosettes, to 2-3 cm diam.; upper surface scabrid or slightly pruinose; lobes deeply incised and mostly concave with a distinct, generally paler, ascending margin, often almost white. True isidia almost always present, simple, finger-like, mostly marginal, the tips white pruinose, often broadened; hypothallus well developed, usually inconspicuous but sometimes extended as a blue-black zone around thallus; tomentum on underside under 100 μ m thick, loose, the hyphae \pm randomly oriented. Apothecia not uncommon, 0.5-1.5 mm diam.; disc concave or flat, red-brown to brown; thalline margin nodulose to isidiate. Hymenium partially I+ persistently deep blue, mainly in vicinity of asci. Spores ellipsoid, 15-19 x 9-10 μ m (20-24 x 10-12 including episore); episore distinctly uneven, acuminate at apices. On bark or mossy rock, S. Dakota to Arizona, east to the Carolinas; Mexico.P. tavaresii

2. Thallus squamulose, Pd-. Upper surface brownish. Marginal lobes not much enlarged, to 1.5 mm long, 0.5-1 mm broad. 3

3. Spores 13-17(-20?) x 5-7.5 μ m. Hymenium I+ strong blue. Upper surface cherry red to brown, gray-brown, or nearly black (blue-black when wet). Marginal lobes not much enlarged, to 1.5 mm long, 0.5-1 mm broad; tips rounded; centrally the ridges and lamina isidiate; isidia true, cylindrical, branched, 0.04-0.12 mm thick, commencing as papillae on the upper surface and eventually covering the center of thallus; upper surface matt, epruinose, esorediate; underside black or blue-black with fine concolorous tomentum. Apothecia adnate, round, without thalline margin; proper margin narrow, entire, dull, concolorous with disc or paler; disc rust red. Hypothecium red-brown. Hypothallus well developed, blue-green to blue-black, extending beyond the thallus 1-1.5 mm; squamules apparent at the thallus margin. Spores ellipsoid, more pointed at one end. No substances. On mosses and soil in the arctic, also on seasonally moistened rock; mainly on trees in open, humid woods further south, at low elevations. Arctic to temperate, south to South Carolina and Louisiana in the east, to Washington state in the west.Parmeliella tryptophylla (syn. P. corallinoides according to Jorgensen, 1978, although Egan lists that name as a separate species)

3. Spores mostly over 17 μ m long, over 7.5 μ m wide. Hymenium I+ blue then reddish. Upper surface brown to reddish brown with bluish pruina (bluish gray when wet), or dirty brownish-yellowish or grayish, or blackening. 4

4. Squamules usually to 1-3 mm long, 0.75-1.5 mm broad, the central ones smaller, thickly beset with \pm erect, finger-like, usually whitish pruinose, accessory lobules producing bluish-gray soredia; margins also with lobules. Upper surface brown to reddish brown or almost black when dry, with bluish pruina, bluish gray when wet;

margins often white felted-tomentose. Apothecia rare, small. Spores (including epispore) with rounded tips. [If upper surface pale to dark medium brown, lobe tips and "isidia" hard-corticate and not pale-felted, forming dense mats completely obscuring substrate, see *Massalongia carnosae*]. (*Pannaria praetermissa*)

4. Squamules (at least central ones) somewhat larger, soon becoming a thick mass of short, stout, irregularly swollen or knotty, coralloid branchlets, leaving no trace of the squamules visible. Upper surface dirty brownish-yellowish, grayish, and blackening. Apothecia numerous, often densely crowded, relatively large. Spores (including epispore, if any?) with pointed tips. Thallus of small or medium sized squamules Apothecia medium to large (this probably means ca. to 2-3 mm diam.), from plane, circular and depressed, becoming convex and irregularly crenate; disk red, red-brown, and blackening, soon excluding the thin, entire, paler proper margin; epithecium pale yellow; paraphyses simple, septate, subconglutinate; hymenium I+ pale blue, the asci then ± dingy reddish-yellowish; Spores 17-24.5 x 8.5-12.25 µm. Chemistry unknown. On mossy sandstone and earth, foothills of central California coast; Alaska. "*Parmeliella lepidiota* [var.?] *coralliphora* (Tuck.) Herre"

5. Marginal lobes enlarged or elongated, over 2 mm long. Thallus foliose. [If lower surface distinctly veined, see *Peltigera collina*]. 6

5. Marginal lobes usually not particularly enlarged or elongated, mostly under 2 mm long. Thallus always squamulose-crustose. 7

6. Thallus Pd+ orange-red (pannarin). Lobes usually concave; lateral lobes not very conspicuous, not very imbricate. Upper surface not appearing undulate, usually glaucous, ashen-blue, sometimes with a ± pale brown (fawn) tinge in more exposed situations. Soralia in the form of partly decorticated squamules or lobules along the margins, often confluent. Crystals not forming in herbarium. Thallus foliose, to 2-3 cm diam., rarely larger, ± forming conspicuous, irregular, entire or fragmentary rosettes; lobes 7-8 mm long, 4-5 mm wide, deeply incised, mostly contiguous, fan-like or somewhat overlapping, ± concave, deeply indented with elongate, ± ascending margins; upper surface often paler and ± scabrid-pruinose towards margins, with numerous, coarse, marginal, at times abraded, knob- or squamule-like simple or coralloid isidia which may cover and obscure the thallus apart from the ± extended marginal lobes; hypothallus well developed, but rarely apparent as a blue-black zone surrounding the thallus. Apothecia very rare, sessile, 0.5-1.5 mm broad; thalline margin distinct, light brown, ± entire but abraded isidiate; proper exciple not visible; disc chestnut brown, smooth, epruinose; hymenium I+ blue, the asci becoming I+ red; spores ellipsoid, 15-19 x 9-10 µm (with perispore 20-24 x 10-12 µm), ellipsoid with ridged perispore, acuminate at one or both ends. On soil and moss, in more southerly portions of the range also on mossy trunks of broad-leaved trees. Boreal, New Brunswick westward, south in the west to California and the central Rocky Mountains (to Arizona and Texas according to Weber). *Pannaria conoplea*

6. Thallus P-. Lobes plane to convex; lateral lobes conspicuous, frequently imbricate; upper surface with an undulate general appearance, pale brown. Soralia true, coarsely granular, not consisting of decorticated squamules, developing from just under the revolute lobe margins, often delimited. Crystals often forming

in herbarium. Thallus foliose, \pm forming rosettes, to 2 cm diam., always with conspicuously enlarged marginal lobes, to 3-4 mm broad, rounded with slightly incised margins, mostly convex, especially so on the frequently developed side lobes. Containing terpenoids and unknown fatty acids. Also reported to contain "steroids". Soralia sometimes almost capitate or maniciform, sometimes more limbiform, never becoming continuous or forming a confluent sorediate crust. Hypothallus well developed, blue-black, rarely extending beyond the thallus itself. Apothecia very rare, 0.5-2.0 mm diam; disc brown; thalline margin thick, nodulose, of same color as thallus, often developing blue-gray soralia. Spores 15-17 x 8-9 μ m (20-25 x 10-11 μ m including epispore), ellipsoid with thick, smooth, distinctly apiculate epispore. Usually on bark of conifers, in very humid localities, mainly in ravines, mostly in wet montane forests. According to ?, mostly in the Appalachians, from North Carolina to Maine, with a few populations in Newfoundland, New Brunswick, and Michigan; according to Goward, et al. (1994), in N. America known only from British Columbia. Pannaria ahlneri

7. Thallus distinctly small-squamulose, blue-gray to olive brown, with white felted-tomentose margin. Containing "steroids". Hymenium I+ blue turning red. 8

7. Thallus entirely granulose (rarely with a few minute squamules in P. cyanolepra). 11

8. Upper surface bearing stiffly erect or appressed-tomentose hairs (check carefully); hypermaritime, rare. (Erioderma and Leioderma)

8. Upper surface lacking hairs (except a few cobwebby hairs rarely present at lobe tips in Pannaria mediterranea); distribution and frequency various. 9

9. Thallus thickly beset with erect, usually whitish pruinose lobules, which have been variously called soredia, isidia, or isidioid soredia, and which do produce bluish-gray soredia. Upper surface brown to reddish brown or almost black when dry, with bluish pruina, bluish gray when wet. Spores 13-23 x 8-11.5 μ m, with broad, even, rounded epispore. On soil and moss, arctic-alpine to boreal, south to California in the west, south to Great Lakes region and Quebec in the east. (Pannaria praetermissa)

9. Thallus with soralia; soralia granular, mainly limbiform, gray or violet-gray, mostly on up-turned, ascending margins, occasionally spreading to upper surface, limbiform. Upper surface blue-gray to olive brown, Spores 13-16 x 7-8 μ m (16-24 x 8-9 μ m including perispore); perispore broadly attenuate. Thallus small-squamulose but appearing crust-like, forming small patches; hypothallus inconspicuous, thin, squamules \pm circular, often irregular, contorted, deeply indented, to 2-3 mm diam. Thallus containing "steroids" (appearing as crystals on herbarium specimens). Soralia often appearing \pm wooly with crystals (50x magnific.). Apothecia very rare; disc brown; thalline margin sorediate. 10

10. Upper surface olivaceous-blue, smooth, not scabrid or pruinose, except along the margins, which are white-pruinose (rarely with a few cobwebby hairs at lobe tips). Without atranorin. Thallus usually less than 2 cm diam. Lobes scale-like/isodiametric, 2-3 mm wide, less than 1(-1.5) mm long. Soredia bluish gray, developing on the recurved margins, often covering thallus. Terpenoid crystals often

developing in herbarium. Apothecia rare, at first with a soresiate thalloid margin. Hymenium I+ green-blue then immediately red-brown. Containing terpenoids and unknown fatty acids. On coarse-barked, conifers or broad-leaved trees and rocks or soil, in old woodlands, in oceanic areas and humid intermontane localities, at lower elevations; more rarely and usually in the north on rocks. British Columbia to Oregon; rare in western Montana. Pannaria mediterranea

10. Upper surface blue-gray (without olive tinge), distinctly scabrid to pruinose (even away from the margins). With atranorin. Otherwise extremely similar to P. mediterranea. Similar to P. leucostictoides but thallus soresiate. California. [If lobes rather elongate, see P. ahlneri]. Pannaria pulveracea

11. Thallus usually distinctly bluish gray (steel blue), matt. Thallus composed of minute, dissected, dusky yellowish or buff squamules, thier edges and soon the whole thallus disappearing under a confused mass of minute, steel blue, continuous and conglomerate soresia-like granules, ordinarily forming a thin, indeterminate, fragile crust, with few or no squamules. Apothecia very rare, 0.3-0.7 mm diam., partly immersed to adnate; disk flat to convex, reddish to blackish; proper margin thin, concolorous with disk, soon disappearing; hypothecium brownish; hymenium I+ bluish; epithecium yellowish brown; spores ovoid-ellipsoid, 16-22 x 7-9 um. On bark, rock, soil or moss, California to Washington; British Columbia (the sterile, blue-gray granular taxon referred to by Noble is undoubtedly this species). Rather common. According to Goward, et al. (1994), this may be just a form of Pannaria mediterranea. According to Nimis (unpubl.), this species belongs in Pannaria. (If apothecia present, with carbonaceous thalline border, and growing on sandy soil, see Moelleropsis nebulosa)..... Parmeliella cyanolepra

11. Thallus brownish, often shiny. On detritus or moss over soil. Thallus entirely granulose; granules 0.1-0.3 mm thick, spherical and unbranched (according to Thomson), or cylindrical to short coralloid, coalescing to form a continuous crust, swelling when wet and drying into wrinkled clumps, lacking squamules even at the margins, grayish, often suffused with brown, often shiny. Apothecia adnate, to 0.5(-1) mm diam.; disc pale red-brown, plane to convex, smooth epruinose; proper margin narrow, entire, paler than disc, non-gelatinous; thalline margin absent. Hypothecium hyaline; hymenium I+ blue then red. Spores ellipsoid with rounded ends, 15-20 x 7-12 um; epispore smooth. Arctic-alpine, very rare in N. America, Alaska, Hudson's Bay, Labrador. Overall appearance of thallus somewhat resembles that of a Collema or Leciophysma. Probably does not belong in Pannariaceae according to Jorgensen, 1978. Santessoniella arctophila

ADD:

EXCLUDED OR DOUBTFUL NAMES:

Pannaria waghornei = doubtful name (type in very poor condition according to Thomson, 1984)

Thallus small-squamulose; squamules when dry concave with the border connivent, when moistened flat to slightly convex, imbricated, 0.5-1 mm across, ca. 0.25 mm thick, with minutely crenulate-globular margins, upon an obscure, brownish black hypothallus; upper surface dark yellowish brown. Apothecia almost entirely covering the squamule, 0.6-1 mm diam., sessile, the disk flat, brownish to dark purplish brown, the proper exciple thin, brownish to brown (paler than disc), rarely disappearing; hymenium 112-120 µm high, I+ blue; epithecium subcontinous, light yellowish brown, gradually paling downward; paraphyses 2-3 µm thick, faintly septate, the slightly clavate tips light brown, some forking above; asci inflated-clavate; hypothecium hyaline to pale straw-colored; spores oblong-ellipsoid, 17-21 x 5.5-7 µm, simple according to Hasse, at least partly 2-3 celled according to Weber. Spermatia oblong, 6-8 x 0.75 µm; sterigma straight. Upper layer of thallus composed of flattened, hyaline cells 4-6 µm thick, resting on a double or triple layer of rounded-quadrangular cells, 10-12 µm thick; below this the algal layer of Nostoc cells, 4-8 µm thick; medulla of smaller colorless cells 6-8 µm thick; hypothallus formed of similar dingy brownish cells. On soil (rocks according to Fink) southern California.
Parmeliella rudratula (= Massalongia microphylliza according to Weber)

Cross references to:

Koerberia spp.

Euopsis spp.

Leciophysma spp.

Massalongia spp.

Erioderma spp.

Placynthium spp.

etc.

Literature

Fink, B. 1935. The Lichen Flora of the United States.

Galloway, D. 1985. Flora of New Zealand Lichens.

Goward, T., B. McCune, and D. Meidinger. 1994. The Lichens of British Columbia.

Hale, M. E. 1979. How to Know the Lichens.

Hasse, E. 1913. Lichen Flora of Southern California.

Herre, A. W. C. T. 1910. Lichen Flora of the Santa Cruz Peninsula, California.

Jorgensen, P.-M. 1978. The lichen family Pannariaceae in Europe. Opera Botanica.

Noble, W. J. 1982. The lichens of the Douglas-fir dry subzone of British Columbia.

Poelt, J. and A. Vezda. 1977. Erg. I.

Purvis, O. W. 1992. Pannaria, and Parmeliella. In: Purvis, et al., Lichen Flora of Great Britain and Ireland.

Rogers, 19 . Genera of Australian Lichens.

Thomson, J. W. 1984. American Arctic Lichens. I. The Macrolichens.

Weber, W. A. 1965. The lichen flora of Colorado: 2. Pannariaceae. University of Colorado Studies, Series in Biology No. 16.

[Author?]. 1993. Lichen Flora of Australia. Part I.