

**Hypogymnia** (Nyl.) Nyl.  
(LECANORALES: HYPOGYMNIACEAE)

After Goward (1988), and Brodo, Hale, and others

June 1995

Thallus foliose to subfruticose, heteromerous, radiate and rosette-forming to irregular, or ascending, prostrate, or subpendulous; corticate on both surfaces; cortex of anticlinal hyphae; medulla very lax, arachnoid, white to dark brown or rarely yellow; lobes weakly to strongly inflated,  $\pm$  tubular, usually hollow, very rarely  $\pm$  solid; upper surface whitish to gray or (especially when wet) greenish, or  $\pm$  suffused brown; perforations absent from upper side; rhizines absent; attached by adhesive discs below, or rarely by most of the lower cortex; lower surface black (to brown near tips), shiny, wrinkled; lower cortex thin, often fissured or irregularly perforate towards the tips. Soredia often present.

Apothecia laminal, sessile to  $\pm$  prominently stipitate, round, sometimes very large (to 5 mm or more); thalline exciple well developed, persistent, concolorous with thallus; disk shining, concave to flat, eperforate or rarely perforate, red- to yellow-brown, epruinose; asci small, cylindrical, unitunicate, I+ blue; spores 8, simple, hyaline,  $\pm$  globose.

Pycnidia when present often very numerous and conspicuous on upper surface (in fertile species), immersed, minute, punctiform, wall blackened around the ostiole pale below; fulcrum endobasidial; pycnospores bifusiform (bacilliform according to Rogers), straight, 5-8 x 1  $\mu$ m. Upper cortex usually with atranorin and often chloratranorin; medulla often with depsidones (including physodic, physodalic and fumaprotocetraric acids). Photobiont Trebouxia. On bark or wood, less often soil or rock, in moist and mostly cool areas, coastal to subalpine.

Differs from most Parmelia-like genera in having inflated lobes and lacking rhizines. Allantoparmelia has solid lobes and a dark color; Menegazzia has regular perforations on the upper surface, a different chemistry and larger, ellipsoid, thick-walled spores. Cavernularia has a smaller thallus with numerous perforation-like depressions below.

This genus is usually easily recognized by the (usually) hollow foliose thallus lacking rhizines and lacking regular perforations on the main parts of the upper and lower surfaces (such as found in Menegazzia and Cavernularia, respectively). Forms with dark, brownish thalli might be confused with Allantoparmelia, which has a solid medulla and lacks atranorin. The lack of rhizines helps distinguish the genus from Anzia, a mostly tropical or subtropical genus that may be superficially similar.

In spite of numerous revisions by various authors, the genus in N. America is still a horrible mess. The following is my latest attempt to compile the various conflicting reports into something halfway coherent and at least partially useable. Lots of luck!

## I. Sorediate

**1. Lobes mainly solid.** Cortex K+ yellow (atranorin); medulla K-, C-, Pd-, KC+ red, with physodic acid complex only, or Pd+ red, KC-, with additional physodalic acid  $\pm$  protocetraric acid. Thallus orbicular, to 15 cm diam. but generally smaller; older central lobes and true marginal lobes adhering to the substrate, generally crowded or contiguous, broad, 3-7(-10) mm wide; peripheral and secondary lobes commonly present, linear, suberect, elongated, 1-2 mm wide, lacking lateral contacts, cartilaginous, repeatedly dichotomously branched, occasionally becoming dominant and accentuating the loosely ramified character of the thallus; upper surface gray, becoming yellowish gray after long storage, commonly with laminal wrinkles, the upper cortex erupting and becoming sorediate, ultimately extensively covered with granular soredia commonly occurring in confluent glomerules 3-5 mm wide; lower surface generally black, sometimes blanching in older highly sorediate specimens, pale brown or off white near the apices, strongly wrinkled; medulla white. Apothecia relatively rare, subpedicellate; margin entire then sorediate, funnel-shaped margin; disc red-brown, 3-7(-12) mm wide, concave then flatter; spores ellipsoid, 6-9 x 4-5  $\mu$ m. Superficially resembling some specimens of H. austerodes. On rock. Very rare in N. America, known thus far only from the east coast of Hudson Bay and from Oregon. .... H. pulverata (Nyl. ex Crombie) Elix

**1. Lobes hollow for the most part.** ..... 2

**2. Soralia developing on the inner surface of burst lobe tips, often lip-shaped.**  
..... 3

**2. Soralia superficial, forming from a breakdown of the upper cortex, not lip-shaped.** ..... 4

**3. Medulla Pd+ red/orange, KC+ pink (physodalic, physodic and oxyphysodic acids, with or without protocetraric acid). Lobes contiguous, lacking marginal lobules; upper surface usually not black-bordered (but is black-bordered in California according to Hale & Cole). Medullary ceiling white throughout (to brown according to Hale & Cole).** Lobes rather short to rather elongated, (0.5)1.5-2(-2.5) mm wide (to 6 mm according to Ozenda & Clauzade), flattened to  $\pm$  convex (inflated according to Hale & Cole), pinnately to irregularly branched, sometimes with smaller lobes irregularly placed, contiguous to imbricated, towards the tips clearly broadened and usually raised; upper surface pale grayish or rarely greenish; lower surface black and matt, brown and shiny at tips, strongly wrinkled, usually not strongly expanded; perforations lacking on underside and generally also on tips; soralia usually abundant but occasionally sparse, usually clearly lip-shaped, whitish gray-green. Apothecia rare. Pycnidia sometimes present (according to Hale & Cole), but usually lacking. On conifers and broadleaf trees and shrubs, old wood, and occasionally on soil, mossy rocks or various other substrates. Rather rare in north coastal forest from near sea level to 2800 ft in California, but extremely common in north temperate and boreal regions (eastern and western); north to southern Canada (BC to SE Canada), south in the Rockies to Arizona and New Mexico in the west; Great Lakes area to New England and south to the Appalachians in the east (Hale, 1979, refers to "H. appalachensis Pike...the sorediate morph of H. krogii"--in which the thallus is only 2-4 cm broad and the upper surface is darker, greener mineral gray; this is a nomen nudum and of uncertain status). Quite variable, with numerous infraspecific taxa described; I won't attempt to make sense out of them at the moment. If thallus with conspicuous laminal perforations, see Menegazzia terebrata. .... H. physodes (L.) Nyl.

**3. Medulla usually Pd- (physodic, 3-hydroxyphysodic, and traces of 2'O-methylphysodic**

and alecoronic acids, sometimes also with vittatolic acids), rarely Pd+ (with additional physodalic acid and sometimes protocetraric acid). Lobes widely separate to imbricate or entangled, often bearing conspicuous and regular marginal lobules at right angles to the main lobes. Upper surface often bordered by a broad black band of the bulging lower surface. Medullary ceiling soon darkening towards thallus center. Thallus forming small rosettes or groups of lobes which spread irregularly and loosely over the substratum. Lobes elongate, to 3-4 cm long, 0.5-2 mm broad, dichotomously or irregularly branched, apices of non-sorediose lobes rarely broadened and often  $\pm$  acute; upper surface greenish or slightly to strongly brownish (except sometimes pale gray in arctic-alpine forms), shiny,  $\pm$  plane, lower surface black or brown-black, shiny, reticulately dented to strongly wrinkled, with large round perforations common and conspicuous at the tips and axils; soralia often sparse, rather irregular and not strongly lip-shaped, white. Infrequent; boreal to arctic-alpine, on conifer trees or soil or mossy rocks, in humid coastal and intermontane forests, Alaska to Oregon. Many early reports from the Pacific NW are misidentifications. According to Hale (1979) this species also occurs in the Appalachians. .... H. vittata (Ach.) Parrique

4. Soredia located at least in part on or near lobe tips; apical perforations present or absent. Medulla Pd+ red or Pd-. .... 5

4. Soredia distinctly and entirely laminal; lobes lacking apical perforations. Medulla P-. .... 8

5. Medulla P+ red, containing physodalic, protocetraric and physodic acids. Lobes distinctly swollen, bearing basally constricted marginal lobules; apical perforations often present; laminal perforations absent. On conifers in open to shady coastal forests at lower elevations, rare in humid intermontane forests, Alaska to Oregon, somewhat infrequent.

Previously misidentified as H. pseudophysodes (not found in N. America), which is usually P-, more or less dichotomously branched, and sometimes has laminal perforations in addition to apical ones. [Need to incorporate full description]. .... H. oceanica Goward

5. Medulla P-, KC+ reddish (physodic acid complex). Lobes not distinctly swollen (except in H. tubulosa), lacking marginal lobules (laminal lobules may, however, occasionally be present); lobe tips rarely perforate. Various distributed. .... 6

6. Lobes  $\pm$  discrete, convex,  $\pm$  tubular (moderately inflated according to Hale & Cole), stiffly suberect (except occasionally rather lax and pendent in shady sites). Soralia common, all apical or subterminal, to 3 mm wide,  $\pm$  capitate and solid, or ring-shaped (with opening into medulla). Upper surface pale whitish gray to greenish gray, without brownish tinges, without black lines or borders. Lobes  $\pm$  elongate (rather short according to Hale, 1979, linear according to Hale & Cole), little branched, 1-1.5(-4) mm wide, relatively thick (0.5-1.5 mm), usually not enlarged at tips, divergent, dichotomously branched. Thallus 2-3(-8) cm across, loosely attached. Lower surface black or very dark brown, often wrinkled. Apothecia rare. Medulla completely black (Hale, 1979) or variably darkened (Hale & Cole), P- (except soralia P+ slowly yellow), KC+ pink, containing physodic acid, plus 3-hydroxyphysodic acid or oxyphysodic and paraphysodic acids. Widespread and frequent (but seldom abundant), especially on twigs of conifers in open woods in the boreal region, also on broadleaf trees or on mosses over rocks. In California from San Benito Co., north in the coast ranges, montane forests, and valley and foothill woodlands, and the Klamath Mountains, from near sea level to 3500 ft, north to Washington (where it occurs mostly at low elevations) and in open forests throughout British Columbia. Also in the east, from Great Lakes area

to New England. .... H. tubulosa (Schaerer) Hav.

**6. Lobes usually contiguous, flattened, closely appressed. Soralia subapical or laminal, or both, smaller (under 1 mm when discrete), more diffuse, never subcapitate or ring-form. Upper surface often with a greenish or brownish cast, often bordered with black and crossed by black lines.** Lobes elongate to more often rather short. Primarily restricted to continental climates. .... 7

**7. Outermost soralia generally small, poorly delimited, punctiform, loosely packed with coarsely granular soredia; laminal soralia generally well developed, often arising from coarse (0.1 mm), pustular papillae or "isidia", becoming diffuse over the upper surface. Upper surface greenish gray, more or less brownish tinged, often rather dark, at least at tips of lobes, often shiny.** Lobules often present. Soralia subapical, mostly small, slightly paler than thallus, forming from isidioid warts filled with rather granular (to farinose) soredia; Lobes 1-5 mm wide at periphery, slightly convex,  $\pm$  imbricate. Medulla containing physodic and 3-hydroxyphysodic acid and sometimes a trace of vittatolic acid or unknown substances. Lower surface entirely black. On bark and wood (especially conifers) and infrequently on mossy rocks in alpine areas, widespread, in open inland forests, boreal and arctic-alpine, Alaska to New Mexico; common in Canada. Closely resembling H. subobscura when soredia are absent or sparse and lobules are present. .... H. austerodes (Nyl.) Räsänen

**7. Outermost soralia larger, at least partly well delimited, capitate, packed with finely granular/farinose soredia; soredia rare toward thallus center, arising through disintegration of upper cortex. Upper surface whitish to bluish gray and matt, or becoming reddish brown to blackish brown and somewhat shiny.** Soralia subapical (to marginal or laminal), round or diffuse, 0.5-1 mm across, whitish or bluish gray, granular (powdery according to Hale, 1979), often little apparent because originating on the lower surface of the tips of ascending lateral branches, but spreading subapically, sometimes becoming  $\pm$  confluent and laminal as well (Ozenda & Clauzade regard the laminal soralia as being of a different type than the terminal ones). Thallus adnate, appressed, 5-10 cm broad; branching pattern various. Lobes adjacent or imbricate, 1-4 mm wide, convex at center of thallus, flattened and slightly broadened at periphery. Lower surface black, rugose. Apothecia rare. Medulla blackening, containing physodic acid complex, and vittatolic acid. Lower surface black, brown at tips. Infrequent; boreal zone (Quebec to Alaska), south to northern California, and in the Rockies south to Mexico, on bark and wood of conifers, occasionally on mossy rocks, in open forests, intermontane. .... H. bitteri (Lyng.) Ahti

**8. Thallus "soft"; upper surface brittle, white to pale gray, at first continuous and shiny, but soon rugose, cracking and flaking,** becoming diffusely sorediate over the whole surface, matt. Thallus closely adnate, 3-6 cm broad; lobes short, ca. 1 cm long, crowded, 1-3 mm wide, little branched. Medullary cavity brown to blackening above and below. Lower surface dull black, rugose, the tips perforate, part of the lower cortex often eroding away to expose the medulla. Medulla containing physodic acid. Rare and restricted to temperate Pacific coast (at present known only from San Luis Obispo and San Diego Counties, California), on bark in open chaparral or scrub. .... H. mollis Pike & Hale

**8. Thallus  $\pm$  firm and tough; upper cortex not distinctly brittle, gray or brown.** Lobes 1-5 mm wide at periphery, slightly convex,  $\pm$  imbricate. Boreal or arctic-alpine. .... 9

**9. Upper surface pale gray (sometimes slightly yellowish or greenish, but not brownish and never very dark), without black lines or borders; soralia arising from a coarsely rugose upper cortex, which then bursts open, producing flakes and granules composed of the upper cortex and algal layer, pale green (slightly yellower than thallus).** Upper surface matt, coarsely rugose, the ridges erupting into soredia; soredia fine granular. Lobes 1-3 mm wide, flattened, coalescing into dense rosettes. Lower surface black at center,  $\pm$  pale brown near tips. Medulla usually containing physodic, 3-hydroxyphysodic and paraphysodic acids,  $\pm$  traces of vittatolic acid. Rare, in western mountains, on trees, Yukon to Colorado. With the general appearance of a shade from of H. austerodes. ..... H. farinacea Zopf

**9. Upper surface brownish, at least at tips of lobes, often shiny, often limited and crossed by black; soralia arising by gradual disintegration of the cortex, either on laminal warts (pustular "isidia") or a roughening upper surface, producing finely to coarsely granular soredia; soredia brownish.** Thallus appressed. Lower surface entirely black. Medulla containing physodic, 3-hydroxyphysodic and sometimes a trace of vittatolic acid. Common; boreal and arctic-alpine, on tree bark, wood and rock. .... (see H. austerodes, above)

ADD:

H. subcapitata (Nyl.) Rass. (also occurs in Russia, but not mentioned by Kopaczewskaja, et al., 1971). The specific epithet probably refers to the soralia, but I have not yet seen any information on it.

Atranorin, physodic acid. Oregon. .... H. subphysodes (Kremp.) Filson v. subphysodes (see Elix's Australian treatment for description)

## II. Non-soresidate

1. Lobes solid or "stuffed". ..... 2

1. Lobes clearly hollow. .... 3

2. Lobes averaging less than 1 mm wide, separate, terete, elongate and little branched, nodulose. Thallus closely adnate but sometimes subascending marginally. Lower surface smooth to wrinkled, black. Medulla Pd-, K-, C-, KC+ reddish, containing physodic acid. Widespread, arctic-alpine, on rock. (If upper surface of thallus olive to brown-black, K- (without atranorin), see Allantoparmelia). ..... (Brodoa oroarctica)

2. Lobes averaging more than 1 mm wide. Medulla Pd+ red and then containing physodalic acid, or occasionally Pd-. Restricted to temperate and boreal western N. America, on bark (very rarely on rock). ..... (rare form of H. imshaugii)

3. Upper surface dark brown or blackish (to occasionally grayish in shade), usually bearing small papilliform lobules or isidia, or both, towards center of thallus and on edges. Cortex mostly K- (without atranorin), but K+ yellow (atranorin) in pale areas. Upper surface shiny towards the tips, black bordered; lobes swollen at tips, elongate, finger-like divergent, pinnate or dichotomously divided, tips  $\pm$  raised. Thallus more or less rosette-forming. Lower surface black. Medulla P-, KC+ reddish, containing physodic usually together with vittatolic acid and often paraphysodic acid. Common; arctic-alpine, on soil or mosses, in windblown localities, Quebec to Alaska, infrequent southward, to British Columbia and Colorado. .... H. subobscura (Vainio) Poelt

3. Upper surface pale whitish gray or green-gray, sometimes mottled with black; lobules, if present, strictly marginal; isidia absent. Cortex K+ yellow (atranorin). Primarily temperate and boreal, on bark and wood (very rarely on rock). ..... 4

4. Lobes mostly short, or if somewhat elongate, then usually broadly and  $\pm$  closely appressed to substrate (except in one form of H. enteromorpha, which has distinctly "knobby" lobes), often swollen; branching lateral or palmate (often very irregular), usually not predominantly isotomic-dichotomous (but see H. apinnata and H. rugosa); lobe tips mostly hemispherical; apical perforations present or absent. Inland or coastal. .... 5

4. Lobes mostly elongate, at least in part suberect or loosely pendulous, or both; branching predominantly isotomic and  $\pm$  regularly dichotomous; lobe tips mostly tapered and broadly pointed; perforations mostly absent or restricted to lower surface. Mostly coastal (except H. imshaugii). ..... 13

5. Broadest lobes averaging 3-6 mm wide, sometimes  $\pm$  "knobby" (nodulose); medullary cavity dark. .... 6

5. Broadest lobes to 1-2(-3) mm wide; not at all "knobby"; medullary cavity white or dark. I have collected several specimens, in California and British Columbia, that have very small, flattened, appressed lobes and a dark medulla, which do not seem to fit any of the taxa below. .... 10

6. Upper side strongly rugose-pitted (without lens), especially towards thallus center.

**Medulla usually Pd+ slowly yellow, containing hypoprotocetraric acid,  $\pm$  paraphysodic or physodic acids, or rarely Pd-. Thallus with a soft papery texture when dry, often forming large (10-25 cm across) rosettes on trunks. Lobes generally short,  $\pm$  swollen (rather weakly) throughout, even the most elongated ones not at all "knobby".** Upper surface ashy gray (turning buff in herbarium); black mottling or margins inconspicuous or absent. Marginal lobules generally poorly developed or absent; branching often neatly isotomic dichotomous, sparse; lobes often contiguous. Lower surface wrinkled, black, with irregular perforations. Lobes thick and crowded, swollen, irregular. Medullary cavity entirely blackened. Apothecia common. Without conphysodic acid. Infrequent, on upper trunks of conifers in open coastal and especially intermontane forests, usually at upper elevations, restricted mostly to humid districts in the Cascades (British Columbia and Washington), rare eastward in the Rockies. (If medulla P-, without lichen substances, branching at least partly anisotomic, and upper surface smooth, see *H. apinnata*). ..... *H. rugosa* (G. K. Merr.) Pike in Hale

**6. Upper side smooth to roughened or slightly wrinkled (or strongly wrinkled in *H. occidentalis*). Thallus with a  $\pm$  cartilaginous texture; rarely forming rosettes over 10 cm diam. Lobes (especially the most elongate ones) often becoming distinctly "knobby" (nodulose), short or long, the broadest ones invariably averaging 3-6 mm wide; marginal lobules well developed or not; lobes not upturned, stiff. Medulla brown-black, thin. Frequent along the humid Pacific coast (California to southern Alaska), and in the northern Rockies. .... 7**

**7. Medulla (usually) P+ red, with physodalic acid,  $\pm$  other acids (diffractaic and physodic acids according to Brodo manuscript; protocetraric acid according to Hale, 1979). marginal lobules (i.e., small, basally constricted adventitious lobes) often well developed,  $\pm$  perpendicular to main branches, giving a somewhat pinnate appearance. Lobes (2-)3-5(-8) mm across (at least near tips), usually strongly nodulose, convex, usually uneven, with slight (to strong) constrictions at intervals and branching points, irregularly to dichotomously branched, usually appressed and crowded, to more rarely free,  $\pm$  loosely adnate but sometimes somewhat trailing, imbricate and attached only centrally, very swollen and irregular, short and broad to or more often elongate and linear, depending on habitat orientation. Medulla thin, brown. Upper surface smooth,  $\pm$  shiny, or becoming rugulose and matt in some older sections, whitish gray to pale glaucous green, often browned at lobe tips, often with black rim when viewed from above [lectotype lacks a conspicuous black rim]. Lower surface matt (Hale, 1979) or shiny (Hale & Cole, 1988), rugose, black (to brown at tips), sporadically perforated. Thallus adnate to loosely attached but not trailing, 6-12 cm broad. Pycnidia numerous. Apothecia occasional to frequent, laminal, on a tumid stipe, urceolate, 2-13(-20) mm wide; disc concave then plane, often cracked. Hymenium 40-55  $\mu$ m high; spores 5-8 x 4-5  $\mu$ m [in the lectotype, nearly spherical, 6 x 5  $\mu$ m]. Medulla KC-, Pd+ red (physodalic and protocetraric acids), or KC+ reddish, Pd- (physodic acid) [an acid-free chemotype "morphologically indistinguishable from P+ plants" is also present on the lectotype sheets]; with accessory diffractaic acid. This taxon as presently delimited is still extremely variable; material from Washington state includes appressed, small-lobed forms that are very difficult to distinguish from *H. occidentalis*, *H. rugosa*, and *H. apinnata*, and a form with very long, rather narrow, trailing lobes and a white upper surface. According to Hale (1979), the species is very common on *Sequoia*, redwoods, and other conifers, along the coast, low to moderate elevations, northern California to Pacific NW, very common in the Cascades, much**

rarer in the northern Rockies (south to western Wyoming). Also on broadleaf trees and fenceposts. According to Noble, in British Columbia it occurs primarily on Pseudotsuga. This is H. enteromorpha in the sense of most authors, including Goward & McCune. The species was lectotypified by Hale & Pike; their article did not provide much morphological information about the type, but Hale & Cole's description (which was made after the lectotypification) applies to this taxon, not to the one referred to by Brodo (see below). ..... H. enteromorpha (Ach.) Nyl. ("H. tumidula Pike ined. var. tumidula")

**7. Medulla P-, KC-, without lichen substances. Marginal lobules usually absent or poorly developed; branching usually anisotomic to isotomic dichotomous, not at all pinnate. Lobes less strongly nodulose, sometimes not nodulose at all, narrower, averaging 3-4 mm across.** Upper surface shiny, convex, smooth to becoming in part weakly rugose, as seen from above usually (but not always!) bordered by the expanded, shiny, black, wrinkled lower surface; pale mineral gray to nearly white. Thallus rather closely appressed to loosely pendulous, orbicular to irregular, to 15 cm diam.; lobes short to more often elongate, often apically perforate; medulla thin, cottony, at first white but soon darkening around central cavity. Apothecia common, short stipitate, to 10 mm diam.; disc medium to dark brown, usually concave; spores subglobose to broadly ellipsoid, 6.5-7.0 x 5.0-5.5  $\mu$ m. Common especially on conifers in coastal localities, especially at low to moderate elevations, in exposed and especially in rather sheltered habitats, but not below the canopy of shady coastal forests. Alaska to central California, and west to Idaho and Montana. According to Noble, the "P- strain of H. tumidula" is somewhat less frequent than the P+ strain, and is found primarily on Pseudotsuga but often on deciduous trees as a secondary substrate after Pseudotsuga. Reference by Hale & Cole to a strain of "H. enteromorpha" lacking medullary substances, and reference by Brodo to a strain of "H. tumidula" lacking medullary substances, apparently refers at least partly to this taxon, which Noble called "H. tumidula Pike ined." var. [or f.] "inactiva (Asah.) ined." [not the same as H. inactiva (Krog) Ohlsson]. ..... H. apinnata Goward & McCune

**8. Lobes mostly crowded-contiguous, distinctly flattened (much like H. physodes), or becoming convex with age or when growing under exposed conditions; apical perforations generally lacking. Medullary ceiling usually white throughout or darkening only gradually inward of the lobe tips (but can be almost entirely dark, at least in British Columbia). Upper surface  $\pm$  plane or at least not strongly convex, often weakly concave near lobe tips; lobes never swollen.** Basally constricted marginal lobules absent. Lobes short, divergent, radiating, mostly less than 2(-3) mm across, closely appressed. Lower medulla brown. Upper surface gray, rather uneven (?). Lower surface wrinkled, black to dark brown, paler towards the swollen apices, rarely perforate. Thallus to 10 cm across. Pycnidia common. Apothecia common, stalked, to 7(-10) mm diam. Medulla KC+ reddish, containing physodic and 3-hydroxyphysodic acids, usually P-, or sometimes (according to Ohlsson) P+, with additional physodalic and protocetraric acids. On trees, especially conifers, in inland forests, common in the intermontane Pacific Northwest, Alaska to Washington, rarer southward to northern California. (Note: presorediate specimens of H. physodes differ in having less copious branching, smooth upper surface, and Pd+ medulla). According to Goward, et al. (1994), the material referred to by this name is heterogeneous and probably represents two distinct species. .... H. metaphysodes (Asah.) Rass.

**8. Lobes separate to crowded-contiguous, swollen and convex from the first, often**



**apically perforate. Medullary ceiling soon darkening inward of the lobe tips. Upper surface distinctly and strongly convex throughout (including near lobe tips), also often swollen.** Basally constricted marginal lobules present or absent. Medulla Pd+ or Pd-. Various distributed. .... 9

**9. Containing conphysodic acid in addition to physodic acid. Upper surface strongly black-mottled, entirely blackened on older portions. Apothecia unknown.** Thallus to 5 cm across; lobes 2-3 mm wide, irregularly branched; upper cortex white, tinged with brown, with numerous black patches, not sharply delimited from lower cortex; lower cortex black, shiny, moderately wrinkled and pitted, with occasional apical perforations, sometimes with white cortex patches; medulla forming a thin, rather compact layer with hyphae sometimes extending into the cavity, wholly or partly blackened. Medulla P-. Rare; Alaska [but not mentioned by Thomson]. (Brodo's manuscript calls this "H. cf. inactiva"). ..... "H. lugubris (Pers.) Krog subsp. beringiana Krog"

**9. Lacking conphysodic acid. Mottling inconspicuous to absent; black rim absent.**

**Apothecia abundant**, substipitate, 3-10 mm diam.; discs plane. Medulla P- or P+, but lacking hypoprotocetraric acid. Upper side usually  $\pm$  smooth. Broadest lobes averaging 1.5-3(-4) mm. Upper surface usually rough or matt. Lobes mostly rather short, crowded, irregularly inflated, swollen or not; marginal lobules present, basally constricted. Upper surface whitish gray; conspicuous perforations often present on lobe tips; pycnidia numerous. Thallus adnate to closely adnate throughout (but occasionally some lobes trailing), (3-)5-10(-12) cm broad. Lower surface black, deeply rugose, shiny, sparsely perforate. Medulla blackening above and below, KC+ reddish, P-, containing physodic acid. Pycnidia abundant. On main trunks of conifers in open to shady forests, from near sea level to 5000 ft (in California), in the north coastal and montane forests. Rather rare in California, from the San Francisco Bay area north to Del Norte Co. in the north coast ranges, Klamath Mountains, and on the western slopes of the Sierra Nevada, north to southern British Columbia, but common more or less throughout the intermontane region of the Pacific NW (east of Cascades, S to NW Wyoming, N to Alaska). In moist lowland forests there are forms with trailing lobes and some adventitious lobes; these differ from H. enteromorpha mainly in chemistry. (If lobes 3 mm or more broad, see H. apinnata, H. rugosa, and H. enteromorpha). ..... H. occidentalis Pike

**10. Restricted to eastern North America.** Medulla Pd+ red, KC+ reddish, containing physodalic acid in addition to physodic acid complex, traces of protocetraric acid, and an unknown. Lobes usually fairly short, 0.8-2.5 mm wide, abundantly palmately branched, especially at tips, imbricate, swollen but somewhat flattened; usually dichotomously divided towards the tips, with few to frequent perforations. Thallus 5-8 cm across, rather closely attached (loosely attached but lobes adnate, according to Hale, 1979), often forming cushion-like colonies; marginal lobes free and slightly upturned. Upper surface greenish gray, brownish towards tips. Lower surface wrinkled, black, becoming light brown towards tips. Upper medulla thick and white, lower medulla thin and brown. Pycnidia common. Apothecia common, stipitate, 2-3 mm diam. Rather common on twigs and branches of conifers at high elevations southward or in exposed sites in the north, locally abundant in spruce forests along the Appalachians, from New England to NE Alabama. .... H. krogii Ohlsson (incorrectly cited by Egan as "krogiae")

**10. Restricted to western North America.** Medulla Pd+ or Pd-. .... 11

**11. Lobes distinctly swollen; lobe tips mostly broadly rounded and perforate.**

..... (see H. occidentalis, H. rugosa, and H. enteromorpha)

**11. Lobes not distinctly swollen; lobe tips predominantly tapered and somewhat pointed, lacking perforations (perforations, however, occasionally present in lower cortex).**

..... 12

**12. Medulla distinctly pale yellow.** Thallus ca. 3-7 cm across, loosely adnate, extending well beyond the branches of the substrate, forming flattened but thick (ca. 5 mm or more) clumps or mats; lobes somewhat radiating or irregularly arranged, crowded, overlapping, 5-15 mm long, 1.5-3(-4) mm wide, irregularly branched to often dichotomous especially at the tips, convex, flattened to moderately swollen, not "knobby", without marginal lobules (but sometimes with short regenerative lobules on surface); upper surface smooth to occasionally rugulose in places, glaucous to greenish gray, matt, not browned at tips, with no trace of a black margin; lower surface dark brown, matt, smoothish, canaliculate (with upper surface curling down and over the edges, forming a distinct pale rim).

Apothecia, when present, to 2-3 mm diam., stipitate. Pycnidia occasional. Medulla P-, containing physodic acid and unknown (UV-, pale yellow after charring, R<sub>F</sub> 2 in solvent C). Channel Islands, California. .... H. sp.

**12. Medulla white to brown or black.** ..... 13

**13. Medullary ceiling white throughout (check thallus center); lower medulla white or darkening;** cortical perforations usually lacking. Medulla KC- or occasionally KC+ rose, and then containing physodic acid. Variously distributed. .... 14

**13. Medullary ceiling darkening towards thallus center; lower medulla dark;** lower surface usually sparsely perforate. Medulla KC+ rose, containing physodic acid. Mostly restricted to humid districts along the Pacific coast and on west side of the Sierras and Cascades. .... 17

**14. Lobes predominantly linear-elongate, 0.6-1.5(-2.0) mm wide, upturned at tips, very soft, pliable, pendulous; upper cortex generally whitish (with a yellowish cast according to Brodo), and with a "tidy" appearance; lower surface frequently much expanded and clearly visible from above as a blackish border.** Lobes ± uniform in width; branching sparse and rarely dichotomous; without lateral narrow branches or lobules. Upper medulla white, cottony. Lower medulla dark brown to black and thin, becoming sac-like, P+ red, KC-, containing physodalic, protocetraric and diffractaic acids and lacking physodic acid. Frequent (especially towards the north) along humid, oceanic west coast, Oregon to southern Alaska. (Non-sorediate specimens of H. vittata might key out here). .... H. duplicata (Sm. ex Ach.) Rass. (including "Parmelia duplicata var. douglasicola Gyelnik")

**14. Lobes at most elongate, never linear, not strongly upturned at tips, ± stiff, appressed or suberect; upper cortex often brownish (sometimes strongly darkened brown-gray in some populations in southern California), and with a "dirty" appearance; lower surface not much expanded, scarcely visible from above.** Lobes terete to compressed, ± branched, ± pointed at tips; Medulla white throughout or only above. .... 15

**15. Medulla white only above, thin and brown below.** Lobes stiff and much branched. Lobes somewhat flattened, upturned at the tips. Rare, California. [I have no other info. on this taxon]. ..... "H. californica Pike ined."

**15. Medulla entirely white, thick and cottony.** Medulla P+ red (physodalic and/or protocetraric acids), KC- or P-, KC+ reddish and then containing physodic acid; other substances (e.g., barbatic acid) may also be present. Common, especially on twigs in western mountains. (The P- strain, which occurs at least in Montana, has been referred to by the name "H. montana Pike ined.") ..... 16

**16. Lobes mostly somewhat elongate, radiating horizontally or more commonly suberect, more or less pointed at the tips; upper surface  $\pm$  smooth,** grayish. Lobes terete, 1.5-2 mm wide, sparingly dichotomously branched. Apical perforations usually absent. Thallus 5-9 cm across, extremely variable, quite appressed especially towards center, or more commonly loosely attached with free lobe ends. Lower surface black to dark brown, matt, strongly rugose. Pycnidia very common. Apothecia abundant, short-stalked, 3-5(-15) mm diam. Medulla P+ red (protocetraric, physodalic and physodic acids, with or without diffractaic acid) or (high elevations in Montana) P- (physodic acid only). The P- specimens are usually more closely adnate. On branches and trunks of oaks and other broadleaf trees, and conifers, in a wide range of habitats, montane to subalpine (to 8000 ft in California), dry to humid, coastal to inland. Common and widespread, southern California to Montana and British Columbia, and southward in the Rockies to SE Wyoming. An extremely variable species as currently delimited. .... H. imshaugii Krog

**16. Lobes rather short, broad, appressed,  $\pm$  blunt at the tips; upper surface often rugose.** Occasional over much of the southern half of California; often, but not always, near cities; perhaps an environmental modification of H. imshaugii due to air pollution. .... H. sp.

**17. Branching predominantly lateral, irregular. Medulla Pd+ red, KC-, containing physodalic acid and, very rarely, diffractaic acid, or (according to Hale & Cole) KC+ pink, with physodic and protocetraric acids.** Lobes little branched, not much inflated, variable in width, generally with more or less broad main branches 1-2.5(-4) mm wide, and numerous, linear, very narrow (0.5-0.75 mm) side branches or lobules which occasionally become quite long, free and trailing. Thallus loosely attached at the base, almost subfruticose, rather soft, 8-15 cm broad. Medulla dark brown above and below, thin. Apical perforations sparse and irregular. Upper surface whitish gray, the margins conspicuously black rimmed. Lower surface shiny, jet black, rugose, conspicuous from above because of lobes twisted upwards. Pycnidia very common. Apothecia common, short stipitate, 3-15 mm diam. On pines and oaks in the drier parts of the humid north coastal forest at lower elevations, from central California to Oregon, and on various conifers north along the coast to southern British Columbia. Rather rare. .... H. heterophylla Pike

**17. Branching isotomic-dichotomous or at least not predominantly lateral; lobes  $\pm$  uniform in width, without lateral narrow branches or lobules.** ..... 18

**18. Lobes irregularly branched or, if dichotomous, not irregularly so.** Lobes long and slender, 0.6-1.5(-2.0) mm; not upturned, stiff; upper surface with a yellowish cast.

Medulla brown-black, thin. California, rare. .... ["H. enteromorpha (Ach.) Nyl. s. str."] (according to Brodo's preliminary key, but that was made before the species was lectotypified; I have no other information on this taxon, whatever it may be)

**18. Lobes  $\pm$  regularly dichotomous. Medulla (usually?) Pd-. .... 19**

**19. Lobes uniformly swollen, very regularly dichotomous; upper surface uniform green-gray without mottling; medulla of lobe tips pale yellow.** Upper surface smooth. Medulla P-, containing physodic  $\pm$  3-hydroxyphysodic acids. Lobes 1-2 mm wide. Oregon. [I have seen such material, and it does seem sort of distinctive; I have one specimen from the northern coast of California that seems to fit here but is P+!]. .... "H. oregonensis Brodo ined."

**19. Lobes irregularly swollen, less regularly dichotomous; upper surface with conspicuous black mottling; medulla of lobe tips brown.** Apical perforations usually frequent. Lower surface black to brown, weakly wrinkled, not conspicuous from above. Thallus 3-12 cm broad; lobes 1-3 mm wide, moderately inflated; upper surface with black pycnidia. Medulla P-, KC+ pink, containing physodic and paraphysodic acids (however, Ohlsson reported a strain containing physodalic acid, which would be P+!). Apothecia frequent, 1-7 mm diam. Common on conifer trees, west coast to mountains (to 4500 ft in California), central California to southern Alaska. .... H. inactiva (Krog) Ohlsson

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