

**Heterodermia** Trevis. em. Poelt  
(LECANORALES: PYXINACEAE)

After Kurokawa, Hale (1979), Trass (1992), Harris (1990),  
and others; need to add some additional key choices, etc. from Moberg & Nash (1992)

Rev. November 18, 1998

Thallus foliose, lobate, dorsiventral, either prostrate, in rosettes or irregular, sometimes combining to form extensive, radiating mats, or ascending to erect, forming thick cushions or tufts; attached by simple to densely branched, white to black rhizines; lobes usually 2-5 mm broad, discrete or  $\pm$  contiguous and closely adpressed or ribbon-like, ascending and loosely attached, linear or linear-cuneate to spatulate, branching  $\pm$  dichotomous to irregular; sometimes channelled below, with thickened margins on the lower side; margins often ciliate; cilia black or pale, hair-like upper surface white to grayish or greenish, K+ yellow (atranorin), with or without pruina; lower surface white, pale to dark grayish or often at least partly yellow-orange (K+ purple) or purplish; medulla white (or partly pigmented in lower part); upper cortex well developed, of longitudinal periclinal hyphae; lower cortex absent, or of periclinal hyphae; medulla woolly. Soredia, lobules, or squamules present or not; isidia rare.

Apothecia often absent, laminal; thalloid exciple thick, well developed, incurved; discs brown or brown-black, often pruinose (epruinose according to Galloway); subhymenium pale; paraphyses unbranched; asci Lecanora-type, unitunicate, clavate, thick walled, I+ blue; tholus I+ blue; spores 8, 1-septate, often with sporoblastidia (additional small locules between main ones and spore wall), dark brown, very thick walled, ellipsoid oblong, smooth.

Pycnidia immersed or prominent; fulcrum endobasidial; pycnosporos bacilliform. Cortex K+ yellow, with atranorin. Medulla with triterpenoids, anthraquinones, norstictic acid, or other substances (depsidones or pigments). Photobiont Trebouxia. On bark or wood, rocks, or ground amongst low vegetation. Best developed in temperate to subtropical areas. Type species: H. speciosa (Wulf.) Trevis.

Distinguished from Anaptychia by the smooth, thick-walled spores, the more complex chemistry (including larger amounts of atranorin in the cortex) and the generally paler colored thallus.

The genus is often a difficult one to recognize, especially in sterile specimens with a corticate lower surface. The presence or absence of a lower cortex is often very difficult to determine, especially without a very high quality dissecting scope.

Note: this is an artificial key, to accomodate sterile thalli; the "natural" classifications of the species, based partly on spores, are given in parentheses (sections or series, based on Kurokawa, 1973; these need to be given a different status now that they are in the genus Heterodermia). The genus is rather difficult, and there are still a lot of problems. Judging from the history of its classification, it is rather heterogeneous. The loosely attached and subfruticose species have a quite different "gestalt" than the appressed,  $\pm$  rosette-forming ones.

More information from Trass needs to go into some of the descriptions; some of the information in the species descriptions needs to be checked, because it is based on the descriptions of groups,

which does not necessarily apply to every species in the group. The earlier editions of this key were really screwed up, and this one still has a few major bugs in it. Need to check Dey, and Swinscow & Krog, again. It is difficult combining the recent treatments of Sonoran region species (Esslinger & Bratt 1998; Moberg & Nash 1999) with earlier ones.

Polyblastidia-type spores (when mature) have sporoblastidia, which are small rounded structures (cellular locules) located near each end of the spore; the lumina are usually somewhat angular, but can be of several different shapes. Pachysporaria-type spores are usually smaller, lack sporoblastidia, and have  $\pm$  rounded lumina which are narrowed towards the septum and broader towards the apices; Physcia-type and Mischoblastia-type spores are included under Pachysporatia-type (see Rinodina key for definitions).

**I. Thallus dichotomously branched; lobes long and narrow;  
with marginal cilia  
(leucomela group)**

**1. Thallus without soralia.** Baja California Sur, Chihuahua. Spores large, over 30 x 15  $\mu$ m.  
[Note: H. erinacea might also seem to key here, since according to Esslinger & Bratt the lobes are  $\pm$  dichotomously branched; however, the lobes of that species tend to be relatively broader and shorter, and the spores are considerably smaller, to 20.5(-24) x 9.5(-10)  $\mu$ m]. ..... H. lineare

**1. Thallus with soralia.** ..... 2

**2. Lobe tips upturned; discrete soralia present on lower surface.** Arizona, Sonora, Chihuahua. .... H. appalachensis

**2. Lobe tips flat; soralia more diffuse on lower surface.** Baja California, Baja California Sur, Chihuahua. Reports from California are apparently based on misidentifications (at least in part of H. namaquana) ..... 3

**3. Medulla P+ yellow-orange, K+ yellow-red, C- (zeorin, two other triterpenes, salazinic acid, consalazinic acid, purple pigment). Lobes wider; tips not very revolute; lower surface pulverulent; soralia frequent; apothecia somewhat infrequent.** Arizona, California, Baja California (Norte & Sur). .... H. leucomela (L.) Poelt ssp. leucomela

**3. Medulla P- or pale yellow, K+ yellow (atranorin, zeorin). Lobes mostly 10-15(-20) mm long, gradually becoming narrower towards the apices; apices usually uncinately or circinately revolute; lower surface arachnoid more often than pulverulent; soralia less frequent; apothecia more frequent.** California, Baja California. . .... H. leucomela ssp. boryi

**II. Thallus irregularly or sympodially branched; lobes broad to narrow;  
with or without marginal cilia**

**II-A. With cilia along margin and sometimes on lobe surface.**

**II-A-1. Lobes erect or suberect.  
(*podocarpa* group)**

**1. Growing in British Columbia.** With soredia. Lobes suberect or ascending (to  $\pm$  appressed). Medulla K+ yellow, C-, KC-, P+ orange (atranorin, zeorin, unknown fatty acids; cause of P+ reaction unknown). Rare. .... *H. sitchensis* Goward & Noble in Goward

**1. Growing in the Southwest, Mexico, or the Eastern U.S.** ..... 2

**2. Growing in the Eastern U.S.** ..... 3

**2. Growing in the Southwest or Mexico.** ..... 4

**3. Thallus without soredia.** Medulla K+ yellow, P- or P+ faint yellow (atranorin, without salazinic or norstictic). Apothecia common. Lobes suberect or ascending. Appalachians and Ozarks..... *H. echinata* (Taylor) W. Culb.

**3. Thallus with soredia.** Medulla K-, P- (norstictic acid lacking) in N. American material. Apothecia usually absent. Lobes flabellate,  $\pm$  appressed according to some authors [but according to Moberg, similar to *H. podocarpa*, which has  $\pm$  ascending lobes]. Florida. .... *H. galactophylla* (Tuck.) Culb.

**4. Lobes erect and paddle-shaped, with cilia on upper side.** Mexico (not presently known from Sonoran part). .... *H. comosa*

**4. Lobes not paddle-shaped, without cilia on upper side.** ..... 5

**5. Thallus sorediate, soredia on lower side.** California, Baja California, Baja California Sur. .... *H. namaquana*

**5. Thallus not sorediate.** ..... 6

**6. Apothecia with prominent lobules.** Arizona, Sonora. .... *H. podocarpa*

**6. Apothecia without lobules.** ..... 7

**7. Saxicolous; apothecia ciliate.** Baja California. .... *H. ciliatomarginata*

**7. Corticolous; apothecia not ciliate.** Baja California, southern California. .... *H. erinacea*

**II-A-2. Lobes  $\pm$  appressed, subascending only near the apices  
(erinacea group)**

- 1. Growing in British Columbia.** ..... (see H. sitchensis)
- 1. Growing in southern or eastern areas.** ..... 2
  - 2. Growing in the Southwest or Mexico.** ..... 3
  - 2. Growing in Eastern U.S.** ..... 4
- 3. Saxicolous; apothecia ciliate.** Baja California. .... H. ciliatomarginata
- 3. Corticolous; apothecia not ciliate.** Baja California, southern California. .... H. erinacea
  - 4. Medulla usually K+ red (norstictic acid).** Florida. .... H. barbifera
  - 4. Medulla K-, P- (norstictic acid lacking) in N. American material.** Florida. Lobes  $\pm$  appressed according to some authors. .... (see II-A-2: H. galactophylla (Tuck.) W. Culb.)

ADD?

H. dendritica sensu Kurokawa non (Pers.) Poelt

**II-B. Without marginal cilia (but long, projecting rhizines may be present);  
Lobes ± appressed (speciosa group and others)**

**II-B-1. Lobes without lower cortex.**

- 1. With isidia or isidia-like squamules or lobules. .... 2**
- 1. Without isidia or isidia-like lobules. .... 4**
- 2. With isidia. Underside orange, K+ purple.** Florida, N. Carolina, Mexico (Chiapas). .... H. crocea R. C. Harris
- 2. With isidia-like lobules. Underside whitish or darkening, not orange.** Need to check Culberson's or Dey's keys to Appalachian species to see how to better these species. .... 3
- 3. At lower elevations, southern Appalachians. Spores usually (except for occasional spores) without sporoblastidia.** Medulla usually K-, P-, containing zeorin, occasionally K+ red, P+ orange (norstictic and salazinic acids); zeorin and physciin-d and traces of physciin b also reported. .... H. microphylla (Kurok.) Skorepa
- 3. At higher elevations, North Carolina northward. Spores with sporoblastidia at maturity (but apothecia rare or absent).** Medulla K+ yellow, without norstictic acid, with zeorin. . .... H. squamulosa (Degel.) W. Culb.
- 4. Thallus without soralia.** Chihuahua, Sonora, Baja California Sur. Also Great Lakes area. [Note: H. echinata sensu Trass will also key out here]. .... H. hypoleuca
- 4. Thallus with soralia. .... 5**
- 5. Lower side with yellow to rusty-brown pigment, K+ violet.** Baja California Sur, Chihuahua. Also Eastern (Great Lakes area and Appalachians, south to Florida),. .... H. obscurata
- 5 Lower side white, or with orange to bluish, purplish, or black pigment, K-.** Need more information to properly distinguish the following two species. .... 6
- 6. Arizona, Chihuahua, Baja California (need to check whether it also occurs in Eastern U.S.). Soralia on lateral or terminal lobes, sometimes spreading along margin, labriform. .... H. japonica**
- 6. Appalachians south to Florida, west to Ozarks. Soralia predominantly apical, covering small lateral lobes in the central part of the thallus, capitate to labriform, .... H. casarettiana (Massal.) Trevisan**

ADD?

H. dendritica (Pers.) Poelt

Non-North American species:

Medulla K+ yellow turning reddish yellow, containing norstictic acid. Similar to the typical variety but with microphyllous or subisidial branches at the margins of the lobes. Japan. .... [H. dissecta (Kurok.) Awasthi]

**II-B-2. With lower cortex (but lower cortex sometimes eroding!);**

- 1. Thallus with isidia.** Sonora, Chihuahua; Ozarks and Appalachians. [Note: H. antillarum (Vainio) Swinscow & Krog, found on bark on non-Sonoran parts of Mexico, will also key out here; at present I do not have enough information to characterize it]. ..... H. granulifera
- 1. Thallus without isidia.** ..... 2
- 2. Thallus with soralia.** ..... 3
- 2. Thallus without soralia.** ..... 6
- 3. Soralia mainly marginal; thallus K+ yellow then red, with salazinic or norstictic acid.** ..... 4
- 3. Soralia mainly apical; thallus K+ yellow, without salazinic or norstictic acid.** ..... 5
- 4. Soralia mostly continuous along lobe margin; salazinic acid present.** Thallus more firmly adnate. Arizona, Sonora, Chihuahua; Appalachians to Florida, and west to Ozarks. .... H. albicans
- 4. Soralia from knob-like, marginal structures; norstictic acid present.** Thallus rather loosely adnate. Sonora; eastern N. America (rare at lower to higher elevations in North and South Carolina, perhaps more common elsewhere?). .... H. pseudospeciosa
- 5. Soralia few, but prominent, spathulate; thallus with “spathulin” (UV+ red after charring, R<sub>F</sub> 4-5 in solvent G).** Not presently known from Sonoran region, but just outside of it. .... H. spathulifera
- 5. Soralia more abundant, lip-shaped; thallus without “spathulin”.** Arizona, Chihuahua; Great Lakes area, Virginia to North Carolina south to Florida. .... H. speciosa
- 6. Colorado. Thallus cartilaginous, with strongly developed upper and lower cortex; medulla virtually obsolete.** Lobes linear, narrow (0.5-0.8 mm wide), convex. Upper surface pruinose on lobe tips. Medulla K-. On vertical or steeply sloping granite cliffs over which water seeps intermittently, 7000 ft to subalpine. Colorado. Section Holanaptychia. .... H. chondroidea W. A. Weber & D. D. Awasthi
- 6. Arizona to Texas and Mexico. Thallus anatomy not as above.** ..... 7
- 7. Thallus distinctly pruinose; mostly with patches of pigment in medulla; thallus K+ yellow, salazinic acid absent.** Arizona, Sonora, Chihuahua, Baja California Sur; east to western Texas. .... H. rugulosa
- 7. Thallus not or weakly pruinose; without medullary pigment; thallus K+ yellow then red, salazinic acid present.** Arizona, Sonora, Chihuahua, Baja California Sur. .... H. tropica

ADD?

Reports from the Sonoran region are erroneous; may not occur in North America at all. .... H. diademata (Taylor) Awasthi

## Descriptions (and Decryptions?)

The “Series” and “Sections” are from Kurokawa, and may not make much sense in view of current concepts.

The distinction between marginal cilia and marginal rhizines is not at all clear to me at present. Rhizines “projecting beyond margins from lower surface” seems straightforward, but “marginal rhizines” (used, e.g., in Moberg & Nash’s descriptions; treated as cilia in their key for some species, but not for others [e.g., *H. hypoleuca*]) is very confusing. For species where no literature citation is given specifically in connection with “cilia”, take the statements about them with a grain of salt.

Calling the lower surface corticate or ecorticate also involves a bit of guesswork; e.g., some authors use “arachnoid” or “fibrous” vs. “smooth”, and high magnification with good light, and/or sectioning, may be required in some cases.

Unfortunately Moberg & Nash don’t give specimen citations (other than the types), and even when they have a map, determining which states of Mexico are involved can occasionally be a bit dicey.

### **H. albicans (Pers.) Swinscow & Krog**

**THALLUS** firmly adnate, orbicular to irregular, 4-6 cm broad (< 3 cm acc. to Moberg & Purvis 1997); densely lobate; **lobes** adjacent,  $\pm$  plane, not ascending, linear-elongate, 0.5(-1) mm wide, to 3 mm long, usually richly branched, dichotomous, with short lateral lobes, often giving a crenate margin to main lobes; widening towards tips, not ascending, upper side weakly convex, upper cortex somewhat uneven; **cilia** absent (Moberg & Nash 1999; but margins with some short projecting rhizines); **soralia**  $\pm$  linear, extended and continuous along margins and round apices of lateral lobes, but generally absent from apices of main lobes, arising from small lateral knoblike structures; soredia finely granular, white to bluish gray; **upper surface** gray to brownish gray, darker at lobe tips, sometimes weakly pruinose, **lower surface** corticate, white to buff, rarely dark gray, weakly to moderately rhizinate with usually short (c. 1 mm) pale to dark brown or black rhizines; **upper and lower cortex** prosoplectenchymatous, together occupying more than 2/3 of the thallus thickness.

**APOTHECIA** rare, subterminal; **spores** 24-35 x 11-15  $\mu$ m, with sporoblastidia.

**PYCNIIDIA**  $\pm$  common, inserted with black weakly protruding tips; **conidia** bacilliform, 4-6 x 1  $\mu$ m.

**CHEMISTRY:** Cortex and medulla K+ yellow to red, P+ yellow-orange; atranorin, salazinic acid, zeorin, and unknown PQ4 or  $\pm$  unidentified terpenes.

**ECOLOGY AND DISTRIBUTION:** Fairly common on roadside trees and in open woods, and also on rocks,  $\pm$  southeastern (Appalachians to Florida, and west to Ozarks). On rocks or mosses on rocks in open situations, southwestern (Arizona, Sonora, Chihuahua).

Series Leucomelaenae.

### **H. antillarum (Vainio) Swinscow & Krog**

**THALLUS lobes** slightly disjunct or adjacent,  $\pm$  plane, not ascending, with short lateral lobes; **cilia** absent; **isidia** cylindrical to flattened, simple or branched, marginal and laminal;

**upper surface** with somewhat uneven cortex; **lower surface** with cortex.

**APOTHECIA** adnate to substipitate; **thalline exciple** isidiate at the outer edge; **spores** 23-30 x 12-18  $\mu\text{m}$ .

**CHEMISTRY:** Atranorin, zeorin, salazinic, unknown.

**ECOLOGY AND DISTRIBUTION:** On bark, Mexico.

**NOTES:** Similar to *H. tropica* but with isidia.

### ***H. appalachensis* (Kurok.) Culb.**

**THALLUS** irregular, to 5 cm diam.; **lobes**  $\pm$  narrow, 0.5-1.0 mm wide, dichotomously divided, towards the center subimbricate but towards the periphery often discrete; margin subentire; **cilia** present, marginal (Moberg & Nash 1999), prominent, pale at base, blackened towards apices, simple or branched at apices, 1-2 mm long; laminal cilia sometimes also present; **soralia** discrete, on underside near tips, bending the tips upwards and appearing labriform (capitulate according to Kurokawa); **upper surface** gray (or glaucous) to dark gray, without or with a weak pruina towards tips; **lower surface** without cortex, mostly with diffuse, yellow to salmon-colored pigment, K-; rhizines present; **medulla** white.

**APOTHECIA AND PYCNIDIA** not seen.

**CHEMISTRY:** Cortex and medulla K+ yellow, P- or P+ pale yellow; atranorin, zeorin, leucotylin.

**ECOLOGY AND DISTRIBUTION:** At lower elevations, Appalachians, infrequent; on tree trunks in open situations in humid places, SE Arizona, Sonora, Chihuahua.

### ***H. barbifera* (Nyl.) K. P. Singh**

**THALLUS** foliose, ca. 5 cm across, loosely attached; **lobes** flabellate,  $\pm$  appressed, mainly dichotomously branched, sublinear-elongate, 1-4(-6) mm wide, subascending only near the apices, distinctly convex; **cilia** occurring along margins and sometimes even on the surface, white, up to 4 mm long; **upper side** grayish white to white, sometimes slightly pruinose near the apices, forming numerous laminal verrucae, often with blackish tips; **lower surface** ecorticate, white, conspicuously arachnoid, canaliculate; **rhizines** densely branched, forming a dense reticulate mat below and along the margins, concolorous, or darkening towards tips.

**APOTHECIA** subterminal, 1-4 mm diam.; **margins** smooth but often becoming lacinulate, often ciliate when young; **disc** brown, pruinose; **spores** 18-20 x 43-49  $\mu\text{m}$ , with sporoblastidia.

**CHEMISTRY:** Medulla usually K+ red, P+ yellow-orange (norstictic acid).

**ECOLOGY AND DISTRIBUTION:** Florida.

**NOTES:** Series *Podocarpae*.

### ***H. casarettiana* (A. Massal.) Trevisan**

**THALLUS** 4-8 cm broad, loosely adnate, brittle; **lobes** long and linear (but broadened and  $\pm$  flabellately branched towards tips), 1-2 mm wide; **cilia** absent; **soralia** predominantly apical, capitate to labriform, covering small lateral lobes in the central part of the thallus, visible from above; **lower surface** purplish black towards center, sometimes yellowish towards tips (pigment in the lower layers of the medulla, not in a superimposed wooly layer of hyphae); ultimate parts white; K-; **rhizines** present towards the tips, black, squarrosely branched, along the margins (projecting somewhat).

**APOTHECIA** **spores** 32-48 x 18-25  $\mu\text{m}$ .

**CHEMISTRY:** Medulla K+ red, P+ orange, with salazinic and norstictic acids (or also K-, P-, without depsidones, according to Hale); always with zeorin, and unknown pigment.

**ECOLOGY AND DISTRIBUTION:** Common at the base of trees and on rocks in open woods, or among grass and bryophytes on soil. Southeastern (Appalachians south to Florida, west to Ozarks).

**H. chondroidea W. A. Weber & D. D. Awasthi**

**THALLUS** foliose, cartilaginous, rigid, forming rosettes to 6 cm diam., strongly adnate; **lobes** narrow (0.5-0.8 mm wide), convex, lobes linear, adnate, imbricate, flabellate, the apices slightly expanded; lateral lobules microphylline isodiametric or slightly elongated, plump, rounded, the apices pruinose; **cilia** ? (check original description); **upper surface** variegated, pruinose on the lobe tips, matt, clay-colored or brownish gray to brown; **lower surface** white or pale, sparingly rhizino-se, **rhizines** brownish black to black, simple or irregularly dichotomously branched, never squarrose, 0.5-1.0 mm long; **upper and lower cortex** strongly developed, vitreous; **medulla** virtually obsolete.

**APOTHECIA** laminal, 2.0-4.5 mm diam., constricted at base, substipitate; **margin** inflexed, entire to strongly lacinate; **disc** concave to plane, dark brown to black, epruinose. **spores** 14-18(-23) x 6-8(-11)  $\mu$ m, Pachysporaria- or Mischoblastia-type, without sporoblastidia, ellipsoid to fusiform, the walls greatly thickened, the lumina globose to angular or truncate.

**PYCNIDIA** laminal, the ostioles brown; **pycnospores** 2 x 1  $\mu$ m, ellipsoid.

**CHEMISTRY:** "Atranorin only" (may not have been TLC'd; if so may have terpenoids also).

**ECOLOGY AND DISTRIBUTION:** On vertical or steeply sloping granite cliffs over which water seeps intermittently, 7000 ft to subalpine. Colorado.

**NOTES:** Section Holanaptychia.

**H. ciliatomarginata (Linder) Essl.**

**THALLUS** foliose to subfruticose, to 6-7 cm diam. but usually smaller, orbicular, loosely adnate; **lobes** radiating, distinctly discrete,  $\pm$  prostrate throughout (although held above the substrate by cilia) or only very indistinctly ascending toward lobe ends, 0.5-1.2(-1.5) mm broad, elongate and linear, **cilia** laminal and marginal (Moberg & Nash 1999; but some of the latter acting like rhizines to weakly attach thallus to the rock substrate), to 5-6 mm long, c. 75-150  $\mu$ m broad at base, simple or sometimes irregularly branched in upper parts, especially those which project downward and contact the substrate), white or darkening in upper parts; laminal ones "stout"; **soralia and isidia** absent; **upper surface**  $\pm$  convex, smooth to weakly lumpy, gray to dark gray, usually minutely bullate; **lower surface** flat or often weakly convex, ecorticate, but with continuous, dense, agglutinate medulla, which usually appears smooth (but dull) on the surface, almost (or indeed) like a cortex, never sorediate or "cottony"/hyphal or veined; fibrous nature often visible at the tips and edges of the lobes.

**APOTHECIA** common, usually present, abundant, laminal and short stipitate, variable in size, to 4 mm diam.,  $\pm$  flat; **margin** ciliate; **disc** black but often pruinose, **spores** (12-)16.5-19.7(-22.5) x (6-)7.5-9.0(-9.5)  $\mu$ m, Physcia-type.

**PYCNIDIA** abundant, large, to almost 500  $\mu$ m wide, inserted, but often bulging the tissues above and protruding above lobe surface ( $\pm$  emergent), black around the ostiole, **conidia** (3-)4-5 x 1  $\mu$ m, ellipsoid to bacilliform, rarely more pointed at one end.

**CHEMISTRY:** Upper cortex K+ yellow, lower surface K- to K+ yellow (positive

especially near some lobe tips but also rarely in some older parts), internal medulla K-. Atranorin, faint traces of several terpenoids.

**ECOLOGY AND DISTRIBUTION:** On rocks in sun-exposed,  $\pm$  coastal habitats, from sea level to 200 m. Baja California (Norte & Sur).

**H. comosa (Eschw.) Follmann & Redón**

**THALLUS** irregular, usually forming small tufts of ascending lobes, to 7 cm across; **lobes** to 5 mm wide, convex; **cilia** marginal (Moberg & Nash 1999), prominent, whitish; laminal cilia also present; **upper side** mostly with cilia if not densely covered by pycnidia; **soralia and isidia** absent; **lower side** without cortex; **rhizines** whitish; **medulla** white.

**APOTHECIA** often absent, to 10 mm diam., situated at end of ascending lobes; **margins** lobulate, ciliate as thallus, **spores** *Pachysporaria*-type, without sporoblastidia, 31-34 x 13.0-15.5  $\mu$ m.

**PYCNIDIA** unknown.

**CHEMISTRY:** Cortex and medulla K+ yellow; atranorin and zeorin.

**ECOLOGY AND DISTRIBUTION:** On tree trunks and branches in fairly open but moist situations. Mexico (presently known only from non-Sonoran parts).

**H. dendritica (Pers.) Poelt**

**THALLUS lobes** 0.7-2 mm wide, with marginal squamules; **cilia** absent (according to Trass); **isidia** and soredia absent; **upper surface** rough, uneven; **lower surface** arachnoid, with yellow pigment present; **rhizines** gray

**APOTHECIA** rare, laminal; **spores** 35-46 x 16-20  $\mu$ m, with sporoblastidia at maturity (section *Polyblastidia*).

**CHEMISTRY:** Medulla K-, without norstictic and salazinic (at least in the holotype and some others); Trass (from whom the morphological description here is taken) implies that the species can sometimes have these substances, as is also stated by Kurokawa (see below).

**ECOLOGY AND DISTRIBUTION:**

**NOTES:** In the holotype, several lobes have some soralia-like regions below their apices (possibly abnormalities) [I'm not sure where this info. came from--probably Swinscow & Krog; it needs to be checked, because in the earlier version of this key, at least some of the info. here referred to *H. dissecta*, which contains dissectic acid, lacks norstictic and salazinic acids, has a lower cortex, and has spores less than 30  $\mu$ m long].

[*H. dendritica* sensu Kurokawa non (Pers.) Poelt]

**THALLUS** foliose, forming extensive colonies to 15 cm or more diam.; **lobes** dichotomously or subdigitately branched, 0.7-2 mm wide, sublinear-elongate, minutely notched; **cilia** black, marginal; **isidia and soredia** lacking; **upper surface** grayish or greenish white, plane, smooth, often lightly pruinose near apices; **lower surface** ecorticate, purple black toward center, K+ purple, white, to yellow or ochraceous (K+) towards the tips; **rhizines** black,  $\pm$  shiny, simple or squarrosely branched, 1-3 mm long.

**APOTHECIA** rather rare, laminal, substipitate, 1-4 mm diam.; **margins** lacinulate, lacinules decorticate and partly yellow on underside; **disc** blackish brown, slightly pruinose; **spores** 35-46 x 16-20  $\mu$ m, with polyblastidia.

**CHEMISTRY:** Medulla K+ yellow/red, P+ yellow to orange (norstictic and salazinic acids) (according to Kurokawa, and Trass).

**NOTES:** Section Polyblastidia. This description differs from the information given by Trass in that cilia are present and the rhizines are black rather than gray.. Compare with H. casarettiana.

**H. diademata (Taylor) D. D. Awasthi**

**THALLUS** 3-6 cm broad, adnate; **lobes** 1-1.5 mm wide,  $\pm$  plane, adjacent (usually crowded) or slightly disjunct, not ascending, with short lateral lobes; **cilia** ? (check the literature); **isidia and soredia** lacking; **upper surface** even, sometimes pruinose; **lower surface** corticate, light tan, K-, with sparse rhizines; **rhizines** long, unbranched..

**APOTHECIA** usually numerous, laminal, adnate to substipitate; **thalline margin** crenulate to squamulose; **spores** 25-35(-40) x 12-17  $\mu$ m, Pachysporaria-type, without sporoblastidia.

**ECOLOGY AND DISTRIBUTION:** On trunks and branches of trees (especially oaks), and also on sheltered rocks, primarily tropical. Reports from the Sonoran region are erroneous.

**NOTES:** Externally very similar to H. hypoleuca, which lacks a lower cortex and rhizines. Sect. Heteroderma series Speciosae.

**H. echinata (Taylor) Culb.**

**THALLUS** 2-3 cm across; **lobes** suberect or ascending, tufted, short, 0.5-2 mm wide, suberect or ascending, tufted; **cilia** marginal, conspicuous (absent according to Trass); **isidia and soredia** absent; **upper surface** rough; **lower surface** white, ecorticate (Kurokawa), arachnoid, reticulately veined; **rhizines** gray.

**APOTHECIA** common, marginal; **margins** with conspicuous cilia on outer edges, without laminal cilia; **cortex** I-; **spores** 30-42 x 13-17  $\mu$ m, with sporoblastidia at maturity.

**CHEMISTRY:** Medulla K+ yellow, P- or P+ faint yellow (atranorin, without salazinic or norstictic).

**ECOLOGY AND DISTRIBUTION:** On juniper twigs and other trees in open pastures. Infrequent (but sometimes locally abundant), at lower elevations, Appalachians and Ozarks.

**NOTES:** Series Podocarpae.

**H. erinacea (Ach.) Hale**

**THALLUS** loosely adnate, 1-5 cm broad, foliose to mostly caespitose-subfruticose, irregular; **lobes** prostrate to more often erect-ascending, (0.5-)1.0-1.5(-2.0) mm wide, linear,  $\pm$  dichotomously divided, often crenate/flabellate near the end; **cilia** primarily marginal or submarginal, less frequent on upper surface (Moberg & Nash 1999), 2-7(-10) mm long and 50-100(-125)  $\mu$ m thick at the base, simple or rarely branched, white or darkening in the upper parts; **soredia and isidia** absent; **upper surface** usually  $\pm$  flat to weakly convex or (rarely) weakly concave, sometimes weakly lumpy, gray to dark gray; **lower surface** flat to weakly concave (not convex), obviously ecorticate essentially throughout, often appearing veined due to downward projecting ridges of the upper cortex appearing among the "cottony"/hyphal medulla, white, **rhizines** lacking; **upper cortex** prosoplectenchymatous; **medulla** lax, usually well developed.

**APOTHECIA** very common (near 100%) and often abundant, laminal, short stipitate, variable in size, to 2.5(-5) mm diam. **disc**, flat to weakly convex, black and becoming  $\pm$  pruinose; **margin** eciliate; **spores** Physcia-type, (16-)18.0-20.5(-24) x (7.5-)8.0-9.5(-10.0)  $\mu$ m; walls thickened; locules apparently without sporoblastidia (uncertain according to Trass)

**PYCNIDIA** usually common, 150-350  $\mu$ m wide, inserted in thallus, sometimes bulging

the tissues above, black around the ostiole and usually conspicuously emergent; **conidia** 3.5-4.5 x <1 um, bacilliform, sometimes more pointed on one end.

**CHEMISTRY:** Upper cortex K+ yellow, lower surface (medulla) K+ yellow. Atranorin, chloratranorin, zeorin, and unidentified trace terpenoids (leucotylin and substance N-3 according to ?).

**ECOLOGY AND DISTRIBUTION:** On trees, shrubs, and cacti, in fog zone, from near sea level to 500 m, coast of southern California and Baja California (Sur & Norte).

**NOTES:** Series Erinaceae

### **H. flabellata (Fée) Awasthi**

**THALLUS lobes** slightly disjunct or adjacent,  $\pm$  plane, not ascending, with short lateral lobes; **cilia** ? (check description); **isidia and soralia** absent; **upper surface** uneven; **lower surface** non-corticate (Kurokawa), with ochraceous orange hyphae, K+ purple, overlying medulla.

**APOTHECIA** laminal, adnate to stipitate; **thalline exciple** crenulate to squamulose at outer edge, inner surface of squamules pigmented; **spores** 30-37 x 12-18 um, with sporoblastidia.

**CHEMISTRY:** Atranorin, zeorin, pigments.

**ECOLOGY AND DISTRIBUTION:** On bark, Mexico.

**NOTES:** Not in key; need to know if it has cilia. Fertile counterpart to H. obscurata. Also compare with H. hypoleuca.

### **H. galactophylla (Tuck.) Culb.** [Aptroot cites Trevisan as the authority for the combination]

**THALLUS** delicate; **lobes** flabellate,  $\pm$  appressed; **cilia** white, occurring along the margins, to 2 mm long, at least in part around the thallus; **soralia** terminal, somewhat labrose soralia on main and lateral lobes; soredia fine; **lower surface** white to brown, ecorticate (Kurokawa), arachnoid or not, K-; **rhizines** pale.

**APOTHECIA** usually absent; **margins** without soralia.

**CHEMISTRY:** Medulla K-, P- (norstictic acid lacking) in N. American material.

**ECOLOGY AND DISTRIBUTION:** Florida.

**NOTES:** Similar to H. podocarpa, which has  $\pm$  ascending lobes.

### **H. granulifera (Ach.) Culb.**

**THALLUS** irregular, sometimes orbicular, adnate, to 3(-6) cm broad, foliose; **lobes** radiating, short and minutely notched, repeatedly irregularly branched, plane, 0.3-1.5 mm broad, overlapping to  $\pm$  discrete, or contiguous at the circumference, adnate to tips,  $\pm$  sinuous, flat to convex, 150-200 um thick; **cilia** and projecting rhizines absent (Moberg & Nash 1999); **isidia** marginal and/or laminal, moderate-sized, papillar, barrel-shaped, constricted at base, becoming granular, variable in length from 1 mm and knob-like to 1 cm and then becoming lobulate; sometimes developing soredia in the openings after isidia are broken; **upper surface** whitish gray to gray, or sometimes greenish white, distinctly pruinose especially near the tips; **lower surface** corticate, pale or sordid brown towards the center, K-, moderately rhizinate; **rhizines** concolorous with thallus or blackening, gray to brown, simple or irregularly thickened; **upper cortex** prosoplectenchymatous, thin, irregularly thickened, 10-60 um thick, I-; **algal layer** subcontinuous, 20-40 um; algae 7-13 um diam.; **medulla** ca. 70 um thick, hyphae sometimes forming sphaeroidal cells; **lower cortex** prosoplectenchymatous, 20-30 um thick

**APOTHECIA** rather rare to  $\pm$  common, laminal, sessile, shortly stalked, 0.5-2.0(-3.0)

mm diam.; **margin** minutely crenate, scabrous, pruinose and isidiate or lobulate; **disc** dark brown, epruinose; **hymenium** ca. 100 µm; **spores** Pachysporaria type, without sporoblastidia, (20.5)21.0-27.0(-30.0) x (8.5-)10.5-14 µm.

**PYCNIIDIA** ± common, inserted in thallus, visible only as black warts on surface; **conidia** bacilliform, 4-5 x 1 µm.

**CHEMISTRY:** Medulla K+ yellow/red, P+ distinctly yellow-orange; atranorin, zeorin, salazinic acid.

**ECOLOGY AND DISTRIBUTION:** On deciduous trees in moist but open conditions, Ozarks and Appalachians; Sonora, Chihuahua, and other parts of Mexico

### **H. hypoleuca (Ach.) Trevisan**

**THALLUS** irregular to orbicular, 3-5(-6) cm broad, loosely adnate; **lobes** radially extending, discrete, adjacent or slightly disjunct, ± plane, not ascending, linear or linear-cuneate, 0.5-2 mm wide, repeatedly branched sympodially, with small adventive lateral lobes at lobe tips, not uncinat; margins becoming sparsely lobulate with adnate lobules in age; **cilia** absent (Moberg & Nash 1999; but projecting “marginal rhizines” may be visible); **soredia and isidia** absent; **upper surface** uneven, “wooly” at the tips, gray to dark gray or brownish, not pruinose, or lobe tips mostly with weak pruina; **lower surface** not bordered by reflexed margin of upper cortex, ecorticate, white to purple or almost black; **rhizines** (“marginal”), pale to black, ± abundantly branched.

**APOTHECIA** frequent, ± common, adnate to sessile or shortly stipitate, variable in size, to 5 mm diam., sometimes cup-shaped; **margins** crenate or lacinulate, with sparse lobules in age; **disc** deeply concave, epruinose; thalline margin crenulate; **spores** ± Pachysporaria-type, (22.5-)23.5-30.5(-35.5) x (11.0)-12.5-16.0(-17.0) µm, usually without sporoblastidia, but occasional spores with one or two simple sporoblastidia; walls thickened.

**PYCNIIDIA** ± common; **conidia** bacilliform, 4-5 x 1 µm.

**CHEMISTRY:** Medulla K+ light yellow, containing zeorin, leucotylin and two pigments, or rarely K+ red (norstictic acid; or salazinic acid?).

**ECOLOGY AND DISTRIBUTION:** On trunks and branches of trees among mosses or on bare wood, in open woodland and parkland. Great Lakes area. On bark in fairly moist, but open conditions, SE Arizona, Sonora, Chihuahua, Baja California Sur

**NOTES:** Sect. Holoanaptychia. Specimens without spores cannot be distinguished from H. magellanica (a mostly Southern Hemisphere species not reported from N. America, having longer spores)..

### **H. japonica (Sato) Swinscow & Krog**

**THALLUS** very variable, irregular, rarely orbicular, foliose, to 5 cm across, or forming extensive colonies 15 cm or more across, loosely adnate; **lobes** ± fan-like, radiating, dichotomously or sometimes subdigitately branched, sublinear-elongate, minutely notched, 0.7-2 mm wide, plane or somewhat convex, contiguous or imbricate, tips ascending, usually widening towards apices to 3(-4) mm, usually discrete, sometimes dissected with lobules along the margin developing small soralia; consistency soft (not stiff); **cilia** absent (Moberg & Nash 1999; but “marginal rhizines” mostly present); **soralia** labiate (or capitate?), apical on short lateral or terminal lobes, sometimes spreading along lobe margin, forming at most a thin border to upper side; soredia farinose to granular, sometimes virtually lacking; soredia farinose to granular; **upper surface** grayish or greenish white or cream colored, but often darkening in the center,

often slightly pruinose towards tips when young; **lower surface** ecorticate, arachnoid, white to brownish or bluish black, often sparsely dotted with brownish orange-red pigment towards lobe apices; **rhizines** 1-3(-7) mm long, black, simple (or becoming squarously branched?).

**APOTHECIA** rather rare, laminal, substipitate, 1-8 mm diam.; **margins** lacinulate; lacinules corticate only on the outer side; **disc** concave, dark brown or blackish brown, lightly pruinose; **spores** *Pachysporaria*-type, (35-)40-45(-95?) x (15-)20-22  $\mu$ m.

**PYCNIDIA** rare; **conidia** bacilliform, 4-5 x 1  $\mu$ m.

**CHEMISTRY:** Thallus K+ yellow to sometimes red, P+ orange, with atranorin, zeorin,  $\pm$  norstictic acid,  $\pm$  salazinic acid and unidentified terpenes.

**ECOLOGY AND DISTRIBUTION:** Usually on bark, on moderately shaded trees, sometimes on rock. On tree trunks or over mosses on rocks in both open and shady situations, SE Arizona, Chihuahua, Baja California

### **H. leucomela (L.) Poelt**

[composite description including ssp. *boryi*, but some parts are based only on ssp. *leucomela*]

**THALLUS** (2-)5-15 cm across, often in loose rosettes or forming  $\pm$  entangled mats,  $\pm$  loosely attached, appearing fruticose; **lobes** disjunct, irregular, narrow, mostly (0.5-)1(-1.5) mm wide (occasionally to 3 mm wide according to some authors), long, to ca. 3-4 mm (sometimes to several cm long according to Moberg & Purvis 1997; to 6 cm long according to Poelt, 1969), strap-like, not narrowing towards apices, mostly dichotomously branched (branches remaining apical), entangled,  $\pm$  ascending at apices, sometimes reflexed (slightly upcurved), tips not revolute; **cilia** marginal (Moberg & Nash 1999), conspicuous, long, gray or black, simple or sparsely branched, 2-4(-9) mm long; **soralia** absent according to Poelt; according to Moberg and others, central part of lower surface usually powdery and  $\pm$  sorediate; irregularly formed soralia common subically on under side, causing the lobes to widen; **upper surface** ivory white or creamy, smooth but cortex uneven, shiny, without pruina; **lower surface** white (to yellowish pink from decomposed salazinic acid; rarely purple), channelled, ecorticate; margin corticate, forming prominent rim; **rhizines** absent; **upper cortex** around half of the lobe thickness.

**APOTHECIA** rather rare, 2(-3) mm diam., laminal or subapical to apical, stipitate; **disc** black,  $\pm$  pruinose, **thalline margin** crenulate to squamulose or lobulate; **spores** *Pachysporaria*-type, (31-)34.5-42.5(-52) x (15.0-)16-20.0(-25)  $\mu$ m, with sporoblastidia.

**PYCNIDIA** rare; **conidia** bacilliform, 4-5 x 1  $\mu$ m

**CHEMISTRY:** Medulla P+ yellow-orange, K+ yellow-red, C- (zeorin, two other triterpenes, salazinic acid, consalazinic acid, purple pigment).

**ECOLOGY AND DISTRIBUTION:** On trees and on mosses on rocks in both moist and fairly dry situations. Baja California Sur. Reports from California northward to British Columbia are apparently based on misidentifications (at least in part of *H. namaquana*). Rather rare in the Appalachians and Florida.

**NOTES:** Characterized by the entangled mats of elongate, linear lobes bearing long, black cilia and the ecorticate lower surface with  $\pm$  thick, corticate margins.

### **ssp. leucomela**

**CHEMISTRY:** Medulla P+ yellow-orange, K+ yellow-red, C- (zeorin, two other triterpenes, salazinic acid, consalazinic acid, purple pigment). Arizona, California, Baja California (Norte & Sur).

[Note: If the two subspecies are to be maintained, a separate morphological description of

ssp. leucomela is needed]

**ssp. boryi**

**THALLUS** loosely adnate, 5-15 cm or more diam.; lobes dichotomously branched, linear-elongate,  $\pm$  ascending, 0.2-1.5 mm wide (less than 2 mm wide in f. circinalis (Zahlbr.) Kashiw.); **lobes** mostly 10-15(-20) mm long, gradually becoming narrower towards the apices, 150-200  $\mu$ m thick; apices usually uncinately or circinately revolute; **cilia** marginal, black except for pale base, simple or sometimes branched, 5-15 mm long; **soralia** sometimes present on lower surface; **upper surface** grayish to greenish white, often turning black in part; **lower surface** ecorticate,  $\pm$  canaliculate, white; **rhizines** absent; **upper cortex**  $\pm$  irregularly thickened, with a grayish outermost layer; **algal layer** continuous; algae 8-15  $\mu$ m diam.

**APOTHECIA** subterminal, sessile or substipitate, 1-5 mm diam.; **margins** with lacinules to 2 mm long, often with sparse short black cilia along their margins; **disc** dark brown, white pruinose, soon naked; **cortex** I-; **hymenium** 160-200  $\mu$ m; **asci** 130-150 x 30-35; **spores** with a median constriction, locules with many sporoblastidia at maturity.

**CHEMISTRY:** Medulla K+ yellow, C-, KC-, P- or P+ pale yellow. Ch.: atranorin and zeorin.

**ECOLOGY AND DISTRIBUTION:** On mosses over bark or rock, Mexico.

**NOTES:** Differs from [typical] H. leucomelos in usually having narrower lobes, more circinately revolute tips to the distal lobes, and arachnoid more often than pulverulent under side, a lower frequency of soralia and a higher frequency of apothecia, and in being P-, K-, lacking depsidones (atranorin and zeorin only).

**H. lineare Moberg & Nash**

**THALLUS** irregular to orbicular, to 10 cm diam.; **lobes** to 3 cm long, to 1 mm wide, distinctly separate, **cilia** marginal (Moberg & Nash 1999), prominent, to 7 mm long, giving margin a comb-like appearance; **soredia and isidia** absent; **upper side** gray to whitish gray; **lower side** white, sometimes bluish, without cortex; **upper cortex** paraplectenchymatous; **medulla** forming lowermost part of lobes.

**APOTHECIA** laminal and/or terminal, shortly stalked, to 5 mm diam.; **margin** shortly lobulate often folded over hymenium; **spores** Pachysporaria-type, sometimes with sporoblastidia, (29.0-)32.5-38.5(-42.0) x (14.0-)15.0-18.0(-21.5)  $\mu$ m.

**PYCNIIDIA** common, immersed, appearing as distinct, black warts on the upper side; pycnoconidia bacilliform, 4-6 x 1  $\mu$ m.

**CHEMISTRY:** Cortex and medulla K+ yellow. Atranorin and zeorin.

**ECOLOGY AND DISTRIBUTION:** Mexico.

**H. microphylla (Kurok.) Skorepa**

**THALLUS lobes** slightly disjunct to adjacent,  $\pm$  plane, not ascending, with short lateral lobes; squamulose; squamules dissected, lobulate, isidia-like, sometimes sorediate; **cilia** ? (need to check description); **isidia and soredia** absent; **upper surface** uneven; **lower surface** pale, ecorticate (Kurokawa).

**APOTHECIA** laminal, sessile to subpedicellate; **thalline exciple** squamulose or  $\pm$  sorediate; **spores** usually (except for occasional ones) without sporoblastidia, Pachysporaria-type, 25-35 x 12-18  $\mu$ m; walls thickened.

**CHEMISTRY:** Medulla usually K-, P-, containing zeorin, occasionally K+ red, P+

orange (norstictic and salazinic acids); zeorin and physciin-d and traces of physciin b also reported.

**ECOLOGY AND DISTRIBUTION:** On coastal rocks, on soil, and on trees and shrubs, in sheltered but open woodland, and on old wayside trees. Southern Appalachians. (Section Holanoptychia). Compare with H. hypoleuca.

### **H. namaquana Brusse**

**THALLUS** irregular, foliose to mostly caespitose-fruticose, mostly 1-3 cm diam., rarely to 5 or 6 cm; **lobes** loosely adnate, erect-ascending, 1-2.5(-3) mm broad, mostly paddle-shaped, sometimes elongate and linear but often somewhat irregular or lacinate, often broader towards the ends; **cilia** marginal and laminal (Moberg & Nash 1999; sometimes submarginal but infrequently laminal according to Esslinger & Bratt 1998), (1-)2-6 mm long, 50-100(-125)  $\mu$ m broad at base, simple or rarely branched, white or darkening in the upper parts; **soralia** present on lower surface of whole lobe as a helmet, sometimes on recurved lobe tips or breaking through upper cortex; **upper side** flat to weakly concave or convex, often appearing uneven or lumpy; **lower surface** flat to weakly concave (not convex), uneven, in mature thalli obviously ecorticate and sorediate throughout (especially in shorter, broader lobed specimens), or some narrower lobed specimens with sorediate areas only toward the (often broadened) ends, the older parts having agglutinated (cortex-like) medulla, sorediate areas often appearing veined due to downward projecting ridges of the upper cortex among the soredia; occasional cilia (rarely more numerous) present among the soredia (originating from lower surface of upper cortex), patchy erosion of the medulla and soredia rarely exposing a  $\pm$  smooth lower surface (actually the lower surface of the upper cortex)..

**APOTHECIA** occasional (present in c. 1/3 of the specimens), often missing but not rare, laminal, shortly stipitate, to 3 mm diam.; **disc**  $\pm$  flat, black and often somewhat pruinose; **margin** eciliate or occasionally (c. 1/4 of fertile specimens) ciliate; **spores** (14-)15.5-18.0(-22.5) x (6-)7.0-8.5(-9.5)  $\mu$ m, *Physcia*-type.

**PYCNIDIA**  $\pm$  common, 150-200  $\mu$ m wide, weakly or not emergent, **conidia** 4-5 x < 1  $\mu$ m, bacilliform but sometimes more pointed at one end.

**CHEMISTRY:** Upper cortex K+ yellow, medulla and soredia on lower surface K+ yellow. Atranorin, chloratanorin, zeorin, and trace terpenoids. Sometimes zeorin is very sparse.

**ECOLOGY AND DISTRIBUTION:** Epiphytic, usually on tree and shrub branches, occasionally on cacti, palm leaf bases, rarely on rock or sandy soil, from sea level to 500 m, coast of California and Baja California (Norte & Sur).

### **H. obscurata (Nyl.) Trevisan**

**THALLUS**  $\pm$  firmly adnate, forming  $\pm$  orbicular rosettes or irregularly spreading, 2-3(-4) cm (or rarely to 8 cm?) diam.; **lobes** regularly but sparsely branched, linear or linear-cuneate, c. 1(-2) mm wide,  $\pm$  discrete, flat to slightly convex; **cilia** lacking (Moberg & Nash 1999; but fasciculate, entirely black, cilia-like rhizines project somewhat beyond the margins); **soralia** labriform, on lateral and terminal lobes visible from above, predominantly covering recurved apices of small lateral lobes in the central parts of the thallus, sometimes confluent forming marginal soralia, often rusty brown colored by the medullary pigment, soredia granular. **upper surface** gray-white to rarely dark gray, shiny, not or rarely pruinose; **lower surface** ecorticate, or indistinctly corticate along the margins, cottony, felted, yellowish or ochraceous orange to rust-colored (K+ purple), with pigment in superimposed layer of hyphae (in high elevation

populations often whitish, with pigment reduced to a one or a few isolated spots, according to Dey); **rhizines** simple or squarrosely branched, black.

**APOTHECIA** very rare (not seen in Sonoran region material), laminal, adnate to substipitate; **thalline margin** crenulate to sorediate; **spores** 25-35 x 15-18 um, with sporoblastidia.

**PYCNIDIA** not seen.

**CHEMISTRY:** Medulla K+ yellow, P- or P+ pale yellow, with atranorin, zeorin, traces of unidentified terpenes, and pigments (physciin-c, and traces of others), without norstictic or salazinic.

**ECOLOGY AND DISTRIBUTION:** Common (at least in southern part of range) on deciduous trees, more rarely on rocks, in open woods and along roadsides, or on sheltered mossy trees and rocks in partial shade. Eastern (Great Lakes area and Appalachians, south to Florida). On trunks of deciduous trees and mossy rocks in open but humid conditions, Chihuahua, Baja California Sur.

**NOTES:** Section Polyblastidia. A possibly undescribed species from coastal Oregon is similar but lacks the orangish lower surface.

### **H. podocarpa (Bél.) Awasthi**

**THALLUS** irregular, to 5 cm broad, but usually smaller; **lobes**  $\pm$  convex, variable in width, to 2 mm, often ascending, sometimes imbricate, with  $\pm$  ascending lobes terminating in squamulose apothecia; **cilia** along margins (Moberg & Nash 1999), whitish; **upper side** gray, sometimes reddish in herbarium caused by poor drying; **soralia and isidia** absent; **lower side** without cortex and appearing sorediate.

**APOTHECIA**  $\pm$  abundant, subterminal and stalked and thus appearing laminal; **margins** with  $\pm$  well developed lobules; **spores** Pachysporaria-type with sporoblastidia, (26-)29.5-35.0(-35.5) x (13.0-)13.5-16.0(-17.0) um.

**PYCNIDIA**  $\pm$  abundant; **conidia** bacilliform, 4-5 x 1 um.

**CHEMISTRY:** Cortex and medulla K+ yellow to red, P+ distinctly yellow to deep yellow atranorin, zeorin, salazinic acid,  $\pm$  norstictic acid.

**ECOLOGY AND DISTRIBUTION:** Arizona, Mexico (Moberg & Nash 1999). Endemic to Asia according to Aptroot in Harris, 1990, but also reported from Africa by Swinscow & Krog.

[H. propagulifera sensu Dey non (Vainio) Dey]

**THALLUS** similar to that of H. obscurata but smaller and with minutely dissected, often densely crowded,  $\pm$  granular, nodulose and eroded, dorsiventral lobules on the upper surface, concentrated at the center of thallus; **cilia** blackish, often branched; **lower surface** arachnoid, yellow or ochraceous at least near tips of lobes, pigment K+ purple.

**APOTHECIA** very rare; **spores** ca. 35-46 x 16-20 um, with sporoblastidia.

**CHEMISTRY:** Medulla K+ yellow/red, P+ strong yellow, with norstictic and salazinic acids, zeorin and traces of unidentified terpenoids.

**ECOLOGY AND DISTRIBUTION:** On rock and hardwood trees at high elevations in the Appalachians.

**NOTES** This description is messed up; it is based on Kurokawa's monograph, and British and European literature (including Trass), all of which refer to the taxon as having a K+, P+ medulla, unlike the holotype according to Swinscow & Krog. Swinscow & Krog, Moberg &

Purvis, and Moberg & Nash treat *H. propagulifera* as a synonym of *H. japonica*, but according to Moberg & Nash, that species lacks marginal cilia.

### ***H. pseudospeciosa* (Kurok.) Culb.**

**THALLUS** foliose, orbicular to irregular, forming rosettes or colonies to 4(-5) cm diam., loosely adnate, densely lobate; **lobes** repeatedly dichotomously or subdigitately branched, rather short, often flexuous, imbricate towards center, 0.7-1(-1.5) mm wide, minutely notched, weakly convex, widening, tips not ascending; in transverse section uniformly 200-300  $\mu$ m; **cilia** absent (Moberg & Nash 1999); **soralia** semi-capitate, apical on main lobes and short lateral lobes, white to bluish gray, sometimes at lobe tips but mainly arising from small, lateral, knob-like structures; **upper surface** gray to brownish gray or grayish white, darker at the tips, sometimes weakly pruinose; **lower surface** corticate, white, turning fuscous towards center, rarely dark gray, sparsely rhizinate; **rhizines** concolorous with thallus or becoming dark brown or rarely black towards the apices, irregularly or fruticoseously branched, usually short (c. 1 mm); **upper cortex** 50-120  $\mu$ m, with a grayish surface layer ca. 15  $\mu$ m thick; **algal layer** continuous, ca. 25  $\mu$ m thick; algae 7-10  $\mu$ m; **medulla** 60-80  $\mu$ m; **lower cortex** 25-40  $\mu$ m, becoming thin or rarely evanescent near the apices.

**APOTHECIA** rare (not seen in Sonoran region material), superficial, sessile, 1-3 mm diam.; **margins** somewhat crenate but soon sorediose; **disc** brown to blackish brown, epruinose; **hymenium** 100-130  $\mu$ m; **spores** 25-35 x 12-18  $\mu$ m, very thick-walled, with subglobose, obovate or obconical locules.

**PYCNIDIA**  $\pm$  common; **conidia** bacilliform, 4-5 x 1  $\mu$ m.

**CHEMISTRY:** Medulla K+ yellow then reddish, C-, KC-, P+ yellow. Atranorin, zeorin, norstictic acid, and  $\pm$  unidentified terpenes.

**ECOLOGY AND DISTRIBUTION:** On rock, eastern N. America (rare at lower to higher elevations in North and South Carolina, perhaps more common elsewhere?). Mainly on rocks, more rarely on trees, in open but humid situations, Mexico (just outside the Sonoran area).

### ***H. rugulosa* (Kurok.) Trass**

**THALLUS** irregular to orbicular, firmly adnate, to 4-5 cm across, or up to 10 cm when confluent with other thalli; **lobes** distinct, usually overlapping, sometimes discrete, flat,  $\pm$  sinuous, usually with peculiar knobs (lobe primordia) along the margins, linear-elongate, 0.7-2 mm wide, dichotomously to partly subpalmately branched, 360-500  $\mu$ m thick; **cilia** absent (Moberg & Nash 1999); **soralia and isidia** absent; **upper surface** gray to dark gray, at first smooth but usually soon becoming densely white pruinose, and slightly rugulose towards center; **lower surface** pinkish to pale brown or brown (to blackish?), paler towards periphery, moderately rhizinate; **rhizines** scattered, short, pale to dark, simple (or branched towards tips?); **upper cortex** subirregularly thickened, 80-200  $\mu$ m; **algal layer** discontinuous; algae 7-13  $\mu$ m; **medulla** white, mostly but not always with patches of yellow to yellow-brown pigment (K+ purple), 110-170  $\mu$ m; **lower cortex** 40-80  $\mu$ m.

**APOTHECIA**  $\pm$  common, (1-)2-4(-6) mm diam.; **margin** sometimes lobulate-crenate, concolorous with thallus, smooth, white pruinose towards outer edge; **discs** concave to almost plane, brown-black, epruinose (Moberg & Nash say that the apothecia often have a rough pruina, but they do not make it clear if this refers to the discs or the margins); **hymenium** ca. 100  $\mu$ m; **spores** *Pachysporaria*-type, without sporoblastidia, (19.5-)21.0-26.0(-29.0) x (9.5-)10.5-12.0(-13.0)  $\mu$ m; locules subglobose to obovate.

**PYCNIDIA**  $\pm$  common, visible as black dots and often concentrated on lobe margins; **conidia** bacilliform, 4-5 x 1  $\mu$ m.

**CHEMISTRY:** Cortex K+ yellow; cortex and medulla P-. Atranorin, zeorin, leucotylin; medulla (especially in apothecia) with yellow to brownish or orangish (K+ purple) anthraquinone pigments.

**ECOLOGY AND DISTRIBUTION:** Common at the base of oak trees in open woods and along roads, from western Texas to Arizona, and southward in Mexico (Sonora, Chihuahua, Baja California Sur). On trunks, twigs, and rocks, apparently preferring open but humid conditions.

**NOTES:** Extremely variable. On bark it is usually broad-lobed with overlapping lobes; on twigs it is short-lobed with  $\pm$  fingerlike lobes, while on rocks it has discrete, distinctly "effigurate" [whatever Moberg & Nash mean by that] lobes.

### **H. sitchensis Goward & W. Noble**

**THALLUS** foliose, semi-erect, cushion-forming, to 2 cm diam.; **lobes** thin, stiff, 0.5-2.0 mm wide, squat to elongate, separate to loosely overlapping, suberect or ascending (to  $\pm$  appressed), sparsely irregularly branched; branching sympodial, with short lateral lobes, not uncinata, on radially extending main lobes; **cilia** marginal, numerous, soon blackening, slender, 0.5-2.0 mm long, sparsely to richly (but irregularly) branched; **upper surface** pale greenish white (but readily discoloring to bluish black), matt, smooth to occasionally bearing scattered verruculae, strongly convex, often with maculae (these laminal, rounded, 0.1-0.4 mm across, sparse to moderately numerous), of uneven thickness, and with ridgelike extensions into the medulla.; **lower surface** white throughout, cottony, ecorticate (except frequently detailed with veinlike extensions of the upper cortex).

**APOTHECIA** stipitate, subapical; **margin** with subgranular, pale whitish green soredia confined to ring-shaped excipular soralia, these 0.5-1.2 mm across, borne within urnlike growths of the apothecial rim, often becoming exposed as the walls of the "urn" gradually subside or flate.

**CHEMISTRY:** Medulla K+ yellow, C-, KC-, P+ orange (atranorin, zeorin, unknown fatty acids; cause of P+ reaction unknown).

**ECOLOGY AND DISTRIBUTION:** On twigs of Picea sitchensis in sheltered, humid situations, outer coast of British Columbia, rare.

**NOTES:** Series Podocarpae

### **H. spathulifera Moberg & Purvis**

**THALLUS** irregular to orbicular, to 3 cm diam.; **lobes** discrete to adjacent, firmly adnate, lobes narrow, to 1 mm, usually flat, not distinctly widening at tips; **cilia** absent (Moberg & Nash 1999; but rhizinae sometimes visible from above); **soralia** labiate, sometimes becoming large (to 5 mm tall) and spathulate; soredia developing into squamules which sometimes cover inner parts of thallus in moist and shaded habitats; **upper side** white to cream-colored, shiny and without pruina; **lower surface** ecorticate, white on outer parts of lobes, pale brown on inner parts (appearing corticate, but in sections this is medulla incrustated by soil particles); **rhizines** sparse, c. 1(-2) mm long, simple, white or cream; upper cortex thick, prosoplectenchymatous.

**APOTHECIA** rare; **spores** Pachysporaria-type, immature in North American material, 36-43 x 15-18  $\mu$ m.

**PYCNIDIA** unknown.

**CHEMISTRY:** Cortex and medulla K+ yellow; atranorin, zeorin, unknown substance, UV+ red after charring Rf 4-5 (G) ['spathulin']

**ECOLOGY AND DISTRIBUTION:** On rocks and tree trunks in open but humid conditions. Southwestern.

See Moberg & Nash

**H. speciosa (Wulfen in Jacq.) Trevisan**

**THALLUS** ± firmly adnate, orbicular to irregular, 2-3(-4) cm diam., often coalescing with other thalli; **lobes** c. 1(-2) mm broad, linear-elongate, plane to convex, slightly widening towards apices; lobe tips not ascending; **cilia** absent (Moberg & Nash 1999; but conspicuous, white or tan [to brown-tipped] rhizines may be visible along margins from above); **soralia** absent from end lobes, strongly crescent-shaped labiate soralia on lateral lobes, sometimes semicapitate, starting from lateral lobes; soredia abundant, whitish or grayish or bluish gray, farinose to ± granular; **upper surface** white to cream-colored or brownish gray, appearing blue-gray from the dense soralia (strikingly contrasting in color with the thallus), ± shiny, the lobe tips sometimes darkening, very rarely pruinose; **lower surface** corticate, sometimes eroding (or decorticate in younger parts of lobes), pale to dark brown, sparsely rhizinate, **rhizines** scattered, short and robust, usually black; **lower cortex** prosoplectenchymatous.

**APOTHECIA** rare (not seen in Sonoran region material); **spores** (20-)25-35(-37) x 12-18 µm.

**PYCNIDIA** not seen.

**CHEMISTRY:** Medulla K+ yellow, P- or pale yellow, with zeorin and 1(to 3) other triterpenoids.

**ECOLOGY AND DISTRIBUTION:** Common on deciduous trees and less often mossy rocks in mature woods and swamps, or on sunny, coastal rocks. Eastern (Great Lakes area, Virginia to North Carolina south to Florida), common at lower elevations in the mountains and piedmont, rarer at higher elevations and latitudes. On sunny but moist rocks or tree trunks, SE Arizona, Sonora, Chihuahua.

**H. squamulosa (Degel.) Culb.**

**THALLUS** fragile, 5-15 cm broad, adnate; **lobes** flabellate, ± appressed, linear and narrow, 1-1.5 mm wide; squamules or lobules erect, abundant and dense on lobe margins and upper surface, occasionally small appearing as soredia or isidia-like in peripheral portions of thallus; **cilia** absent; **lower surface** white at the tips but darkening toward the center, not bordered by reflexed margin of upper cortex; **rhizines** short.

**APOTHECIA** rare or absent, covered by branched squamules; **spores** with sporoblastidia at maturity.

**CHEMISTRY:** Medulla K+ yellow, without norstictic acid, with zeorin.

**ECOLOGY AND DISTRIBUTION:** Common at base of trees and over mosses on trees, in open woods or along roads, high elevations in the Appalachians (N. Carolina to Virginia, and northward); also reported from the Black Hills, but that report may be a misidentification.

**NOTES:** Section Polyblastidia.

**H. tropica (Kurok.) Kurok.**

**THALLUS** orbicular, to 5 cm diam. or irregular and confluent with other thalli, ± closely adpressed; **lobes** radiate, delicate, 0.5-1.5 mm wide, ± elongated, richly branched with ± lobulate

margins; **cilia** absent (Moberg & Nash 1999); **soralia and isidia** absent; **upper surface** rough, gray to dark gray, often with darker margins and tips, sometimes with a weak pruina; **lower surface** corticate, white to pale gray or brownish; **rhizines** abundant, pale gray to black, sparsely branched; **medulla** white; **lower cortex** prosoplectenchymatous

**APOTHECIA** numerous, laminal, to 5 mm diam.; **margin** subentire or crenate (abundantly lobulate when older according to Moberg & Nash); **spores** Pachysporaria-type, without sporoblastidia, (25.0-)27.0-32.0(-37.5) x (12.0-)13.0-17.0(-19.5)  $\mu$ m.

**PYCNIDIA**  $\pm$  abundant; **conidia** bacilliform, 4-5 x 1  $\mu$ m..

**CHEMISTRY:** Cortex and medulla K+ yellow to red, P+ yellow-orange; with atranorin, salazinic acid and zeorin.

**ECOLOGY AND DISTRIBUTION:** Arizona, Sonora, Baja California Sur

**NOTES:** Lacking soredia, otherwise similar to H. albicans. Externally resembles H. diademata, but differs in chemistry.

## Literature

- Awasthi, D. D. 1973. On the species of Anaptychia and Heterodermia from India and Nepal. *Geophytology* 3(1): 113-116.
- Culberson, W. 1966. Chemistry and taxonomy of the lichen genera Heterodermia and Anaptychia in the Carolinas. *The Bryologist* 69: 472-487.
- Esslinger, T. L. and C. Bratt. 1997. The Heterodermia erinacea group in North America, and a remarkable new disjunct distribution. Pages 25-36 in Glenn, et al. (eds.), *Lichenografia Thomsoniana*.
- Galloway, D. 1985. *Flora of New Zealand Lichens*.
- Harris, R. C. 1990. *Some Florida Lichens*.
- Harris, R. C. 1995. New or rare lichens/lichenicolous fungi for North America. *Evansia* 12: 154-156.
- Kurokawa, S. 1962. A monograph of the genus Anaptychia. *Beih. f. Nova Hedwigia* 6: 1-115.
- Kurokawa, S. 1973. Supplementary notes on the genus Anaptychia. *J. Hattori bot. Lab.* 37: 563-607.
- Moberg, R. and T. H. Nash III. 1999. The genus Heterodermia in the Sonoran Desert area. *The Bryologist* 102: 1-14.
- Moberg, R. and O. W. Purvis. 1997. Studies on the lichens of the Azores. Part 4. The genus Heterodermia. *Symb. Bot. Ups.* 32(1): 187-194.
- Purvis, O. W. 1992. Heterodermia. In: Purvis, et al., *Lichen Flora of Great Britain and Ireland*.
- Rogers, 19 . *Genera of Australian Lichens*.
- Swinscow, T. D. V. and H. Krog. 1976. The genera Anaptychia and Heterodermia in East Africa. *Lichenologist* 8: 103-138.
- Trass, H. 1992. Synopsis of the lichen genus Heterodermia (Ascomycotina, Physciaceae sive Pyxinaceae). *Folia Cryptogamic Estonica* 29: 2-24.
- Weber, W. A. and D. D. Awasthi. 1971. A new species of Heterodermia (Physciaceae) from Colorado. *The Bryologist* 74(2): 181- 183.