Four new sorediate species in the *Hypogymnia austerodes* group (lichens) from northwestern North America, with notes on thallus morphology

Author(s) :Trevor Goward, Toby Spribille, Teuvo Ahti, and Celia J. Hampton-Miller

Source: The Bryologist, 115(1):84-100. 2012.
Published By: The American Bryological and Lichenological Society, Inc.
DOI: http://dx.doi.org/10.1639/0007-2745-115.1.84
URL: http://www.bioone.org/doi/full/10.1639/0007-2745-115.1.84

Four new sorediate species in the *Hypogymnia austerodes* group (lichens) from northwestern North America, with notes on thallus morphology

Trevor Goward[1,5], Toby Spribille[2], Teuvo Ahti[3], and Celia J. Hampton-Miller[4]

[1] *UBC Herbarium, Beaty Museum, University of British Columbia, Vancouver, B.C. V6T 1Z4, Canada. (Mailing address: Edgewood Blue, 5369 Clearwater Valley Road, Upper Clearwater, B.C. V0E 1N1, Canada);* [2] *Institute of Plant Sciences, University of Graz, Holteigasse 6, A-8010 Graz, Austria;* [3] *Botanical Museum, Finnish Museum of Natural History, P.O. Box 7, FI-00014 University of Helsinki, Finland;* [4] *University of Alaska Museum Herbarium, Fairbanks, AK 99775, U.S.A.*

Abstract. The *Hypogymnia austerodes* group is an assemblage of mostly boreal and arctic-alpine lichens traditionally comprising three wide-ranging sorediate and/or isidiate species, *H. austerodes*, *H. bitteri* and *H. subobscura*. Here we describe four additional members of this group – *H. dichroma* sp. nov., *H. protea* sp. nov., *H. salsa* sp. nov. and *H. verruculosa* sp. nov. – which have until now been treated within *H. austerodes* s. lat. Our new species are primarily epiphytic, and are currently known only from Cordilleran western North America. They differ from other members of the *H. austerodes* group both morphologically and in their virtually consistent production of apinnatic acid. *Hypogymnia protea* is by far the most variable of the new species, uniting two putative taxa here designated as morphs "disjuncta" and "tessellata". Reliable discrimination of the segregate species requires careful attention to their vegetative reproductive structures, which are described in detail. A key to all treated species and their recognized morphs is provided. Earlier reports of *H. farinacea* from western North America appear to be based on schizidiate material of *H. protea* morph "tessellata". Whether *H. farinacea* actually occurs in North America remains an open question.

Keywords. Apinnatic acid, British Columbia, Lecanorales, lichens, Parmeliaceae, vegetative propagules.

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The North American members of the lichen genus *Hypogymnia* have received considerable attention by taxonomists in recent decades, resulting in an increase from nine accepted species in 1960 (Hale & Culberson 1960) to 33 species at the present time (Esslinger 2011; McCune 2008). Most studies to date have focused on the *H. enteromorpha* and *H. imshaugii* groups, in which reproduction of the fungal partner is effected via meiotic spores. By contrast the North American species of the vegetatively reproducing *H. austerodes* group have received little attention.

[5] Corresponding author e-mail: trevor.goward@botany.ubc.ca
DOI: 10.1639/0007-2745-115.1.84

As circumscribed here, the *H. austerodes* group is a small, predominantly boreal to arctic-alpine assemblage characterized by black mottling over the upper surface, a tendency to turn chestnut brown in high light, a PD- medulla, a white medullary ceiling, and the frequent presence of laminal soredia and/or isidia. In North America this group encompasses three wide-ranging species, i.e., *H. austerodes* (Nyl.) Räsänen, *H. bitteri* (Lynge) Ahti and *H. subobscura* (Vain.) Poelt. To these might also be added *H. farinacea* Zopf, which shares most of the above characters, but which lacks black mottling, apparently never turns chestnut brown, and is restricted mostly to temperate latitudes.

Lately we have become aware of a perplexing degree of morphological variation within *H. austerodes* in northwest North America. Much of this variation has yet to be discussed in the literature, prompting us to undertake a critical examination of *H. austerodes* and its allies in North America. In light of our studies, this paper has four main objectives: (1) to describe four new *Hypogymnia* species until now included within *H. austerodes*; (2) to call attention to the diagnostic value of vegetative reproductive structures in the *H. austerodes* group; (3) to characterize the secondary chemistry of this group; and (4) to provide an identification key to all sorediate members currently known to occur in northwest North America. *Hypogymnia subobscura* was excluded from our study owing to its production of isidia and isidioid outgrowths in place of soredia.

Species delimitations based on thallus morphology are effectively hypotheses about what constitutes a reproductively isolated, genetically distinct unit, i.e., a biological species. Testing this experimentally is prohibitively difficult in lichens; nor has the application of molecular approaches to *Hypogymnia* yet satisfactorily clarified its terminal clades (McCune & Schoch 2009; but see Miadlikowska et al. 2011). Here we advance a new species hypothesis for the *H. austerodes* group in western North America, with emphasis on thallus morphology, vegetative propagule ontogeny and secondary metabolite chemistry. Propagule ontogeny is highly evolved in this group, spanning a range of variation otherwise unknown within *Hypogymnia*. Because this variation is not readily accommodated using the standard lichenological terminology, we find it useful to introduce a set of terms specially adapted to the *H. austerodes* group, as described below. These terms are not intended to for use outside of *Hypogymnia*; but within it they help to focus attention on certain taxonomic nuances critical to the recognition of our new species.

Materials and Methods

Approximately 400 herbarium specimens labeled as *H. austerodes, H. bitteri* and *H. farinacea* were examined by us during this study, including North American and European material from ALA, CANL, GZU, H and UBC, as well as personal collections by Ed Berg, Curtis Björk and Karen Dillman, and the type material of *H. austerodes* in H. A rich collection was also assembled during our own field studies in Alaska, the Yukon, British Columbia, and the American Northwest. Only a few specimens were available to us from south of the Canada-U.S. border, where the *H. austerodes* group appears to be rather infrequent – as inferred, e.g., from the work of Imshaug (1957).

Two hundred specimens were selected for chemical testing by thin-layer chromatography (TLC). TLC was performed following the methods of Culberson (1972) and Culberson & Johnson (1982), with relative Rf values calculated from atranorin and norstictic acid as controls. No attempt was made to distinguish atranorin from chloroatranorin.

Lobe width refers to the "average" width of the broadest peripheral lobes (see below). Soredia and gymnidia (see below) were mounted in water and measured in light microscopy. Measurements were taken in the original condition, i.e., without application of pressure to the cover slip. Because soredia in *H. austerodes* s. lat. often tend to aggregate into consoredia (sensu Tønsberg 1992: 34), we standardized our measurements by assessing only individual granules, with emphasis on the largest ones within each consoredium. In the case of corticate diaspores – isidia, cortidia – we restricted our measurements to recently formed propagules. Ascospore and conidiospore measurements were made in light microscopy. Ascospore measurements are based on well-formed spores free from the ascus. A minimum of ten spores from each ascus were measured. Unfortunately, apothecia are sparse or poorly developed in the *H. austerodes* group, resulting in a small number of available asci.

Results and Discussion

Diagnostic characters.

Careful examination of a rich material confirmed our initial impression that *H. austerodes* as currently conceived in western North America is morphologically highly diverse – much more so than in Europe, where *H. austerodes* has its type locality. We further succeeded in resolving the North American material into four discordant elements additional to *H. austerodes* s. str. These four segregate taxa differ across several characters, including propagule ontogeny, and are recognized here as distinct species.

Structures marked with an asterisk are additional to the lichen propagules covered by Büdel & Scheidegger (2008).

Thallus attachment appears to have moderate taxonomic value in the *H. austerodes* group. Two character states can be recognized, i.e., lobes loosely attached, and lobes appressed more or less throughout. Only in *H. austerodes* s. str. have both types of attachment been observed, the former being most frequent in thalli growing on thin twigs.

Lobe type. For descriptive purposes we recognize two lobe types in *H. austerodes* s. lat.:

(1) **First-tier lobes** can be described as ‘‘pioneer’’ lobes; they extend the thallus outward across its substrate. These lobes often become laterally expanded toward the tips, providing a useful point of measurement for maximum lobe width.

(2) **Second-tier lobes** arise as lateral offshoots of first-tier lobes, which they soon overlap. In the loosely attached species, they can completely overgrow the first-tier lobes, and hence extend to the thallus periphery; such lobes are here described as ‘‘trailing’’ (**Fig. 1C**). In *H. austerodes* s. lat., only second-tier lobes bear the vegetative reproductive structures.

Vegetative reproductive propagules and structures. Isidia, soredia, schizidia and vegetative propagules of other kinds provide key diagnostic characters for our new species. Critical here are details of early propagule development. Below we provide a brief summary of these propagules, with emphasis on the structures that bear them. Terms marked with an asterisk are proposed here for the first time.

1. **Soralopodia*** are mounded to steeply conical or even capitate, soredia-bearing outgrowths positioned at or near the lobe tips. In some species they can also develop along the lobe margins, albeit apically on short side lobes. Fully mature soralopodia measure up to about 0.2–0.5 (–0.8) mm across by 0.2–0.4 mm high, and either burst open into true soredia or else disintegrate above into cortidia; see below. Especially noteworthy are the highly characteristic subapical soralopodia of *H. bitteri*, which measure up to 2–4 (–6) mm across and, only in this species, sometimes arise also over the laminal surface. Whereas soralopodia are otherwise essentially peculiar to the lobe tips, the following seven structures are restricted to laminal portions of the thallus.

2. **Papillae** are defined here as tiny, compact, semi-translucent structures less than 0.05 mm in diameter and distinctly hemispherical in outline. They differ from similar structures mostly in being rather uniformly spaced. Papillae should not be regarded as propagules *per se* as typically they remain attached – yet at maturity they do give rise to isidia and/or gymnidia and, secondarily, to soredia. Their resemblance to papillae in some species of *Usnea* is striking.

3. **Micropustules*** are low, weakly mounded, radially symmetrical upwellings of the cortical surface. At maturity they give rise to rounded soralia that in turn tend to dissolve outward from the base, at length often becoming coalescent. Unlike glebulae, which are larger and tightly packed, micropustules measure only about 0.05-0.10 mm across and are generally rather sparse.

4. **Glebulae*** Like micropustules, glebulae are radially symmetric upwellings of the laminal cortex. They differ, however, in being larger (about 0.15–0.20 mm across), more blocky, and much more tightly packed. Somewhat similar structures occur also in *H. farinacea;* but as these are typically detached from the underlying medulla, they are classified here as exfoliation ridges; see below.

5. **Verrucae** are larger and more mounded than glebulae. In *H. austerodes* s. lat., they take the form of laminal wart-like outgrowths about 0.5–1.0 mm across. At maturity each verruca characteristically gives rise to two or often more soralia.

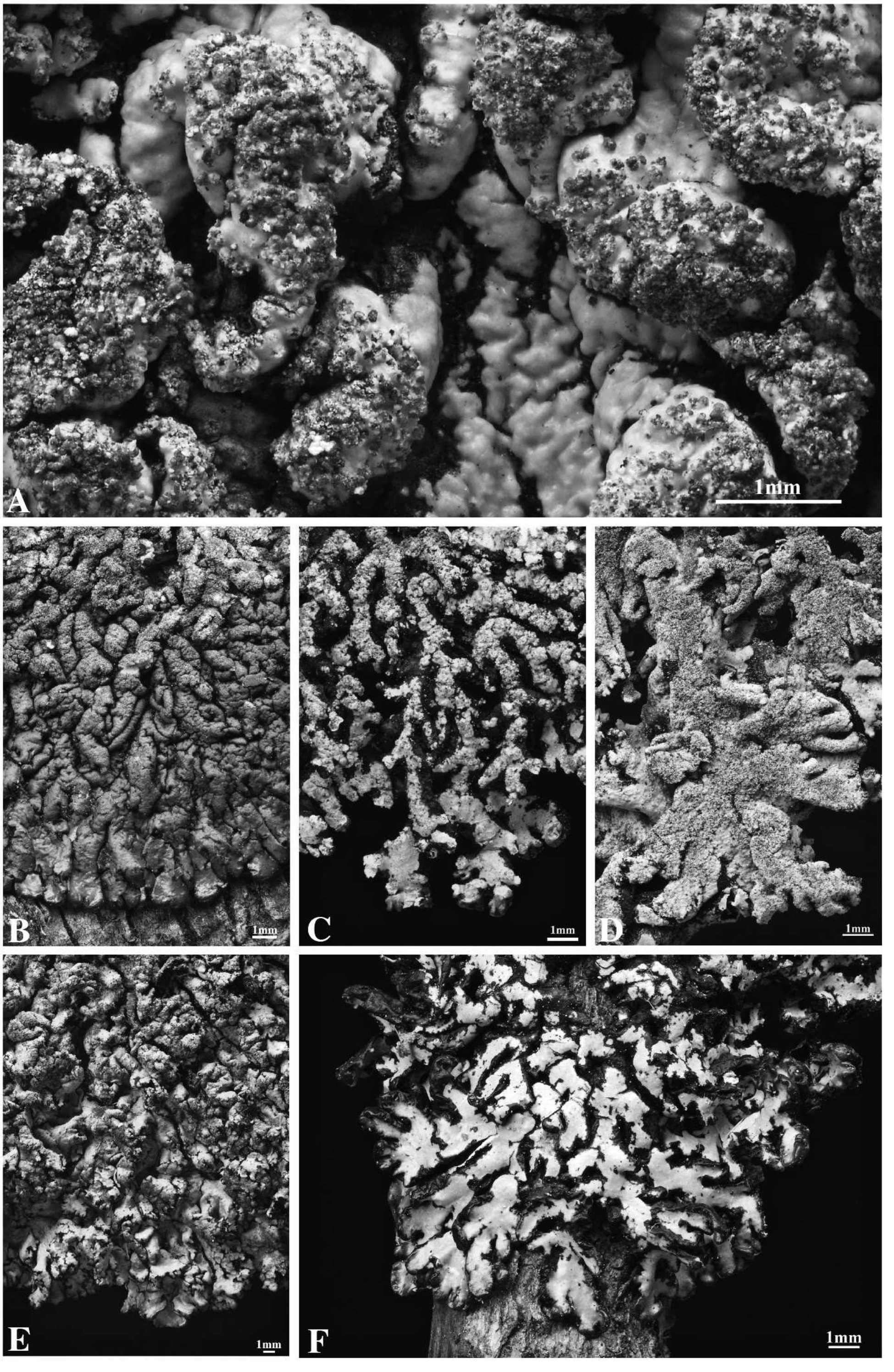

Figure 1. *Hypogymnia austerodes* and its segregates in western North America. **A.** *H. austerodes*; detail, showing isidia and gymnidia, some of which are grading into soredia. **B**. *H. dichroma* (holotype); lobes contiguous and appressed. **C.** *H. protea* morph *disjuncta* (holotype); lobes open and trailing. **D.** *H. salsa* (holotype). **E.** *H. verruculosa* (holotype). **F.** *H. protea* morph *tessellata*. Photos and plate by Tim Wheeler.

Table 1. Secondary metabolites in the species of the *H. austerodes* group in northwest North America as detected by TLC. Numbers indicate percentage of samples in which substance was detected. Trace accessory substances found in fewer than five samples overall are not shown.

	N	atranorin	physodic	3-hydroxy-physodic	2′-*O*-methyl-physodic	apinnatic acid	vittatolic
Established taxa:							
austerodes	34	0.88	1.00	0.47		0.12	0.47
bitteri	15	0.87	1.00		0.33		0.93
farinacea	3	1.00	1.00	1.00	0.67		
New taxa:							
dichroma	16	1.00	1.00	0.88	0.50	0.75	0.19
protea	41	0.88	0.98	0.78	0.51	0.85	0.34
salsa	6	0.50	0.67	0.17	0.50	0.50	
verruculosa	7	1.00	1.00	1.00	0.57	1.00	

6. **Rugulae*** are low ridges oriented perpendicular to the main lobe axis and frequently dissolving into diffuse soredia-bearing soralia. In some species they may become subdivided laterally into numerous small, tightly packed glebulae. Unlike exfoliation ridges, rugulae remain attached to the underlying medulla. In some cases the upper surface of rugulae may dissolve into cortidia; see below.

7. **Exfoliation ridges*** form when the laminal cortex expands, becomes detached from the underlying medulla, and buckles upward. When ultimately an exfoliation ridge breaks open at the ridge line, it forms a pair of parallel cortical flaps; see next.

8. **Cortical flaps*** are up-turned, page-like portions of the cortex no longer in contact with the medulla. These structures may arise along the margins of cortical cracks, or form through the break-up of exfoliation ridges. In both cases they presumably contribute to vegetative reproduction not only as thallus fragments (i.e., in the form of schizidia), but also through fine-scale cortical disintegration, and hence the production of cortidia; see below. Cortical flaps sometimes also arise in connection with the soralopodia or laminal soralia, which they may encircle. These structures may also arise toward the thallus centre, though here the margins appear to break down directly into true soredia.

9. **Gymnidia.** *Hypogymnia austerodes* s. str. produces highly characteristic laminal outgrowths variously referred to as "isidioid soredia" (Büdel & Scheidegger 2008), "subisidiate granules" (McCune 2002a), and "isidia-like pustules" (Brodo et al. 2001). These propagules are not strictly speaking corticate, hence can't be termed true isidia; yet at the same time they are too compact to qualify as soredia. Actually such structures are rather widespread among the macrolichens, occurring for example in *Letharia vulpina*, *Lobaria scrobiculata*, *Massalongia carnosa*, *Parmelia fraudans* and *P. hygrophila*. Similiar structures in *Pannaria* have been termed "gymnidia" by Jørgensen & Kashiwadani (2001); and here we adopt this term, which can thus be defined as rather compact (but non-corticate), granular outgrowths of the thallus surface containing both fungi and algae/cyanobacteria.

10. **Schizidia** are flake-like propagules formed when portions of cortex become detached from the medulla and scale off, carrying with them at least some underlying algal cells.

11. **Cortidia.*** Like schizidia, cortidia can be interpreted as a byproduct of programmed cortical disintegration. But whereas schizidia scale off in dorsiventral flakes, cortidia are small and spheroid-granular. In appearance they resemble gymnidia, but arise as a result of cortical disintegration rather than as cortical outgrowths. All soralopodiate members of the *H. austerodes* group are probably capable of producing apical or subapical cortidia, whether along cortical flaps (= rim cortidia) in the case of burst soralopodia, or over the upper surface (= extension cortidia). True laminal cortidia, by contrast, arise only in *H. farinacea* and *H. protea*. Because cortidia

often soon disintegrate into true soredia, their presence must be confirmed during the early stages of their development.

12. **Isidia** are corticate outgrowths of the cortex, usually somewhat constricted at the base. True laminal isidia are rare in *Hypogymnia*; in the *H. austerodes* group they may be intermixed with or, in some cases, replaced by gymnidia. They should be searched for especially in depressions between the main thallus ridges. Some thalli develop "adventitious" isidia but these are usually very sparse, mostly confined to the inner portions of the thallus.

13. **Soredia** are a characteristic feature of all species included in our study. In some thalli soredia are present from the first (primary soredia), whereas in others they arise only later, through dissolution of structures such as gymnidia and/or isidia or cortidia.

Secondary thallus chemistry. Chemical diversity in the *Hypogymnia austerodes* group (**Table 1**) is broadly similar to that in the *H. metaphysodes* group (Goward et al. 2010): in addition to near-ubiquitous atranorin and physodic acid, the suite of substances alternates between 3-hydroxyphysodic acid, 2′O-methylphysodic acid, vittatolic acid and the aliphatic compound apinnatic acid. Diffractaic acid was found as a trace substance in only one specimen of *H. bitteri* and one of *H. dichroma* and is not shown in **Table 1**. Physodalic acid and its satellites, common in the *H. physodes* and *H. imshaugii* groups in North America, are not known from this group. Noteworthy trends between taxa in the *H. austerodes* group includes the characteristic absence of 3-hydroxyphysodic acid from *H. bitteri* and its absence from *H. salsa* in 5 of 6 samples studied, and the high incidence of vittatolic acid in *H. bitteri*. Another conspicuous pattern is the high incidence of the fatty acid apinnatic acid in the newly described taxa and its near-absence from previously described members of this group.

Apinnatic acid was mentioned as a common constituent of *Hypogymnia apinnata* and *H. occidentalis* by Spribille et al. (2010), who referred to Goward et al. (2010) for its R_f values and identification characteristics. However, R_f values were inadvertently omitted from that publication. Apinnatic acid – a trivial name for 2-methylene-3*R*-carboxy-18*R* hydroxy-nonadecanoic acid – runs in our solvent systems at relative R_f values of A18, B′27, C33. *Hypogymnia apinnata* provides an excellent standard to visualize this compound since it is not concealed by physodic acid or its satellites in solvent systems A and B′. In species such as those of the *H. austerodes* group, it is often clearly visible only in solvent system C, where it migrates farther than physodic or its satellites. When dry, developed plates are sprayed with H_2O or immersed in a water tank, apinnatic acid appears quickly, but disappears faster than most other aliphatic compounds, which may explain why this compound has remained unnoticed in the past. We have found it useful to keep a digital camera handy to photograph aliphatic compounds in the seconds after the plate is removed from the tank to avoid overlooking such substances. Over time apinnatic acid develops a light brownish color. Apinnatic acid has been reported from only a few species of *Hypogymnia*, *Parmotrema* and *Usnea* (Goward et al. 2010). Remarkably, it was recently also reported from *Lecanora phaeostigma* (Czarnota et al. 2010).

Summary of diagnostic characters.

Some of the propagule types outlined in the preceding section are admittedly rather subtle, their reliable recognition often requiring careful examination at an early stage of propagule development. Nevertheless they do seem to represent discrete products of evolutionary process and, as such, provide important characters to diagnose species. **Tables 2 and 3** summarize the apportioning of these characters across our four new segregate species (and two additional morphs), and at the same time survey their occurrence in *H. austerodes, H. bitteri* and *H. farinacea* . The following key further emphasizes their diagnostic value.

Key to sorediate members of the *H. austerodes* group in northwest North America

Note: Specimens lacking vegetative propagules often cannot be determined with certainty.

1. Thallus loosely attached or in part trailing; second-tier lobes often in part forming thallus periphery 2
1. Thallus more or less closely appressed; second-tier lobes rarely if ever forming the thallus periphery (Note: specimens with isidia and/or gymnidia key here) 4
    2. Upper surface minutely roughened (check thallus centre), usually bearing at least some tiny hemispheric papillae; well developed marginal soralopodia often present at the tips of short, stiff, non-tapering lobes;

Table 2. Vegetative reproductive structures and other characters diagnostic for the four members of the *H. austerodes* group described in this paper, with *H. austerodes* s.str. for comparison. Measurements represent the average of the largest units for the structures indicated. Bolded characters are diagnostic; see also **Table 3**. Spore measurements for *H. austerodes* are based on European material (Westberg et al. 2011).

	***austerodes* morph "austerodes"**	***dichroma***	***protea* morph "*disjuncta*"**	***salsa***	***verruculosa***
attachment	appressed or trailing	appressed	**loose/trailing**	**loose**	appressed
lobes up to (mm)	2.5–4.0 (–6.0)	2–3 (–3.5)	2–3 (–4)	2.0 (–2.5)	3.5–4.0 (–6)
soralopodia (mm diameter)	none/few 0.1	none/few 0.4–0.8	**some/many** 0.4–0.8	none/few 0.4–0.6	none/few 0.3–0.4
soralopodial cortidia (μm diameter)	none	none	none/**some** 20–25	none	none
stress cracks	gen. few	none	gen. few	none	gen. few
isidia/gymnidia	**some/many**	none	none	none	none
papillae	**few/some**	none	none/few	**few/some**	none
micropustules	few	none	**some/many**	few/some	some
glebulae	none	**few/many**	none	none	some
verrucae	none/some	none/few	none/few	none	**many**
rugulae	few/some	**few/many**	**none**	none	few
exfoliation ridges	none	none	none	none	none
cortical flaps	none/few	none	none/some	none	none
laminal cortidia (μm diameter)	none	none	**none/some 30–40 (–50)**	none	**some/many 50–70 (–80)**
laminal schizidia	none	none	none	none	none
apothecia	not seen	gen. none	gen. none	not seen	not seen
spores (μm)	(6.5–7.5 × 4.5–5.0)	**6.0–6.2 × 4.0–4.2**	**5.2–6.0 × 4.2–4.5**	not seen	not seen
pycnidia	not seen	gen. none	gen. none	not seen	**few/some**
conidia (μm)	not seen	4.2–5.5	4.5–5.0	not seen	4.5–5.0

second-tier lobes stiff, not trailing; northern, south to about 58°N .... *H. salsa*

2. Upper surface more or less smooth throughout, or at any rate not roughened, usually without papillae; soralopodia sparse to abundant, but scarcely if at all well developed at tips of short, stiff, non-tapering marginal lobes; second-tier lobes usually trailing; widespread, south to about 48°N .... 3 (*H. protea*)

3. Laminal soralia present, usually closely spaced, more or less protuberant; soralopodia usually numerous, conspicuous, the largest ones 0.4–0.8 mm across; eroded lobe tips rarely opening into thallus interior; stress cracks at most few and inconspicuous .... *H. protea* morph "disjuncta"

3. Laminal soralia absent or, if present, then usually sparse, scarcely elevated above the cortical surface; soralopodia absent or, if present, usually rather inconspicuous, the largest ones 0.2–0.3 mm across; eroded lobe tips, if present, often opening into thallus interior; stress cracks often numerous and conspicuous (check near thallus centre)............. .... *H. protea* morph "tessellata"

4. Soralopodia well developed at or near lobe tips, the largest ones usually more than 2 mm across, disintegrating above into coarse cortidia up to 50–80 μm across (check recently formed soralopodia) .... *H. bitteri*

4. Soralopodia absent or at most poorly developed and small, less than 1 mm across, usually exfoliating, not giving rise to cortidia 5

5. Upper surface bearing at least some granular or elongate isidia and/or gymnidia (check depressions) (Note: specimens with eroded lobe tips opening into the thallus interior key here) .... 6 (*H. austerodes* s. str.)

5. Upper surface without isidia and/or gymnidia 7

6. Broadest first-tier lobes more than (3–) 4–5 mm wide, more or less contiguous, usually entirely obscuring the underlying substrate; thallus usually without isidia-like lobules along the lobe margins .... *H. austerodes* morph "austerodes"

6. Broadest first-tier lobes less than 2 (–2.5) mm wide, rather sparsely branched, usually not entirely obscuring the underlying substrate; thallus usually bearing at least some isidia-like lobules along the lobe margins............. .... *H. austerodes* morph "depauperata"

7. Upper surface pale greenish, without black mottling; cortex conspicuously brittle, soon dissociating from the underlying medulla, forming exfoliation ridges, cortical flaps and/or coarse cortidia up to 60–80 μm across; soredia present or absent; temperate to low boreal, not definitely known from North America .... *H. farinacea*

Table 3. Vegetative reproductive structures and other characters diagnostic for morphotypes of *Hypogymnia austerodes* and *H. protea*, compared with *H. bitteri* and *H. farinacea*. Measurements represent the average of the largest units for the structures specified. Terms accompanied by an asterisk are described in the text. Bolded characters are diagnostic; see also **Table 2**. Spore and conidia measures for *H. farinacea* are taken from Westberg et al. (2011) based on European material.

	austerodes **morph "depauperata"**	***bitteri***	***farinacea*** **(Europe)**	***protea*** **morph** ***disjuncta***	***protea*** **morph** ***tessellata***
attachment	loosely appressed	appressed	appressed	**loose, often trailing**	**loose, often trailing**
lobes up to (mm)	1.5–2 (–2.5)	3–4 (–5)	2.5–4 (–5)	2–3 (–4)	2–3 (–4)
soralopodia	none/few	few/many	not seen	**some/many**	**none/few**
(mm diameter)	0.1	**2–4 (–6)**		**0.4–0.8**	**0.2–0.3**
soralopodial cortidia	not seen	many	none	none/few	none/few
(µm diameter)		**50–80 (–90)**		20–25 (–30)	20–25 (–30)
stress cracks	gen. few	gen. none	none	gen. few	**gen. many**
isidia/gymnidia	**some/many**	gen. none	none	none	none
papillae	**few/some**	none	none	none/few	none
micropustules	none	none	none	**some**	none/few
glebulae	none	none/many	none	none	none
verrucae	none	none	none	none	none
rugulae	none	none/many	some/many	none	none
exfoliation ridges	none	none	**some/many**	none	none
cortical flaps	none	none	**some/many**	none/some	**none/many**
laminal cortidia	none	none/some	**many**	none/some	none/many
(µm diameter)		**50–80 (–90)**	**(40–) 60–80**	**(30–) 40–50**	**25–35**
laminal schizidia	none	none	**few/many**	none	none/few
apothecia	not seen	not seen	not seen	gen. none	not seen
spores (µm)	not seen	not seen	(6–7.5 × 3–4.5)	5.2–6.0 × 4.2–4.5	not seen
pycnidia	not seen	not seen	not seen	gen. none	not seen
conidia (µm)	not seen	not seen	(5.0–8.0)	4.5–5.0	not seen

7. Upper surface pale greenish to more often brownish, flecked with irregular black mottling; cortex not conspicuously brittle, not dissociating from the medulla, lacking exfoliation ridges and cortical flaps, but sometimes bearing coarse cortidia; soredia present; distribution various 8
   8. First-tier lobes up to 3.5–4.0 (–6.0) mm wide, generally distinctly thickened at the tips; laminal soredia arising through dissolution of granular cortidia up to 50–90 µm across; upper surface variously colored but not whitish toward the thallus centre .... *H. verruculosa*
   8. First-tier lobes up to 2–3 (–3.5) mm wide, scarcely if at all swollen at the tips; laminal soredia arising directly from dissolution of the cortex, at most up to only 30–40 µm across; upper surface usually becoming whitish toward the thallus centre, hence appearing "two-toned" .... *H. dichroma*

New taxa and morphotypes.

Here we describe four new species within *H. austerodes* s. str., i.e., *H. dichroma*, *H. protea*, *H. salsa* and *H. verruculosa*. With the segregation of these species, *H. austerodes* in western North America conforms well to the European species concept. In both regions, however, *H. austerodes* s. str. retains two rather distinct, but apparently intergrading morphotypes; these are designated here, without taxonomic rank, as morphs "austerodes" and "depauperata". *Hypogymnia protea* can likewise be divided into two morphotypes, designated below as morphs "disjuncta" and "tessellata".

The Species

Diagnostic characters for the species are given in **Tables 2 & 3**, which for comparison include two additional sorediate members of the *H. austerodes* group, i.e., *H. bitteri* and *H. farinacea*. Also noteworthy in this context are *H. bryophila* McCune from Portugal (McCune 2002b), and *H. laminosorediata* D. Hawksw. & Poelt from Morocco and Greece (Hawksworth 1973), both of which are morphologically rather close to *H. farinacea.* Neither species, however, is likely to be confused with our segregate species owing, for example, to their lack of black mottling and tendency to remain pale (never chestnut brown) in high light.

Hypogymnia austerodes (Nyl.) Räsänen Fig. 1A

Note: Included in our circumscription of *H. austerodes* s. str. is material falling roughly in two size classes. Broad-lobed thalli (largest lobes > [3–] 4–5 mm wide) measuring up to 15 cm across are consistent with the type of the species and are referred to here as morph "austerodes", while small (< 3 cm across) and narrow lobed (largest lobes < 2 [–2.5] mm wide) thalli are recognized as morph "depauperata". Both morphs occur in western North America as well as in northern Europe (see selected specimens, below).

Diagnosis: Thallus closely appressed (sometimes loosely attached when growing on twigs), highly variable, up to 5–10 (–15) cm across; lobes irregularly branched. First-tier lobes up to 2.5–4.0 (–6) mm wide (1.5–2.0 [–2.5] mm wide in morph "depauperata"), usually contiguous, obscuring the substrate (branching more open in morph "depauperata"), at the tips weakly plane to concave in cross-section, inwards becoming convex. Second-tier lobes usually well developed, appressed, not trailing, usually without conspicuous soralopodia, in older thallus portions generally massing into high ridges and deep intervening depressions. Upper surface whitish to pastel green in sheltered sites, otherwise chestnut brown, weakly shiny throughout or sometimes dull toward thallus centre, firm or rarely in part thin and fragile (see below), sometimes with sparse transverse stress cracks, irregularly flecked with black mottling, also usually with conspicuous black borders as seen from above; bearing isidia, gymnidia and often soredia. Vegetative propagules mostly restricted to second-tier lobes, arising in three ontological contexts: (1) apical soralopodia, these at most sparse, inconspicuous, positioned mostly on extreme lobe tips, capitate, up to 0.1 mm across and 0.1–0.2 mm high, at length either exfoliating (and then revealing the thallus interior) or bursting open into punctiform, soredia-bearing soralia, adjacent portions of lobe margins frequently bearing three or four short, narrow, tapering lobules, these giving a coxcomb-like appearance, readily eroded at the tips, opening into the thallus interior; (2) laminal isidia and/or gymnidia, these sparse to copious, positioned both on ridges and in intervening depressions, arising mostly from tiny hemispheric papillae (also rarely from mounded verrucae), more or less evenly spaced from the first, individually up to 0.05–0.10 mm across (check detachment scars), sometimes becoming coalescent on the ridges, but in the depressions remaining discrete, expanding upwards from the narrow base into coarse soredia; and (3) laminal diffuse soralia infrequent, localized, consisting of thin, erodible patches often flecked with tiny rust-coloured speckles. Perforations sparse to frequent on second-tier lobes, also rare at tips and lower surface of first-tier lobes, the openings usually > 0.2 mm across. Medullary ceiling white except darkening in vicinity of old ruptures in the lower surface. Lower surface mostly black, shiny, thin, easily torn, sharply winkled or folded. Apothecia not observed in North American material, but in northern Europe rare, sessile, up to 6 mm across, disc dark reddish brown. Spores broadly ellipsoid, up to 6.5–7.5 × 4.5–5.0 μm (Westberg et al. 2011). Pycnidia not observed.

Chemistry: atranorin (cortex), physodic acid (major, constant), 3-hydroxyphysodic (submajor, sometimes in trace amounts or absent altogether), 2′-*O*-methylphysodic and vittatolic acid (present in about half the specimens studied). Apinnatic acid was detected in only four of 34 specimens tested. Spot tests: cortex K+ yellow, KC-, C-, PD-; medulla K- (except often K+ pink after 30 minutes!), KC + pink, C-, PD-.

Ecology: In northern portions of its range, *H. austerodes* is most frequent over (mossy) rock in well illuminated sites. Farther south, it becomes more common on the trunks and branches of conifers. In southern inland British Columbia, *H. austerodes* seems to occur most frequently on conifer branches within the dripzones (sensu Goward & Arsenault 2000) of deciduous trees, especially *Populus.*

Distribution: Most common at arctic and boreal latitudes, but extending southward in the mountains at least to southern British Columbia, and reportedly at scattered locations in Washington, Montana, Wyoming, Nevada, Colorado and New Mexico (Ohlsson 1973), as well as Arizona (McCune 2002a).

***Differentiation*:** *Hypogymnia austerodes* s. str. can be distinguished from other sorediate members of the *H. austerodes* group by its characteristic production of well-spaced isidia/gymnidia both over the lobe ridges and in the intervening depressions. These structures sometimes become sorediate and coalescent over the ridges, but remain discrete in the depressions, where they are thus easily discerned. The larger lobes also often bear a small number of closely spaced marginal outgrowths recalling a coxcomb. These typically erode at the tips, and hence open into the thallus interior. *Hypogymnia austerodes* usually grows appressed, though when occurring on twigs it can sometimes adopt a much looser habit. Such forms might be confused with *H. salsa,* in which, however, the central portions of the cortex usually breaks up into minute cracks and cortidia-bearing cortical flaps, and the lobe tips, though sometimes eroding, rarely open into the thallus interior. Some forms of *H. protea* are also similar, though here the soredia normally initiate within rounded, ultimately coalescent soralia; see the discussion under that species. Medullary chemistry is also usually diagnostic, inasmuch as apinnatic acid is rarely detectable by TLC in *H. austerodes*, but usually so in *H. protea*; see Table 1.

Morph "depauperata" differs from morph *austerodes* not only in having smaller lobes and more open branching (see above) but also in producing numerous conspicuous marginal lobules usually longer than wide. Similar structures are also sometimes observed in regenerating portions of morph *austerodes*, suggesting that these two morphotypes may indeed be conspecific; see **Tables 2 & 3**.

Notes: The chemistry of an isolectotype (in Norrlin & Nylander, Herb. Lich. Fenn. no. 209b, H) of *H. austerodes* was analyzed using HPLC. This specimen contains atranorin (minor), chloroatranorin (minor), physodic acid (major), vittatolic acid (minor), 2′-*O*-methylphysodic acid (minor), alectoronic acid (minor), dehydroalectoronic acid (trace), apinnatic acid (minor). The absence of 3-hydroxyphysodic acid in the type specimen is not surprising given that this substance was detected in only about half of specimens studied by us. More surprising is the presence of apinnatic acid. Only four specimens of *H. austerodes* tested by us – one from Sweden, the others from southern British Columbia – were found to contain this substance. By contrast, apinnatic acid was present at detectable levels in most specimens of *H. dichroma*, *H. protea*, *H. salsa* and *H. verruculosa* (**Table 1**). We speculate that this substance will eventually be found to occur also in *H. austerodes* s. str. – even if at concentrations insufficient for detection by TLC.

The specimen pictured in Brodo et al. (2001: p. 355) as *H. subobscura* certainly belongs to *H. austerodes* morph "depauperata". On the other hand, the illustrations attributed to *H. austerodes* in Thomson (1984: p. 237) and Hinds & Hinds (2007: p. 271) more closely resemble *H. bitteri*, though in the absence of soralopodia, this must remain inconclusive. See **Tables 2 & 3** for points of distinction.

Selected specimens examined with TLC (morph "austerodes"). CANADA. BRITISH COLUMBIA: 26 km north of Clearwater Village, west of park road, 710 m, 51°52′N, 120°01′W, open mixed forest, on branch of *Picea*, 19 IV 2009, *T. Goward 09-40* (UBC); 35 km north of Clearwater, Murtle Plateau, southeast of park road, 825 m, 51°58′N, 120°07′W, edge of forest near wetland, on branch of *Picea* under *Populus,* 17 IV 2009, *T. Goward 09-29* (UBC); Liard River Basin, Wokkpash Lake, 4200′, 58°27′N, 124°53′W, on dead *Salix* in fen, 23 VII 1977, *I.M. Brodo 21602* (CANL); Fairy Lake, alpine ridges west of lake, 5350′, 57°20′N, 123°56′W, on stone on ground, 25 VII 1977, *I.M. Brodo 21654* (CANL). U.S.A. ALASKA: Alaska Peninsula, Mother Goose Lake area, 30 m, 57°11′N, 157°14′W, in *Populus-Viburnum* forest, on *Populus balsamifera*, 28 VI 1998, *S. Talbot 072-60X* (UBC); Survey Pass Quad., near confluence of Alatna and Nahtuk rivers, 1000′, 67°25′N, 153°43′W, white spruce forest, on twigs, 21 VI 1973, *B.M. Murray 73-107* (ALA). NORWAY. NORD-NORDLAND: Saltdalen, Junkersdalsuren, on stone, 4 VII 1916, *E. Häyrén s. n.* (H). SWEDEN. JÄMTLAND: Frostviken parish, Hällingsåfallet, on spruce, 22 VIII 1937, *S. Ahlner s. n.* (H).

Selected specimens examined with TLC (morph "depauperata"). CANADA. BRITISH COLUMBIA: Alaska Highway, 2–4 km east of Summit Lake 1350 m, 58°37′N, 124°50′W, open spruce forest, on branch of

Picea, 24 VII 1982, *T. Goward 82-1253* (UBC); Alaska Highway, mile 418.7, mossy spruce forest, on branches dead willow, 17 VII 1976, *G.F. Otto 6137* (UBC); Clearwater Valley, just south of Spahats Creek, west-facing basalt talus slope, 450 m, 51°44′N, 120°01′W, on decaying log, 10 IV 1994, *T. Goward 94-03* (UBC). NORTHWEST TERRITORIES: Nahanni National Park, floodplain near mouth of Prairie Creek, 1300′, 61°16′N, 124°26′W, on *Picea* twigs, 15 VII 1976, *G.W. Scotter 23803* (H); Ram Creek, spruce forests, 1150′, 61°14′N, 124°23′W, on branch of conifer, 11 VII 1976, *G.W. Scotter 23841, 23845* (H); Southwestern Mackenzie region, east end of Brintnell Lake, in shale gorge, 62°05′N, 127°35′W, on rock, 24 VII 1939, *L.C. Raup 3214* (CANL), U.S.A. ALASKA: Denali National Park, Mt. Healy, 63°44.439′N, 148°57.193′W, south-facing wet rock, 969 m,19 VIII 2008, *T. Spribille 27950* (hb. Spribille). RUSSIA. Murmansk Region: Kutsa Reserve, Nivajärvi, Hirveäkallio, metabasic rocks on open lakeshore, 31 VII 1939, *M. Laurila s. n.* (H). SWEDEN. Jämtland: Åre parish, Handöl, mixed, mainly evergreen forest near waterfall, 11 VIII 1975, *R. Alava 15378* (H).

HYPOGYMNIA DICHROMA Goward *sp. nov.* **Fig. 1B**

MycoBank # MB 563095.

Sicut Hypogymnia austerodes *sed cortex eradiens versus centrum thalli et soredia laminalia ex rugulis transversalibus nascentia, non sursum proliferantia. Acidum apinnaticum vulgo praesens. Crescit ad arbores et saxa.*

TYPE: CANADA. BRITISH COLUMBIA. Clearwater Valley, Spahats Creek, north face of Raft Mtn, 51°44′ N, 119°51′ W, windswept pass on branch of *Picea*, 2200 m, 20 VIII 2009, *T. Goward 09-696 & J. Hollinger* (holotype: UBC; isotypes: CANL, GZU, H).

***Diagnosis*:** Thallus closely appressed, moderately variable, up to 5–6 (–8) cm across; lobes irregularly branched. First-tier lobes up to 2.0–3.0 (–3.5) mm wide, mostly contiguous, obscuring the substrate, at the tips weakly plane to concave in cross-section, inwards becoming convex. Second-tier lobes closely appressed, not trailing, occasionally bearing apical and/or subapical soralopodia (see below), older thallus portions usually massing into low, side-on ridges and intervening depressions, usually perforate (see below). Upper surface pale pastel green in sheltered sites, otherwise usually distinctly two-toned, i.e., chestnut brown in distal portions, grading to whitish inwards, shiny at thallus periphery, usually becoming dull toward thallus centre, firm except thin and fragile over rugulae (see below), sometimes with sparse transverse stress cracks, irregularly flecked with black mottling, also usually with conspicuous black borders as seen from above; usually sorediate. Vegetative propagules mostly restricted to second-tier lobes, arising in two ontological contexts: (1) apical and/or subapical soralopodia, these at most sparse, inconspicuous, capitate to mound-forming, in the latter case up to 0.4–0.5 (–0.7) mm across and 0.2–0.3 mm high, dissolving above into soredia-bearing soralia; and (2) laminal rugulae (and verrucae), these sparse to copious on lobe ridges, absent in intervening depressions, sometimes replaced by blocky, closely packed glebulae, at length dissolving above into diffuse soredia up to 30–40 μm across. Perforations sparse to many on upright lateral outgrowths of second-tier lobes, apparently lacking on lower surface of first-tier lobes, the opening usually > 0.2 mm across. Medullary ceiling white except darkening in vicinity of old ruptures in the lower surface. Lower surface mostly black, shiny, thin, easily torn, sharply winkled or folded. Apothecia rare, laminal, short stalked, the disc concave, pale brown to dark brown, the largest ones 2–3 mm across, usually aborting; ascospores ellipsoid, at maturity up to 6.0–6.2 × 4.0–4.2 μm. Pycnidia absent or sparse over upper surface; conidiospores dumbbell-shaped, 4.2–5.5 × 0.8–1.0 μm.

***Chemistry*:** Atranorin (cortex), physodic acid (major, constant), 3-hydroxyphysodic (submajor, present in most specimens), and 2′-*O*-methylphysodic (often trace, present in about half the specimens), vittatolic acid present or usually absent. Apinnatic acid present in 75% of samples studied. Spot tests: cortex K+ yellow, KC-, C-, PD-; medulla K- (except often K+ pink after 30 minutes!), KC + pink, C-, PD-.

***Etymology*:** *Dichroma* is from Greek *di-*, two, and *chroma*, surface colour. It refers to the characteristic two-toned upper cortex.

***Ecology*:** *Hypogymnia dichroma* appears to be primarily epiphytic on conifers, though a few saxicolous specimens have been examined. Different from other members of the *H. austerodes* group, it frequently occurs on acidic substrates apparently not subject to nutrient enrichment.

***Distribution*:** So far known only from western North America. Most common in boreal and oroboreal regions, ranging from Alaska and the Yukon south at least to southern British Columbia.

***Differentiation*:** *Hypogymnia dichroma* is readily distinguished from other sorediate members of the *H. austerodes* group by its thin, appressed lobes, low ridges (rugulae) aligned perpendicular to the main lobe axis, and tendency to dissolve directly into rather fine soredia up to 30–40 µm across. Well developed thalli of *H. dichroma* also generally have a two-toned appearance, the central portions being distinctly paler than the thallus periphery. *Hypogymnia verruculosa* also sometimes bears rugulae, but these are invariably accompanied by coarse, wart-like verrucae that disintegrate above into cortidia. Cortidia are never present in *H. dichroma. Hypogymnia protea* morph *disjuncta* can also be similar, differing in its at least partly loosely attached lobes and presence of apical and/or subapical soralopodia.

Notes. Typical material of *Hypogymnia dichroma* grades from shiny near the thallus periphery to dull toward the thallus centre. Somewhat challenging our circumscription of this species are specimens having a more or less uniformly shiny cortex. However, such material differs also in having rather well delimited soralia that rarely if ever become diffuse. This material is excluded from further consideration here, pending further study in the field.

The specimen pictured in Brodo et al. (2001: p. 347) as *Hypogymnia austerodes* (*Sharnoff & Sharnoff 1395.06*, CANL) has been examined by us, and can now be redetermined as *H. dichroma*. The photograph attributed to *H. austerodes* in McCune & Geiser (1997: p. 121; 2009: p. 145) also appears to represent this species.

Additional specimens examined with TLC. CANADA. ALBERTA: Banff National Park, Johnston's Canyon, by trail to Lower Falls, 400 m, 50°13′ N, 122° 52′ W, open mixed forest, on branch of *Picea*, 16 XI 2006, *A. R. Prince 63-228b* (H); Bow River Forest Preserve, 21.5 miles west of Turner Valley. 5000′, in lodgepole pine forest, 10 VI 1966, on log, *S.D. MacDonald s.n.* (CANL 22827). BRISTISH COLUMBIA: Alaska Highway, mile 33, in dry *Pinus* forest, on boulder, 15 VII 1976, *G.F. Otto 6083* (UBC); in Terminal Range, 3 km west of Muncho Lake, 1600 m, 58°57′N, 125°55′W, open forest on *Abies* trunk, 25 VII 1982, *T. Goward 82-1372* (CANL, UBC) ; Cassiar region, Howling Wolf Reserve, 35 miles north junction, 792 m, 59°27′N, 129°12′W, in black spruce bog, on dead branches, 7 VII 1973, *G.F. Otto 4400* (UBC); Tatshenshini River, 1 km southwest of confluence with Tats Creek, 200 m, 59°31′N, 137°27′W, in sheltered hollow on *Picea glauca* branch, 29 VII 1992, *T. Goward 92-1074* (UBC). YUKON: Haines Triangle, south of Haines Junction, near Million Dollar Campground, on dead *Picea*, 27 VI 1994, *S. & S. Sharnoff 1395.06* (CANL). U.S.A. ALASKA: Survey Pass Quad., near confluence of Alatna and Nahtuk rivers, 1000′, 67°25′N, 153°43′W, west facing slope with scattered spruce forest, on *Picea glauca* twigs, 21 VI 1973, *B.M. Murray 73-99* (ALA).

HYPOGYMNIA PROTEA Goward, T.Sprib. & Ahti *sp. nov.* **Fig. 1C**

MycoBank # MB 563096.

Thallus valde variabilis, plerumque sicut Hypogymnia austerodes *sed non adpressus, soredia laminalia ex pustulis corticalibus, non ex isidiis vel gymnidiis, evolventia. Acidum apinnaticum vulgo praesens. Fere semper crescit ad arbores.*

TYPE: CANADA. BRITISH COLUMBIA. Clearwater Valley, base of Battle Mtn, 1 km north of Philip Creek, 51°52′ N, 119°59′ W, on branch of *Picea*, 800 m, 2009, *T. Goward 09-737* with T. Spribille & C. Björk (holotype: UBC; isotypes: CANL, GZU, H).

Note: *Hypogymnia protea* is a strikingly variable species in which two apparently intergrading morphotypes can be recognized, i.e., morphs "disjuncta" (**Fig. 1C**) and "tessellata" (**Fig. 1F**). For further characterization, see **Table 2** and the diagnostic keys. Unless otherwise stated, the following description is based on *H. protea* morph "disjuncta", which serves as the type of the species.

***Diagnosis*:** *Thallus* loosely appressed to trailing, extremely variable, up to 5–8 (–13) cm across; lobes irregularly branched. First-tier lobes up to 2–3 (–4) mm wide, contiguous or loose, obscuring the substrate or sometimes not, at the tips weakly plane to concave in cross-section, inwards becoming convex. Second-tier lobes loosely overlapping or trailing, furnished with conspicuous apical and subapical soralopodia (see below), often massing into low side-on ridges and intervening depressions. Upper surface whitish to pastel green or blue, except chestnut brown in exposed sites, weakly shiny throughout, usually firm, except often readily abraded at lobe tips and in vicinity of soralia, with sparse or numerous (morph "tessellata") stress cracks, irregularly flecked with black mottling, usually with black borders as seen from above; soredia present or sometimes not (morph "tessellata"). Vegetative propagules mostly restricted to second-tier lobes, arising in five ontological contexts: (1) apical and/or subapical soralopodia, these copious to sparse (morph "tessellata"), capitate to mound-forming, in the latter case up to 0.8–1 mm across and 0.3–0.4 mm high (0.2–0.3 mm across in morph "tessellata"), at length disintegrating or bursting open above, and then giving rise respectively to expansion cortidia or to rim cortidia 20–25 μm across; (2) laminal micropustules, these copious to sparse or often (in morph "tessellata") lacking, arising on ridges alone, absent in intervening depressions, up to about 0.1 mm across, unevenly spaced, at length replaced by ultimately coalescent, soredia-bearing soralia, the soredia to 30–40 μm across; (3) laminal diffuse soralia, these often present toward thallus centre, bearing copious soredia. (4) laminal stress cracks and cortical flaps, these sparse or often (in morph "tessellata") copious, sometimes disintegrating along the margins and then giving rise sparse to copious cortidia; and (5) laminal schizidia, these absent or, if present (morph "tessellata"only), then usually sparse, patchy, restricted to to one side of the second-tier lobes, consisting of tiny cortical flakes up to 0.3–0.4 mm across. Perforations sparse or lacking on lower surface of first-tier lobes, sparse to copious along margins of second-tier lobes, the openings usually $>$ 0.2 mm across. Medullary ceiling white except darkening in the vicinity of old ruptures in the lower surface. Lower surface mostly black, shiny, thin, easily torn, sharply winkled or folded. Apothecia rare, laminal, short stalked, the disc concave, pale brown to dark brown, the largest ones 2–4 (–6) mm across, usually aborting; ascospores ellipsoid, at maturity up to (5.0–) 5.2–6.0 × 4.5–5.0 μm. Pycnidia absent or sparse over upper surface; conidiospores dumbbell-shaped, 4.5–5.0 × 1.0 μm.

Chemistry: Atranorin (cortex), physodic acid (major, constant), 3-hydroxyphysodic acid (submajor, usually present), 2′-*O*-methylphysodic acid (present to trace, in about half the samples studied), and vittatolic acid (present to trace, in about one third of samples studied). Apinnatic acid is abundant and found in most samples at detectable levels in TLC. Spot tests: cortex K+ yellow, KC-, C-, PD-; medulla K- (K+ pink after 30 minutes!), KC + pink, C-, PD-.

Etymology: *Protea* derives from Proteus, the Greek sea god renowned for his ability to change shape at will.

Ecology: Both of *Hypogymnia protea*'s morphotypes are apparently restricted to the trunks and branches of trees. In southern inland British Columbia *H. protea* is most frequent within the dripzones (sensu Goward & Arsenault 2000) of deciduous trees, especially *Populus*. In nutrient-rich localities, however, it often becomes established – especially on *Abies* and *Picea* – in habitats not associated with dripzones.

Distribution: So far known only from western North America. *Hypogymnia protea* occurs in inland regions from Alaska east to the Northwest Territories, and south at least to Montana. South of the Canadian-American border, however, this species becomes infrequent (C.R. Björk pers. comm., T. Spribille pers. obs.).

Differentiation: Within the *Hypogymnia austerodes* group, *H. protea* s. str. (= morph "disjuncta") is most reliably distinguished by its loosely attached, often partly trailing lobes, conspicuous apical and subapical soralopodia, and production of variously spaced micropustules at length giving rise to rounded soralia. Morph "tessellata" is also loosely attached, but has fewer, much smaller soralopodia, more numerous stress cracks, and overall a "tidier" appearance (**Fig. 1F**). When abraded, its lobe tips often open into the thallus interior – a phenomenon common also in *H. austerodes* s. lat., but rarely seen in morph "disjuncta". See **Table 2** for further points of distinction between these two morphotypes. Some forms of *H. dichroma* are morphologically similar, but have a more closely appressed thallus in which the rather loosely spaced soralia of *H. disjuncta* are replaced by tightly packed, elevated glebulae. See also the notes under *H. farinacea.*

Notes. While morphs ''disjuncta'' and ''tessellata'' appear to us to intergrade, we nevertheless wish to leave open the possibility that they will eventually be found to warrant recognition as separate species. For this reason we tie the type of *H. protea* to morph ''disjuncta''.

The specimen (*Goward 79-882* UBC) illustrated by Goward et al. (1994: p 59) as *H. austerodes* belongs to *H. protea* morph ''disjuncta''.

Additional specimens examined with TLC (morph ''disjuncta''). CANADA. BRITISH COLUMBIA: Tulsequah Valley, at confluence of Taku and Tulsequah Rivers, 150 m, 58°40′N, 133°35′W, conifer forest on branch in crown of *Picea sitchensis*, 10 VII 1982, *T. Goward 82-622* (UBC); Cariboo region, north of Vert Lake in Dog Creek area, 1080 m, 51°39′N, 122°11′W, branch of *Pseudotsuga*, 21 VII 1994, *T. Goward 94-601* (UBC); Clearwater Valley, 35 km north of Clearwater, Murtle Plateau, southeast of park road, 825 m, 51°58′N, 120°07′W, edge of forest clearing, on branch of *Picea*, 8 IV 2009, *T. Goward 09-10* (UBC); 26 km north of Clearwater Village, west of park road, 700 m, 51°52′N, 120°02′W, open mixed forest, on branch of *Picea*, 20 IV 2009, *T. Goward 09-54* (UBC); east of park road, 700 m, 51°52′N, 119°59′W, mixed forest, on branch of *Pseudotsuga*, 28 VII 2009, *T. Goward 09-660* (UBC); Prince George area, 50 km west of Highway 16, 800 m, 53°55′N, 122°45′W, branch of *Larix laricina*, 14 V 1980. *T. Goward 80-206* (UBC). U.S.A. MONTANA: Lake County, Jocko Canyon Road, 3600′, 47.180952N, 113.950217W, on wood of *Pseudotsuga*, 9 VI 2005, *T. Wheeler 851* (UBC).

Selected specimens examined with TLC (morph "tessellata"). CANADA. ALBERTA: Turner Valley area, 20 miles west-southwest of town, Sheep River, 5250′, 50°36′N, 114°45′W, *Picea glauca* woods on *Picea glauca*, 17 IV 1965, *C.D. Bird 11510* (CANL); 16 miles west of Marlboro on Highway 16, in *Picea mariana* mire, 53°33′N, 117°00′W, on branch of *Picea*, 4 IX 1969, *Brodo 15879* (CANL). BRITISH COLUMBIA: Clearwater Valley, 26 km north of Clearwater Village, west of park road, 700 m, 51°52′N, 120°01′W, open mixed forest, on branch of *Picea*, 19 IV 2009, *T. Goward 09-36B* (UBC); east of park road, 1000 m, 51°52′N, 119°59′W, mixed forest, on branch of *Picea*, 28 VII 2009, *T. Goward 09-657* (UBC); 750 m, 51°43′N, 119°59′W, on branch of *Picea*, 25 XI 2009, *T. Goward 09-738* (UBC); 35 km north of Clearwater, Murtle Plateau, southeast of park road, 825 m, 51°58′N, 120°07′W, edge of forest clearing, on branch of *Picea*, 8 IV 2009, *T. Goward 09-09A* (UBC).

HYPOGYMNIA SALSA Goward *sp. nov.* **Fig. 1D**

MycoBank # MB 563097.

Sicut Hypogymnia austerodes *sed non adpressa, soredia laminalia ex papillulis et/vel disintegratione corticis, non ex isidiis vel gymnidiis, evolventia et non sursum proliferantia. Arboricola.*

TYPE: U.S.A. ALASKA. Mt. Hayes Quadrangle. Upper Tanana River near the Gerstle River, 63°54′ N, 144°53′ W, lower branches of *Picea glauca*, 370 m, 23 VII 1965, *L. Viereck 7749A* (holotype: ALA; isotype: UBC).

***Diagnosis*:** Thallus loosely attached, moderately variable, up to 6–8 (–12) cm across; lobes irregularly branched. First-tier lobes up to 2.0 (–2.5) mm wide, loose, usually not entirely obscuring the substrate, at the tips weakly concave in cross-section to weakly convex, inwards becoming more strongly convex. Second-tier lobes loosely appressed or trailing, occasionally bearing inconspicuous apical soralopodia (see below), older thallus portions often massing into low symmetrical ridges and intervening depressions. Upper surface whitish to pastel green, brownish in exposed sites, weakly shiny throughout or occasionally dull toward thallus centre, cortex usually firm except often readily abraded near lobe tips, with occasional stress cracks, irregularly flecked with black mottling, with or without black borders as seen from above; sorediate. Vegetative propagules restricted to second-tier lobes, arising in three ontological contexts: (1) apical and marginal soralopodia, these sparse to copious, capitate to rim-forming, in the latter case up to 0.4 mm across (0.5–1.0 mm along long axis) and 0.2–0.3 mm high, at length dissolving above into soredia-bearing soralia, the marginal soralopodia borne at the tips of short, scarcely tapering lobes; (2) laminal micropustules, papillae and other irregularities of the cortical surface, these abundant but localized, arising over ridges and in intervening depressions, up to 0.05–0.10 mm across, closely spaced from the first, only gradually expanding outwards from the base, at length giving rise to soredia-bearing soralia, the soredia up to 20–30 μm in diameter; and (3) laminal diffuse soralia, these often well developed toward thallus centre, bearing copious diffuse soredia. Perforations sparse, inconspicuous, often arising on lower surface of first-tier lobes (check tips), also along margins of second-tier lobes. Medullary ceiling white except darkening in vicinity of old ruptures in the lower surface. Lower surface mostly black, shiny, thin, easily torn, sharply winkled or folded. Apothecia not seen. Pycnidia not seen.

Chemistry: Atranorin, physodic acid, 3-hydroxyphysodic acid, 2′-O-methylphysodic acid, and apinnatic acid. Spot tests: cortex K+ yellow, KC-, C-, PD-; medulla K-, KC + pink, C-, PD-.

Etymology: *Salsa* is from Latin, *salsus*, salted: a reference to the tiny, pale, nonclumping soredia spread diffusely over the upper surface.

Ecology: All specimens examined by us are from the lower branches of *Picea*, both in old spruce stands, and in mixed forests with *Populus*.

Distribution: So far known only from western subarctic North America, apparently rare and disjunct between western Alaska and the Mackenzie delta of the Northwest Territories. Further study is needed to confirm the species' distribution and rarity status.

Differentiation: *Hypogymnia salsa* is most reliably distinguished by its loosely attached lobes, minutely roughened upper surface often bearing tiny closely spaced papillae and micropustules less than 0.1 mm across, and its ultimately diffuse soredia up to 20–30 μm across. In the central portions of the thallus the soredia are diffuse. *Hypogymnia protea* morph "disjuncta" is superficially similar, but here the upper surface is smooth, not roughened, and the laminal soredia are larger, usually up to 30–40 μm. That species also often has trailing lobes and much more numerous (and conspicuous) soralopodia. For points of distinction with *H. austerodes*, see the discussion under that species.

Additional specimens examined. Canada. british columbia: Cassiar area, Pyramid Creek near Anvil Lake, 59°12′N, 129°40′W, on twigs of *Abies,* 462 m, 13 VII 1973, *G.F. Otto 4551* (h); Northwest Territories: Nahanni National Park, along Meilleur Creek, 61°15′N, 124°34′W, white spruce black cottonwood community, 1100′, 27 VI 1970, *G.W. Scotter 13038* (h), Floodplain near mouth of Prairie Creek, 61°16′N, 124°26′W, branch of *Picea*, 1300′, 14 VII 1976, *G.W. Scotter 23803* (h). U.S.A. alaska: Mt. Hayes Quadrangle. Tanana, 2.3 km upriver from Cummings Landing, 63°55′ N, 144°52′ W, lower branches of spruce trees, 370 m, 25 VII 1965, *L. A. Viereck 7767* (ala). Big Delta Quadrangle. Delta River floodplain, vicinity of Big Delta Airfield, 64°01′ N, 145°45′ W, dead white spruce branches, 360 m, 25 VI 1966, *L. A. Viereck 8009* (ala).

Hypogymnia verruculosa Goward *sp. nov.* **Fig. 1E**

MycoBank # MB 563098.

Sicut Hypogymnia austerodes sed soredia laminalia ex verruculis corticalibus, non ex isidiis vel gymnidiis, evolventia, tandem sursum proliferantes. Acidum apinnaticum vulgo praesens. Arboricola et terricola.

Type: Canada. yukon. Near Otter Falls, 61°04′ N, 136°59′ W, aspen – white spruce community, 2800 ft, 6 VIII 1972, *G.W. Scotter 20337* (holotype: canl).

Diagnosis: Thallus appressed, moderately variable, up to 5–10 (15) cm across; lobes irregularly branched. First-tier lobes up to 3.5–4.0 (–6) mm wide, contiguous, obscuring the substrate, at the tips weakly plane to concave in cross-section, inwards becoming convex. Second-tier lobes closely appressed, usually bearing at least some soralopodia (see below), older thallus portions massing into high, symmetrical ridges and intervening depressions. Upper surface whitish to pastel green in sheltered microsites, otherwise rich chestnut brown, weakly shiny to more often dull, especially toward thallus centre, cortex firm, with occasional stress cracks, irregularly flecked with black mottling, also often with black margins as seen from above; cortidiate, gymnidiate and/or sorediate. Vegetative propagules restricted to second-tier lobes, arising in two ontological contexts: (1) apical and/or subapical soralopodia, these sparse (sometimes lacking), mostly mound-forming, up to 0.5–1.5 mm across and 0.3 mm high, at length dissolving above into granular cortidia; (2) laminal verrucae, these sparse to copious, arising both over ridges and (to a lesser extent) in intervening depressions, up to 0.5–1.0 (–1.5) mm across and 0.5 mm high, usually closely spaced from the first, remaining discrete, at length disintegrating above into coarse granular cortidia up to (40–) 50–70 (–80) μm across, these soon further dissolving into coarse proliferating soredia that often become deeply piled where sheltered (check depressions). Perforations inconspicuous, rare over lower surface of first-tier lobes, also sometimes lateral along second-tier lobes, the openings mostly tiny, < 0.2 mm across. Medullary ceiling white except darkening in vicinity of old ruptures in the lower surface. Lower surface mostly black, shiny, thin, easily torn, sharply winkled or folded. Apothecia not seen. Pycnidia sparse to numerous over upper surface; conidiospores dumbell-shaped, 4.5–5.0 × 0.8 μm.

Chemistry: Atranorin (cortex), physodic acid (major, constant), 3-hydroxyphysodic acid (major, constant), apinnatic acid (major, constant), and 2′-O-methylphysodic acid (present to trace, occasionally absent). Spot tests: cortex K+ yellow, KC-, C-, PD-; medulla K-, KC + pink, C-, PD-.

Etymology: *Verruculosa* is from Latin *verrucula,* small wart, referring to the warty outgrowths characteristic of this species.

Ecology: On trunks and branches of conifers and nutrient-rich deciduous trees, also over boulders in areas of low snow pack. Known only from rather dry regions.

Distribution: So far known from rainshadow regions of inland western North America, from Alaska and the Yukon southward to southern British Columbia. Mostly at lower to middle forested elevations, especially south of the main limits of *H. austerodes* s. str.

Differentiation: *Hypogymnia verruculosa* is most reliably distinguished by its appressed habit, broad lobes (often > 4 mm diameter), frequent presence of pycnidia, and especially its coarse laminal verrucae that at length disintegrate above into granular cortidia 50–70 μm across. The cortidia, however, quickly dissolve into soredia, and hence need to be checked in the early stages of development. *Hypogymnia austerodes* s. str. is similar in general habit, but always bears at least some well spaced isidia and/or gymnidia and usually lacks well developed pycnidia.

Additional specimens examined. CANADA. ALBERTA: Jasper area, Snaring River. 13 VI 1966, *L. L. Kennedy s.n.* (CANL 55533). 1 mile W of Oldman River in Dutch Creek Valley, on boulder, 5000′, *C. D. Bird 15809* (CANL). BRITISH COLUMBIA: 10 km SSE of Tatla Lake, 51°49′N, 124°36′W, corticolous on *Picea* in open mature *Picea glauca* forest, 1050 m, 14 VII 1981, *T. Goward 81-1505* (UBC). Cariboo: Dog Creek area, 3 km west-northwest of village, 51°35′N, 122°16′W, on mossy rock, 720 m, 5 VII 1994, *T. Goward 94-445* (UBC); Lower Alkali Creek ("China Flats"), 51°43′N, 122°21′W, sheltered treed gully, on trunk of *Pseudotsuga*, 680 m, 13 VI 1994, *T. Goward 94-85* (UBC); Chilcotin Plateau: 7 km W of Satah Mtn, 52°23′N, 125°32′W, sheltered gully on trunk of leaning *Populus tremuloides*, 1275 m, 27 IX 1995, *T. Goward 95-1496* (UBC). U.S.A. ALASKA: Southeast Fairbanks Census Area: Fielding Lake, S of Delta Junction, 63°12′N, 145°39′W, on *Populus*, 17 VI 1994, *S. D. Sharnoff 1420.3* (CANL).

Hypogymnia farinacea Zopf

Hypogymnia farinacea is a widespread species of temperate latitudes. Originally described from Europe (Bitter 1901; Zopf 1907), it has since been reported also from Asia (Urbanavichus & Andreev 2010) and North and Central America (Louwhoff 2009). In western North America it is usually characterized as rare in the American Rocky Mountains (McCune & Geiser 2009), ranging from Wyoming (Eversman 1998) south to Arizona (Nash et al. 1998; McCune 2002a). Several Canadian specimens previously identified as *H. farinacea* have been examined during the course of this study, and all proved to be *H. protea* – as indicated, e.g., by the looser attachment, copious presence of soralopodia, fine laminal cortidia (30–40 μm diameter versus 60–70 μm in *H. farinacea*), and production of apinnatic acid (see also **Table 2**). It thus remains an open question whether *H. farinacea* actually occurs in western North America.

In eastern North America, this species was recently reported by Hinds & Hinds (1998, 2007) on the basis of a single specimen from Maine, collected by G.K. Merrill in 1914. This report likewise warrants checking.

Acknowledgments

We thank the curators of ALA, CANL, GZU and H for providing critical material in support of this study. Jack Elix is warmly thanked for performing HPLC on an isolectotype specimen of *H. austerodes.* Ed Berg, Karen Dillman and Karen McKeown kindly provided specimens from their personal herbaria, while Curtis Björk provided technical support throughout. The manuscript benefitted from comments by Curtis Björk and two anonymous reviewers. Special thanks to Tim Wheeler both for supplying the photos in Figure 1 and for preparing the figure itself.

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ms received Feb. 18, 2011; accepted Jan. 18, 2012.