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Lecanorales: Parmeliaceae

Cover image: *Parmelia saxatilis*, on maritime granite, Lamorna Cove, West Cornwall.

Revisions of British and Irish Lichens is a free-to-access serial publication under the auspices of the British Lichen Society, that charts changes in our understanding of the lichens and lichenicolous fungi of Great Britain and Ireland. Each volume will be devoted to a particular family (or group of families), and will include descriptions, keys, habitat and distribution data for all the species included. The maps are based on information from the BLS Lichen Database, that also includes data from the historical Mapping Scheme and the *Lichen Ireland* database. The choice of subject for each volume will depend on the extent of changes in classification for the families concerned, and the number of newly recognized species since previous treatments.

To date, accounts of lichens from our region have been published in book form. However, the time taken to compile new printed editions of the entire lichen biota of Britain and Ireland is extensive, and many parts are out-of-date even as they are published. Issuing updates as a serial electronic publication means that important changes in understanding of our lichens can be made available with a shorter delay. The accounts may also be compiled at intervals into complete printed accounts, as new editions of the *Lichens of Great Britain and Ireland*.

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Lecanorales: Parmeliaceae

including the genera *Alectoria*, *Allantoparmelia*, *Arctoparmelia*, *Brodoa*, *Bryoria*, *Cetraria*, *Cetrariella*, *Cetrelia*, *Cornicularia*, *Evernia*, *Flavocetraria*, *Flavoparmelia*, *Hypogymnia*, *Hypotrachyna*, *Imshaugia*, *Melanelia*, *Melanelixia*, *Melanohalea*, *Menegazzia*, *Montanelia*, *Nesolechia*, *Parmelia*, *Parmelina*, *Parmeliopsis*, *Parmotrema*, *Platismatia*, *Pleurosticta*, *Protoparmelia*, *Pseudephebe*, *Pseudevernia*, *Punctelia*, *Raesaenenia*, *Tuckermannopsis*, *Usnea*, *Vulpicida* and *Xanthoparmelia*.

by

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PARMELIACEAE F. Berchtold & J. Presl (1820)

Thallus foliose in most species, in some fruticose, filamentous or crustose; very rarely absent and then lichenicolous; corticate on both surfaces, sometimes with rhizoids underneath, pale grey to yellowish, green or brown to black, sometimes with pseudocyphellae; many species forming **soralia** or **isidia** and then frequently sterile. **Photobiont** trebouxoid or chlorococcoid. **Ascomata** apothecia, usually sessile on the thallus, rarely immersed or \pm stalked, laminal or marginal, with a usually persistent cupulate exciple. **Hamathecium** of sparingly branched paraphyses, the apices often pigmented and/or swollen. **Asci** *Lecanora* type, usually cylindric-clavate, the apex with a well-developed I+ blue apical cap and a more weakly I+ internal column. **Ascospores** aseptate, colourless or rarely brownish, sometimes with a distinct external sheath. **Conidiomata** pycnidia, frequent, immersed in the thallus. **Conidia** bacilliform to filiform. **Chemistry** very varied. **Ecology**: on bark and siliceous rocks, rarely on the ground and overgrowing vegetation.

The largest family of lichens, with around 2800 species occurring in a very broad range of habitats worldwide (Lücking *et al.* 2016). It is one of the most well-researched groups for phylogenetics, with much attention paid to generic limits. Unusually, several of the recent improvements in knowledge have led to reduction in numbers of genera. This account partly follows the major genus-focused treatment of Divakar *et al.* (2017), leading to the synonymy of *Cavernularia* with *Hypogymnia* that was previously proposed by Miadlikowska *et al.* (2011), and *Parmelinopsis* with *Hypotrachyna*. Their approach was partially adopted by Thell *et al.* (2018), and largely accepted by Wijayawardene *et al.* (2020). Additionally, Thell & Divakar (2022) argued that the revised generic circumscription of *Cetraria* and *Nephromopsis* proposed by Divakar *et al.* (2017) should be accepted as the alternative would be division into further new genera, and that arrangement is supported by characters of conidia and ascospores (Thell *et al.* 2009).

However, Thell *et al.* (2018) and Lücking (2019) argued against the strict application of temporal phylogenetics methodology for genus delimitation in the *Parmeliaceae*, which would have led to several further synonymies of genera accepted in edition 2 of this publication, with names that are familiar to all lichenologists in Britain and have important implications for conservation legislation. For pragmatic reasons, we therefore retain the genera *Cetrariella* and *Vulpicida* (included within *Cetraria* by Divakar *et al.* 2017), and *Flavocetraria* and *Tuckermannopsis* (included within *Nephromopsis*).

There are three genera of Parmeliaceae that are lichenicolous rather than lichenized (see Divakar *et al.* 2015). Two of these (*Nesolechia* and *Raesaenenia*) occur in our region. It is very unusual for lichenicolous fungi to parasitise other members of their own families, and these nutritional interactions deserve further research. In addition, species of *Protoparmelia* (also included in Parmeliaceae) appear initially to grow as a parasite of unrelated lichens but then develop independent thalli.

Literature:

Amo de Paz *et al.* (2011), Blanco *et al.* (2004b), Crespo *et al.* (2007, 2011, 2020), Divakar *et al.* (2015, 2017), Elix (1993), Elix & Hale (1987), Esslinger (1977, 1978), Grewe *et al.* (2020), Hawksworth *et al.* (2008), Lücking (2019), Mattsson & Wedin (1999), Nelsen *et al.* (2011), Peršoh & Rambold (2002), Pizarro *et al.* (2018), Thell *et al.* (2002, 2004, 2009, 2012, 2018), Thell & Divakar (2022), Thell & Moberg (2011), Wijayawardene *et al.* (2020).

1	Lichenized.....	2
	Lichenicolous.....	48
2(1)	Thallus crustose, rarely scurfy	<i>Protoparmelia</i>
	Thallus fruticose or filamentous.....	3
	Thallus foliose.....	12
3(2)	Thallus flattened, strap-shaped, distinctly dorsiventral (with differently coloured upper and lower surface); algae concentrated near the upper surface only	4
	Thallus ± terete or, if flattened, lower and upper sides ± concolorous	5
4(3)	Thallus green, sorediate; lower surface white, never black (see also <i>Ramalina lacera</i>)	<i>Evernia</i>
	Thallus grey, isidiate; lower surface at least partly black	<i>Pseudevernia</i>
5(3)	Thallus with a tough axial strand, not easily broken when branches are pulled	<i>Usnea</i>
	Thallus without a tough, axial strand (breaking cleanly when pulled apart)	6
6(5)	Thallus pale yellow to yellowish-green.....	7
	Thallus greyish, brown or brown-black.....	8
7(6)	Thallus ± filamentous, with distinct white ± elongate, often raised pseudocyphellae	<i>Alectoria</i>
	Thallus distinctly dorsiventrally flattened, ± erect, wrinkled and lacunose with wavy margins; pseudocyphellae on the lower surface only, ± inconspicuous and sunken	<i>Flavocetraria</i>
8(6)	Thallus hair-like, often decumbent or pendent, rarely erect (some <i>Bryoria</i> spp.)	9
	Thallus not hair-like, with hollow branches or dorsiventrally flattened lobes.....	11
9(8)	Thallus densely divergently branched, dark brown-black; forming a dense spreading strongly decumbent mat attached by spreading hapters; usually on rocks	<i>Pseudephebe</i>
	Thallus not densely branched, or if so then ± erect; pale to brown-black, mostly only attached at one end ; usually on trees or soil	10
10(9)	Thallus erect; pseudocyphellae conspicuous, white, flat or slightly raised (<i>Gowardia</i>).....	<i>Alectoria</i>
	Thallus erect or pendent; pseudocyphellae absent, or inconspicuous and sunken.....	<i>Bryoria</i>
11(8)	Thallus dark brown to black, forming compact firmly attached sparingly branched tufts on rocks, the branches <1 mm broad; apothecia terminal.....	<i>Cornicularia</i>
	Thallus olive-brown, fruticose to minutely foliose, forming richly branched tufts; branches >1 mm broad; apothecia laminal	<i>Cetraria</i>
12(2)	Thallus lobes olive to brown or blackish grey throughout	13
	Thallus lobes yellow-green, green to grey-green or whitish	25
13(12)	Thallus erect, ± tufted	14
	Thallus adnate to loosely overlapping	16
14(13)	Thallus lobes strap-shaped or <2 mm broad, soralia very rare; on soil	15
	Thallus lobes rounded, overlapping, with marginal soralia; on bark or rarely rock	<i>Tuckermannopsis</i>
15(14)	Medulla C-; conidia lemon-shaped.....	<i>Cetraria</i>
	Medulla C+ red; conidia wine-bottle shaped.....	<i>Cetrariella</i>

- 16(13) Rhizines absent, lobes convex, contorted and closely adpressed to the substratum *Allantoparmelia*
Rhizines present at least in the centre of the thallus, lobes loosely to closely attached to
the substratum 17
- 17(16) Thallus lobes with globose pycnidia along the margins *Cetrariella*
Thallus lobes with laminal pycnidia, or pycnidia absent 18
- 18(17) Cortex K+ yellow; thallus grey or brownish, with linear to reticulate pseudocyphellae *Parmelia*
Cortex K- (medulla rarely K+ yellow); thallus greenish to brown; pseudocyphellae punctiform
if present 20
- 20(19) Medulla Pd- (without lichen substances in British material); conidia cylindrical to fusiform 21
Medulla Pd+ yellow or red; if Pd- than with convex lobes and whitish punctiform
pseudocyphellae; conidia bifusiform *Melanelia*
- 21(18) Thallus lobes short and narrow, plane to convex; saxicolous *Montanelia*
Thallus lobes broad, plane to concave; mostly corticolous *Melanohalea*
- 22(18) On bark 23
On rock 24
- 23(22) Thallus olive green to olive brown; medulla K ± purple, KC+ red, Pd- *Melanelixia*
Thallus grey-green to brown-grey; medulla K+ red, KC-, Pd+ orange *Pleurosticta*
- 24(22) Cortex N+ blue-green; medulla K-, UV+ white (sometimes appearing so due to reflectance)
..... *Xanthoparmelia*
Cortex N-; medulla K ± purple, UV- *Melanelixia*
- 25(12) Thallus lobes inflated, hollow in section, lower surface without rhizines 26
Thallus lobes solid in section, flat or convex 27
- 26(25) Thallus without perforations on the upper surface *Hypogymnia*
Thallus with perforations on the upper surface *Menegazzia*
- 27(25) Thallus strap-like, foliose to fruticose in structure, usually with a single holdfast 28
Thallus usually with broad lobes, attached at various points on the undersurface 30
- 28(27) Thallus of erect foliose, dichotomously branched lobes; on the ground in montane moss-heaths
..... *Flavocetraria*
Thallus usually ± pendent, on bark, wood and rocks; if on the ground then not montane 29
- 29(28) Thallus green, sorediate; lower surface white, never black (see also *Ramalina lacera*) *Evernia*
Thallus grey, isidiate; lower surface at least partly black *Pseudevernia*
- 30(27) Thallus yellow, or at least with some yellow tinge; usnic acid present 31
Thallus green, grey, cream or white; usnic acid not present 37
- 31(30) Thallus bright cream-yellow, sometimes greenish when wet, foliose to subfruticose 32
Thallus yellow-grey to yellow-green; foliose, ± strongly appressed 33
- 32(31) Thallus intermediate between fruticose and foliose in structure, medulla pale, UV-;
on the ground *Flavocetraria*
Thallus ± foliose, medulla bright yellow, UV+ dark red; on bark or lignum *Vulpicida*

- 33(31) Medulla Pd⁻, UV⁺ white (divaricatic acid) *Parmeliopsis*
 Medulla Pd⁺ orange or rust-red, UV⁻ or UV⁺ vivid glaucous blue 34
- 34(33) Thallus strongly appressed, rosette-forming with narrow radiating convex lobes, medulla
 K⁻, UV⁺ vivid glaucous blue (alectoronic acid) *Arctoparmelia*
 Thallus weakly to strongly appressed, if strongly appressed then with flattened lobes; medulla
 K⁺ yellow, brown or red, UV⁻ 35
- 35(34) Thallus with broad lobes with discrete or pustular soralia; usually on bark *Flavoparmelia*
 Thallus with narrow or ± contorted lobes 36
- 36(35) Rhizines branched, often extending beyond lobe margins; on bark *Hypotrachyna*
 Rhizines unbranched, usually with a bare margin to the undersurface; on rock *Xanthoparmelia*
- 37(30) Pseudocyphellae present on upper surface of thallus, punctiform or elongate 38
 Pseudocyphellae absent 40
- 38(37) Pseudocyphellae elongate, sometimes forming reticulate patterns *Parmelia*
 Pseudocyphellae punctiform 39
- 39(38) Thallus lobes overlapping with wavy crisped margins, marginal soralia and sparse rhizines *Cetrelia*
 Lobes with soredia developing from laminal and marginal pseudocyphellae, with numerous
 rhizines *Punctelia*
- 40(37) Rhizines absent; thallus closely attached, rosette-forming, with narrow intertwined lobes;
 on rock *Brodoa*
 Rhizines present (at least in the older part of the thallus) 41
- 41(40) Thallus closely appressed to the substratum 42
 Thallus not closely appressed to the substratum, or with overlapping lobes 43
- 42(41) Thallus grey-white, the lower surface pale tan to white, medulla K⁺ bright yellow and UV⁻,
 densely isidiate *Imshaugia*
 Thallus pale grey or grey-blue, the lower surface dark brown to black, medulla K⁻ and
 UV⁺ glaucous white, with pustular laminal soralia *Parmeliopsis*
- 43(41) Medulla C⁺ red 44
 Medulla C⁻ 45
- 44(43) Thallus surface faintly maculate; lobes rounded at the margins, the axils rounded with marginal
 unbranched cilia *Parmelina*
 Thallus surface smooth; lobes usually ± truncate, sometimes upturned; axils rounded or not,
 marginal cilia branched if present *Hypotrachyna*
- 45(43) Lower surface strongly veined and wrinkled *Platismatia*
 Lower surface not strongly wrinkled 46
- 46(45) Lower surface pale tan to white *Pleurosticta*
 Lower surface dark brown to black 47
- 47(46) Thallus small (to ca 5 cm diam.) with lobes mostly <3 mm broad; medulla K⁻, PD⁻
 (*Parmelinopsis*) *Hypotrachyna*
 Thallus large (mostly to 15–20 cm diam.) with lobes at least 5 mm broad; medulla usually
 K⁺ yellow, Pd⁺ yellow, orange or red *Parmotrema*

- 48(1) Initially lichenicolous, but developing an independent crustose thallus..... *Protoparmelia*
Thallus not present, lichenicolous for the entire life-cycle..... 49
- 49(48) Ascomata elongate, 2–2.5 × 0.5–1.1 mm, convex, causing shiny blackish geniculate
deformations on *Bryoria* species..... *Raesaenenia*
Ascomata 0.15–0.3 (–0.45) mm diam., round with flat to convex red-brown to dark brown
discs, associated with contorted, gall-like, often bleached malformations of thalli of a broad
range of Parmeliaceae species..... *Nesolechia*

ALECTORIA Ach. (1809)

Thallus shrubby, erect, decumbent or pendent, greenish yellow or brown-black; branches generally terete and smooth, occasionally becoming compressed and striately ridged towards the base and axils, in one subspecies markedly expanded and dorsiventrally compressed. **Isidia** and **soredia** absent. **Pseudocyphellae** always present, conspicuous, fusiform, white, flat to markedly raised. **Photobiont** trebouxiod. **Ascomata** apothecia, lateral, rare. **Thalline margin** persistent, concolorous with the thallus. **Asci** clavate, thick-walled, 2- or 4-spored, *Lecanora*-type. **Ascospores** generally large, aseptate, ellipsoidal, colourless to brown, with a distinct colourless external sheath. **Conidiomata** pycnidia, black, globose, immersed to slightly erumpent. **Conidia** bacilliform to narrowly fusiform. **Chemistry**: usnic acid present in all but one species, orcinol and β -orcinol depsides frequent. **Ecology**: on rock, bark, lignum and over soil.

Readily separable from *Bryoria* and *Pseudephebe* by the characteristic chemistry as well as the abundance and structure of the pseudocyphellae, and also by apothecial characters. Some forms of *Ramalina chondrina* (Lecanorales: Ramalinaceae) can resemble an *Alectoria* but they have a cartilaginous subcortex and hook-tipped lobe ends. The genus is phylogenetically related to *Nodobryoria* (not present in Britain and Ireland) and *Pseudephebe*.

Literature:

Brodo & Hawksworth (1977), Divakar *et al.* (2017), Gilbert & Purvis (2009a), Halonen *et al.* (2009), Hawksworth (1972), McMullin *et al.* (2016), Myllys *et al.* (2014), Velmala & Myllys (2011).

- 1 Thallus pink-grey to pale grey-brown at base, dark grey-brown to grey-black towards the apices; medulla C+ red *nigricans*
Thallus uniformly pale yellow or yellowish green, sometimes blackened at the apices; medulla C- 2
- 2(1) Thallus branches with fine linear or dot-like pseudocyphellae 3
Thallus branches without pseudocyphellae *Bryoria capillaris*
- 3(2) Thallus pendent; on bark or rocks *sarmentosa* subsp. *sarmentosa*
Thallus ascending or prostrate; scrambling on low vegetation or over the ground 4
- 4(3) Thallus ascending; main stems \pm terete, usually <2.0 mm diam.; medulla KC-, UV- *ochroleuca*
Thallus sprawling/prostrate; main stems becoming dorsiventrally flattened and striately ridged, often >2.0 mm in width; medulla KC red or KC-, UV+ ice-blue *sarmentosa* subsp. *vexillifera*

Alectoria nigricans (Ach.) Nyl. (1861)

LC

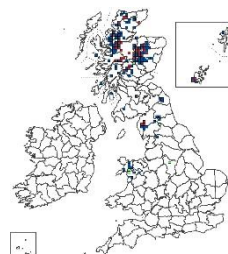
Gowardia nigricans (Ach.) Halonen, Myllys, Velmala & Hyvärinen (2009)

Thallus to 5 (–8) cm, erect, sometimes sprawling; branching moderate, ± anisotomic-dichotomous; branches to 1.5 mm diam., mostly terete, becoming tangled, compressed basally, pink-grey to pale grey-brown towards the base, dark grey-brown to sooty grey-black towards the apices, ± matt, smooth or pitted at the base; pseudocyphellae to 0.8 mm long, white, elliptical in outline, flat or slightly convex, usually conspicuous on thicker branches; soralia and apothecia unknown in Britain and Ireland. Cortex and medulla C+ red, K+ yellow, KC+ red, Pd+ yellow, UV– (alectorialic and barbatolic acids). **BLS 0039**.

Locally abundant in arctic-alpine moss-lichen heaths, mostly above 600 m. N. England, N. Wales, Scotland (Highlands).

A. nigricans is easily separable from other *Alectoria* species by thallus colour and chemistry, and it was placed in the segregate genus *Gowardia* by Halonen *et al.* (2009) and Myllys *et al.* (2014). *Gowardia* is a sister group to *Alectoria* in phylogenetic terms, but the combined taxon is also monophyletic and the generic separation was not supported by Divakar *et al.* (2017). Distinguishing the two groups at subgenus level might be the best compromise.

Bryoria bicolor differs from *A. nigricans* by the absence of conspicuous pseudocyphellae, the presence of short, lateral, perpendicular, spinulose branches and by being C–, K–.

**Alectoria ochroleuca** (Hoffm.) A. Massal. (1855)

VU(B) NR

Thallus to 8 (–12) cm, erect or becoming sprawling; branching moderate, ± anisotomic-dichotomous; branches 0.5–2 mm diam., the main stems terete, never strongly compressed, yellowish green to bright yellow, the apices often black or greenish black, ± matt; pseudocyphellae ca 1 × 0.1 mm, abundant, elliptical in outline, white. Apothecia unknown in Britain and Ireland. Pycnidia frequent, to 0.15 mm diam., ± apical, black. Medulla C–, CK+ yellow, K–, KC–, Pd–, UV– (diffractaic acid); cortex KC+ pale yellow (usnic acid). **BLS 0040**.

On the ground or among dwarf shrubs in *Racomitrium-Empetrum* communities, above ca 800 m; rare and decreasing. C. Scotland (Cairngorms).

Sometimes confused with *A. sarmentosa* subsp. *vexillifera*, which is prostrate, has compressed and ± flattened main stems, and a UV+ ice-blue medulla reacting usually KC+ red but never CK+ yellow.

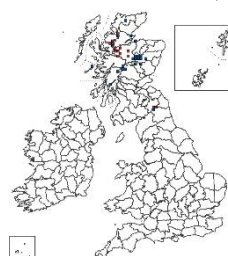
**Alectoria sarmentosa** (Ach.) Ach. (1810) subsp. *sarmentosa*

NT

Thallus to 20 (–80) cm, pendent; branches to 2.5 mm diam., terete, occasionally flattened at the axils and towards the base; branching moderate, isotomic-dichotomous, sparser towards the base which may become pitted, greenish grey, yellow to bright golden yellow, the apices usually concolorous or ± blackened, matt. Pseudocyphellae ca 1 × 0.2 mm, elongate, ± fusiform, flat or convex, often abundant and conspicuous. Soralia unknown Britain and Ireland. Apothecia to 5 mm diam., lateral; thalline margin concolorous with the thallus; disc orange-yellow to dark brown or black, matt or ± shiny; ascospores 25–40 × 12–25 µm. Medulla C–, CK–, K–, KC+ red or KC–, Pd–, UV+ ice-blue (alectoronic, squamatic and perhaps α-collatolic acids); cortex KC+ pale yellow (usnic acid). **BLS 0041**.

On *Pinus* bark and lignum, and old *Betula*, in relict Caledonian woodlands, rarely on rock. N.E. England (Northumberland), Scotland (Highlands).

Thin-branched morphs may resemble *Usnea* species, but thalli do not have the tough internal axial strand typical of that genus.

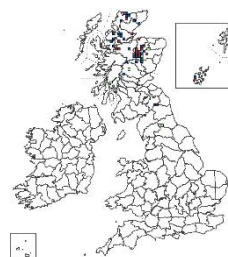
**Alectoria sarmentosa** subsp. *vexillifera* (Nyl.) D. Hawksw. (1970)

Nb

Differs from subsp. *sarmentosa* in that the thallus is prostrate. The branches are up to 8 mm broad, often markedly flattened, expanded, striately ridged and pitted. The thallus base degenerates and is then supported by hapters attached to surrounding vegetation. **BLS 0042**.

Decumbent over low vegetation in montane areas, to 1100 m; also rare on coastal sand/shingle in N.E. Scotland. N.E. England (Northumberland), Scotland (Highlands).

Subsp. *vexillifera* varies considerably in the degree of flattening and width of the main branches and is sometimes difficult to separate from subsp. *sarmentosa*, with which it intergrades in some parts of Europe, including in our region. Molecular studies (Myllys *et al.* 2014, McMullin *et al.* 2016) have not demonstrated conclusively that the two subspecies are phylogenetically distinct, and there is doubt that North American populations identified as either subspecies are equivalent to the European taxa.



ALLANTOPARMELIA (Vain.) Essl. (1978)

Thallus foliose, black to dark olive or yellow-brown, closely appressed, sometimes appearing crustose, attached to the substratum by irregular peg-like cortical outgrowths; rhizines absent; lobes convex, dorsiventrally flattened, corticate on both sides. **Upper surface** without pseudocyphellae, soredia or isidia. **Cortex** formed from hyphae perpendicular to the surface, K-, N-; upper and lower cortex similar in structure. **Photobiont** chlorococcoid. **Ascomata** apothecia, laminal, sessile; disc brown-black. **Thalline margin** present. **Hymenium** colourless. **Asci** 8-spored, *Lecanora*-type. **Ascospores** colourless, ellipsoidal to globose, aseptate. **Conidiomata** pycnidia, ± immersed in the thallus. **Conidia** colourless, bifusiform to bacilliform or slightly clavate. **Chemistry**: 2 benzyl ester depsidones unknown elsewhere in the foliose Parmeliaceae. **Ecology**: on exposed, siliceous rock.

The genus is chemically distinct from *Hypogymnia* and *Brodoa*, both of which have atranorin in the upper cortex. Other species of brown Parmeliaceae have thalli that are not so closely appressed to the substratum, with the lower surface with rhizines at least in part. Its phylogenetic placement within Parmeliaceae remains uncertain.

There is only one species known from Britain and Ireland.

Literature:

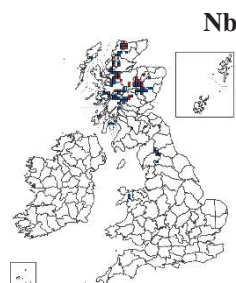
Divakar *et al.* (2015), Duke & Purvis (2009a), Esslinger (1978), Westberg & Thell (2011a).

Allantoparmelia alpicola (Th. Fr.) Essl. (1978)

Thallus to 6 cm diam., forming rosettes or irregularly spreading, closely appressed; lobes 0.2–1 mm broad, convex, elongate, somewhat gnarled, contiguous, often overlapping and entangled (particularly in older parts), at times so tightly compacted as to appear crustose towards the centre; upper surface dark brown to black, grey-black, rarely dark olive; soralia and isidia absent; lower surface black, ± pleated; rhizines absent but peg-like outgrowths occasionally present. Apothecia frequent; disc to 5 mm diam.; margin entire, rarely crenate. Ascospores $7.5\text{--}10 \times 5\text{--}7 \mu\text{m}$. Conidia $4.5\text{--}6 \times ca 1 \mu\text{m}$. Medulla C+ rose-red, K+ yellow, KC+ red, Pd+ bright yellow, UV- (alectorialic and barbatolic acids). **BLS 0043**.

On exposed siliceous boulders in montane situations, usually above 700 m. Locally abundant in Scotland, less frequent in N. England (Cumbria, Durham, Northumberland) and Wales (Snowdonia).

Distinguished by the dark colour, absence of rhizines and Pd+ bright yellow reaction; in time specimens stain paper red-brown in the herbarium due to the presence of alectorialic acid. *Melanelia stygia* has rhizines and pseudocyphellae and a Pd+ rust-red or Pd- medulla. *Brodoa intestiniformis* has a Pd+ rust-red medulla (fumarprotocetraric acid).



ARCTOPARMELIA Hale (1986)

Thallus foliose, closely appressed, dull grey to greenish-yellow, often pruinose, corticate on both sides; **lower surface** white to pale brown, finely pubescent, attached by rhizines. **Rhizines** unbranched, sparse. **Cortex** composed of isodiametric cells, without pseudocyphellae. **Photobiont** trebouxiod. **Soralia** present (may be absent in non-British or Irish species). **Ascomata** apothecia, laminal, sessile; **disc** red-brown. **Thalline margin** persistent, concolorous with the thallus. **True exciple** visible only in section, colourless. **Hymenium** colourless, I+ blue. **Hypothecium** colourless. **Hamathecium** of paraphyses, sparsely branched, apices somewhat swollen, often pigmented. **Asci** clavate, 8-spored, *Lecanora*-type. **Ascospores** colourless, aseptate, ellipsoidal to spherical, without an external sheath. **Chemistry**: cortex with atranorin, usnic acid, medulla orcinol and β -orcinol depsidones, particularly alectoronic acid. **Ecology**: on siliceous rocks, rarely on wood in exposed situations.

Some species of *Xanthoparmelia* are very similar to *Arctoparmelia* but they lack alectoronic acid (medulla UV+ glaucous blue). However, it is phylogenetically distant from that genus, and groups within the hypogymnioid clade (Divakar *et al.* 2015).

Literature:

Divakar *et al.* (2015), Duke (2009), Hale (1986a), Moberg & Thell (2011a).

Arctoparmelia incurva (Pers.) Hale (1986)

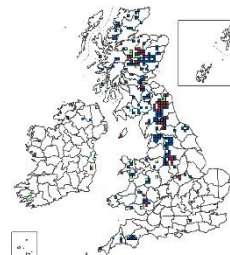
Thallus 0.5–2 cm diam., often coalescing to form much larger thalli, very closely appressed, the inner part often \pm degenerating; lobes narrow, to 3 (–4) mm broad, radiating, intricate, not overlapping, markedly convex; upper surface dull yellow-grey, becoming darker grey-yellow at the centre; soralia 2–4 mm diam., on the ends of smaller, inner lobes within the thallus, globular, scattered; lower surface pale, finely pubescent; rhizines sparse, dark, short, aseptate. Apothecia rare; disc brown. Medulla and soralia C–, K–, KC+ pink, Pd+ rust-red or Pd–, UV+ vivid glaucous blue (alectoronic, sometimes also α -collatolic and/or protocetraric acids); cortex KC+ yellow (usnic acid). There is considerable variation in the protocetraric acid content; in some populations it is absent, in others it is predominant. **BLS 1000**.

On well-lit siliceous rocks, very rarely on wood, acid pollution-tolerant; rather local. Upland Britain, from W. Cornwall to Sutherland, a few scattered records in Ireland, with the range expanding on man-made substrata during the era of high sulphur dioxide pollution. There is a solitary record from S.E. England on imported stone.

Arctoparmelia incurva resembles *Xanthoparmelia mougeotii* which differs in the flatter lobes, laminal, more flattened, circular soralia, the medulla which is K+ yellow→red, UV–, and the smooth shiny cortex. *Parmeliopsis ambigua* has few or no rhizines, spreading soralia and the medulla is K–, Pd–, UV–. The similar *A. centrifuga* (L.) Hale (1986), which has been erroneously reported from Scotland, lacks soralia and usually has well-developed apothecia.

Host to the plurivorous *Lichenocodium erodens* M.S. Christ. & D. Hawksw. (1977).

LC



BRODOA Goward (1986)

Thallus foliose to subfruticose, closely appressed to cushion-forming. Lobes narrow, stiff, swollen, solid, contiguous to overlapping. **Upper surface** pale grey to nearly black, shiny, convex, soredia and isidia lacking. **Lower surface** dark, wrinkled, without rhizines. **Photobiont** trebouxiod. **Medulla** white throughout. **Upper cortex** composed of hyphal tissue, covered in an epinecral layer. **Lower cortex** of hyphal tissue, without an epinecral layer. **Ascomata** apothecia, laminal, sessile. **Thalline**

margin well-developed, persistent. **Disc** concave, to 5 mm diam. **Asci** clavate, 8-spored; apex strongly thickened with an I+ blue apical dome, *Lecanora*-type. **Ascospores** aseptate, ellipsoidal, colourless. **Conidiomata** pycnidia, abundant, black, immersed in the upper cortex. **Conidia** fusiform. **Chemistry**: β -depsides (atranorin and chloratranorin) in the upper cortex and orcinol and β -orcinol depsidones in the medulla. **Ecology**: on siliceous rocks.

There are two species, both arctic-alpine in the N. Hemisphere. Only one occurs in our region. *Hypogymnia* has hollow lobes, usually with soralia; *Menegazzia* has lobes perforate on the upper or lower surface; *Allantoparmelia* has a brown upper surface and differs chemically in lacking fumarprotocetraric acid and atranorin. *Brodoa* is a sister group to *Hypogymnia* and *Pseudevernia*.

Literature:

Gilbert (2009a), Thell & Westberg (2011).

Brodoa intestiniformis (Vill.) Goward (1987)

Thallus to 5 cm diam., closely attached, forming rosettes or irregularly spreading; lobes narrow, 0.5–1 mm broad, \pm convex, nodular-uneven, contiguous, overlapping, often narrower and ascending towards the centre; upper surface pale grey, tinged brown especially towards the apices, shiny; lower surface black. Apothecia rare, to 8 mm diam.; thalline margin often irregular and sub-lobulate. Pycnidia numerous. Cortex K+ yellow (atranorin); medulla C-, K-, KC-, Pd+ rust-red, UV- (fumarprotocetraric acid). **BLS 0581**.

On exposed siliceous boulders above 900 m; very rare. Scotland (E. Cairngorms).

The centre of the thallus often has somewhat flattened decumbent branching, and \pm unoriented finger-like lobes. It can be confused in the field with small specimens of *Allantoparmelia alpicola* (medulla KC+ red, Pd+ bright yellow). The other species, *B. oroartica* (Krog) Goward (1987) which contains physodic acid (medulla UV+ blue-white), could also occur in the Scottish Highlands.



BRYORIA Brodo & D. Hawksw. (1977)

Thallus shrubby, erect, decumbent or pendent, dark brown to pale greyish brown; branches \pm terete and smooth, hair-like, occasionally becoming flattened and pitted towards the base, with or without lateral spinules; branching aniso- or isotomic dichotomous. **Soralia** frequent, tuberculate or fissure-like. **Pseudocyphellae** present or absent, usually inconspicuous. **Cortex** composed of cells with elongate lumina. **Photobiont** trebouxoid. **Ascomata** apothecia, lateral, very rare. **Thalline margin** persistent to excluded, concolorous with the thallus. **Asci** clavate, thick-walled, *Lecanora*-type, (6-) 8-spored. **Ascospores** aseptate, ellipsoidal, colourless. **Conidiomata** pycnidia, usually rare. **Conidia** minute, cylindrical to fusiform. **Chemistry**: usnic acid absent, atranorin, chloratranorin, alectorialic and barbatolic acid frequent, β -orcinol depsidones (fumarprotocetraric, norstictic acids) predominating or sometimes absent. To observe some of the Pd and K reactions the filter paper method must be used (see glossary). **Ecology**: calcifuge, in saxicolous, corticolous and terricolous habitats.

Distinguished from *Alectoria*, *Cornicularia*, and *Pseudephebe*, even in the absence of apothecia, by the characteristic chemistry, and the scarce, inconspicuous pseudocyphellae. The pendulous species of the *B. fuscescens* complex are sometimes host to *Raesenenia huuskonenii* (syn. *Phacopsis huuskonenii*, *Protousnea huuskonenii*), the development of which gives the thallus a shiny black 'dog-leg' appearance.

The phylogeny of *Bryoria* has been addressed in several papers since the publication of edition 2 of this volume, notably by Myllys *et al.* (2011b, 2014) and Velmala *et al.* (2014). Species concepts in the *B. fuscescens* complex have been studied by Boluda *et al.* (2015, 2019). This research has highlighted a lack of congruence between phenotypic and genotypic information for the genus, suggesting a complex evolutionary pattern that has not yet resolved into multiple distinct species. The eleven morphotaxa recognized within this group were therefore subsumed into four species, three of which are cryptic in morphological terms (and do not occur in Great Britain and Ireland).

Literature:

Boluda *et al.* (2015, 2019), Brodo & Hawksworth (1977), Myllys *et al.* (2011b, c, 2014), Velmala *et al.* (2014).

1	Lateral spinules (fibrils) frequent; thallus erect or prostrate	2
	Lateral spinules usually absent or sparse; thallus pendent or prostrate	7
2(1)	Apices usually paler than the base of the thallus	3
	Apices \pm concolorous with the base of the thallus	5
3(2)	Soralia present, with tufts of spinules; medulla and soralia Pd–	<i>smithii</i>
	Soralia absent; medulla Pd+ red (fumarprotocetraric acid)	4
4(3)	Thallus with infrequent branching; lateral spinules and ultimate branches attenuated and hair-like	<i>tenuis</i>
	Thallus densely branched; lateral spinules and ultimate branches with blunt ends	<i>bicolor</i>
5(2)	Thallus K+ yellow, KC+ red (barbatolic and alectorialic acids); on rock	<i>nadvornikiana</i>
	Thallus K–, KC– (fumarprotocetraric acid only); on trees or on the ground	6
6(5)	Soralia present, with tufts of spinules; on trees	<i>furcellata</i>
	Soralia absent; on the ground (probably extinct).....	<i>nitidula</i>
7(1)	Thallus K+ yellow, KC+ red.....	<i>capillaris</i>
	Thallus K–, KC–.....	<i>fuscescens</i>

***Bryoria bicolor* (Ehrh.) Brodo & D. Hawksw. (1977)**

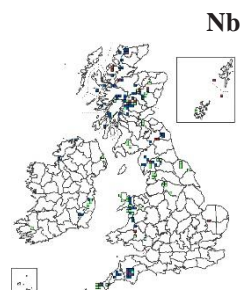
Thallus to 4 (-10) cm, erect, rarely decumbent, forming densely branched, dark cushions; branches 0.2-0.7 mm diam., terete, occasionally compressed towards the base; branching isotomic- to anisotomic-dichotomous; basal branches black or brownish black, the apices olive-grey to pale brown, shiny, blunt; lateral spinules 1.5-5 mm, numerous, with constricted bases, arising at right angles from main stems, often bow-like, usually unbranched; pseudocypbellae absent; soralia absent, but soredia occasionally present at ends of broken branches. Apothecia unknown in British material. Medulla C–, K–, KC–, Pd+ red (often patchy) (fumarprotocetraric acid). **BLS 0188.**

Amongst mosses, sometimes on soil or rock in hilly areas; local and decreasing. N. & W. Britain (one record in E. Anglia), scattered in Ireland.

Distinguished from *B. smithii* by the lack of soralia and associated clusters of spinules, and the Pd+ red medullary reaction, and from *Alectoria nigricans* by the smaller size, absence of conspicuous pseudocypbellae, presence of short lateral perpendicular spinulose branches and by being C– and K–.

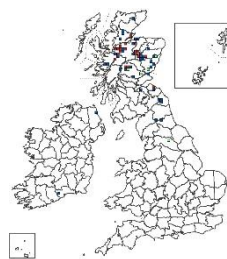
***Bryoria capillaris* (Ach.) Brodo & D. Hawksw. (1977)**

Thallus to 10 (-30) cm, pendent, rarely prostrate, the base often not persistent, often fragmenting with black and colourless areas; branches 0.3–0.5 mm diam., terete or compressed at the axils, abundant;



Nb

branching irregular isotomic-dichotomous, greyish white to pale to dark brown; true lateral spinules \pm absent; pseudocyphellae 0.1–0.25 mm, oval in outline, inconspicuous; soralia to 0.5 mm diam., mainly tuberculate, abundant to rare, or absent. Apothecia and pycnidia not observed in British material. Medulla C+ red or C–, K+ yellow, KC+ red, Pd+ yellow (barbatolic and alectorialic acids); soralia Pd+ orange-red (fumarprotocetraric acid). **BLS 0189.**



On conifers and *Betula* bark in relict pinewoods, mainly on twigs; also on exposed *Betula* and *Fagus* in S.E. Scotland (E. Lothian); rare but locally abundant. C. & E. Scotland; also in Ireland.

Exhibits considerable variation in colour and abundance of soralia. Distinguished from most other British species by not being K– and KC–. *B. nadvornikiana* which is KC+ red, C+ red has spinulose lateral branches and dark main stems.

Along with several other species, *B. capillaris* was included in a broad concept of *B. fuscescens* by Boluda *et al.* (2019), but the chemical distinction is consistent and the synonymy has some implications for recording in Britain and Ireland.

There is a single report of *Raesaenenia huuskonenii* (q.v.) as a parasite of this species.



Bryoria branching types. Left: anisotomic (*B. bicolor*). Right: isotomic (*B. fuscescens*). Bar = 15 mm.

***Bryoria furcellata* (Fr.) Brodo & D. Hawksw. (1977)**

Thallus 3–5 (–12) cm, tufted; branches 0.3–0.5 mm diam., terete, sometimes compressed towards the base; branching regularly isotomic-dichotomous, pale to dark brown to black, \pm shiny; lateral spinules usually present, occasionally abundant; pseudocyphellae absent; soralia 0.3–1 mm in length, white, usually abundant, oval to fusiform in outline, grooved, sometimes slightly raised, becoming covered with tufts of spinules 0.5–2.5 mm in length. Cortex, medulla and soralia C–, K–, KC–, Pd+ red (fumarprotocetraric acid). **BLS 0191.**

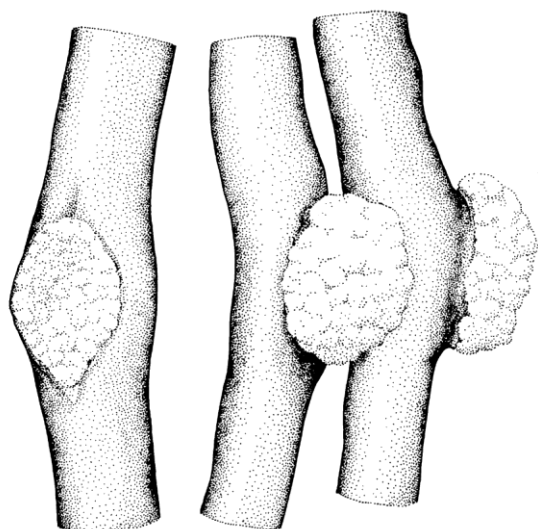
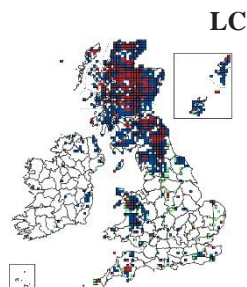
On bark and lignum of *Pinus* trunks, twigs of *Betula*, old *Calluna* and fence posts in a few relict pine woodlands; rare. Scotland (Easternness: Glen Affric, Glen Strathfarrar, Glen Moriston, Abernethy Forest).

A well-delimited species, characterized by the uniform pale brown \pm shiny tufted thallus, the short perpendicular lateral spinules and the soralia, which develop tufts of spinules. *B. smithii*, which shares this last feature, has paler apices, lacks detectable lichen products, has a different ecology and is south-western in the British Isles.



Bryoria fuscescens (Gyeln.) Brodo & D. Hawksw. (1977)*Bryoria chalybeiformis* (L.) Brodo & D. Hawksw. (1977)*Bryoria implexa* (Hoffm.) Brodo & D. Hawksw. (1977)*Bryoria lanestris* (Ach.) Brodo & D. Hawksw. (1977)*Bryoria subcana* (Nyl. ex Stizenb.) Brodo & D. Hawksw. (1977)

Thallus 5–15 (–30) cm, pendent or prostrate; branches to 0.5 (–2) mm diam., terete, becoming compressed towards the base and axils, occasionally contorted or pitted; branching irregularly isotomic-dichotomous, pale grey to dark brown, rarely blackish, the basal parts usually paler or concolorous with the apices; fragmented black regions occasionally present, ± matt; lateral spinules absent, pseudocypbellae absent or inconspicuous; soralia to 0.75 mm diam., abundant to scarce, rarely absent, tuberculate or fissure-like. Apothecia very rare; disc 1–1.5 mm diam., brown to dark brown. Thallus K+ yellow to orange-red or K–, KC+ red, Pd+ red or Pd–; medulla Pd+ red or Pd–; soralia C–, K–, KC–, Pd+ red (fumarprotocetic acid). **BLS 0192**.



Bryoria soralium types. Left: fissural; centre and right: tuberculate.

On acid-barked trees, siliceous rocks, amongst mosses, on walls and worked timber; common in hilly areas but decreasing. Throughout Britain and Ireland, but much commoner in the north and west. Rapidly declining in areas with even slightly elevated ammonia pollution.

The commonest species of the genus in the Britain and Ireland. Very variable, becoming contorted and spinulose in exposed situations, but generally easily recognizable by the tendency to have a pale base, fissure-like as well as tubercle-like soralia, the matt surface and smoky-brown colour; the soralia are always Pd+ red, but the thallus can be Pd+ or Pd–.

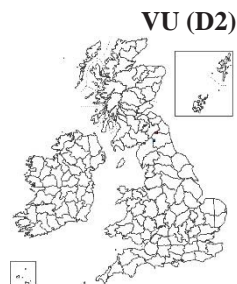
Several semi-cryptic morphotypes were accepted as distinct species by Brodo & Hawksworth (1977) and in the second edition of this publication, but Boluda *et al.* (2015, 2019) have shown that these do not correspond to phylogenetic units. *B. capillaris* was distinguished primarily by a K+ yellow, KC+ red medulla; *B. chalybeiformis* by relatively broad main stems with a PD– medulla; *B. implexa* by the production of norstictic acid (K+ yellow to orange-red); *B. lanestris* by the dark and very narrow flexuous stems; and *B. subcana* by the paler grey-green to whitish grey thallus.

The principal host of *Raesaenenia huuskonenii*, seen as black ‘dog-legs’ in the branches. Also host to *Lichenocodium erodens*, *L. usneae* (Anzi) D. Hawksw. (1977) and *Lichenostigma maureri* Hafellner (1983).

Bryoria nadvornikiana (Gyeln.) Brodo & D. Hawksw. (1977)

Thallus 5–15 cm, erect, becoming pendent; branches 0.2–0.3 mm diam., terete or rarely ± compressed at the axils; branching isotomic-dichotomous towards the base, anisotomic-dichotomous towards the apices; basal branches black; apical branches pale greyish green to pale brown or olivaceous brown; lateral spinules arising at right angles, frequent; pseudocypbellae absent; soralia, apothecia and pycnidia not observed in British material. Medulla C+ pink or C–, K+ yellow, KC+ red, Pd+ orange-red (barbatolic and alectorialic acids). **BLS 0195**.

Known only from a few sandstone crags, where it is associated with *Usnea dasopoga*. N. England (Northumberland-Cumbria border).



Only this species and *B. capillaris* (sometimes regarded as a chemotype of *B. fuscescens*) react KC+ red and K+ yellow; the latter lacks lateral spinules and black basal branches. This chemistry is shared by the montane, terricolous *Alectoria nigricans*, which differs in having conspicuous pseudocyphellae.

Bryoria nitidula (Th. Fr.) Brodo & D. Hawksw. (1977)

NE

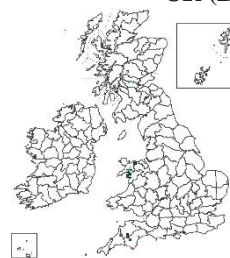
Thallus to 5 (–8) cm, erect, sometimes decumbent, dying away at the base; branches 0.5–0.8 mm diam., terete, shiny, dark brown to black; branching anisotomic-dichotomous; basal branches black; apical branches pale greyish green to pale brown or olivaceous brown; lateral spinules arising sparsely from main stems, concolorous with the thallus; pseudocyphellae and soralia absent. Apothecia and pycnidia unknown. Cortex and medulla C–, K–, KC–, Pd+ orange-red (fumarprotocetraric acid). **BLS 0196.**

Characteristic of arctic and subarctic heaths, particularly of ‘snow-patch’ communities. Scotland (Cairngorms). Collected on two separate occasions in the 19th century; probably extinct in our region. The provenance of British material is considered doubtful.

Bryoria smithii (Du Rietz) Brodo & D. Hawksw. (1977)

CR (B)

Thallus 4–7 (–12) cm, decumbent; branches *ca* 1 mm diam., frequent, terete or slightly compressed towards the base, frequently with depressions; branching isotomic-dichotomous, the basal branches dying away, dark brown to black, the apices paler, olivaceous to pale brown, exceptionally concolorous with the main stems; lateral spinules 2–7 mm long with slightly constricted bases, numerous, arising at right angles to the main stems, frequently bow-like; soralia present, arising from pseudocyphellae, grooved, concave to flat; soredia often sparse, mixed with short spinules arising in tufts from the soralia. Apothecia and pycnidia unknown. Medulla and soralia C–, K–, KC–, Pd– (lichen products not detected by TLC). **BLS 0198.**



On ancient trees of *Quercus* in sheltered but rather well-lit situations, occasionally on boulders; very rare. S.W. England (Devon, Dartmoor). Formerly collected in N. Wales (Merioneth) & S.C. Scotland (Perthshire) but probably extinct there, though potentially overlooked on moorland boulders.

A well-defined species, characterized by its soralia mixed with short spinules and its Pd– reaction; it most resembles *B. bicolor*, which lacks soralia, has a medulla which is Pd+ red, and is rarely on trees (except on Dartmoor). See also *B. furcellata*.

Bryoria tenuis (A. E. Dahl) Brodo & D. Hawksw. (1977)

Nb

Thallus erect to decumbent or subpendulous, 4–6 cm long, branching infrequent, isotomic-dichotomous towards the base, becoming anisotomic-dichotomous towards the apices, angles between the branches usually acute, branches terete, of uniform diameter, occasionally slightly compressed towards the base, to 0.4 mm diam., ultimate branches and lateral spinules attenuated and thread-like; base becoming black, apical branches pale brown to brown, paler than the base; some lateral spinules at right angles to the main stem, pseudocyphellae sparse to absent, grooved, dark, soralia lacking. Inner cortex and medulla C–, K–, KC–, Pd+ red at least in part (fumarprotocetraric acid). **BLS 2331.**



Growing among other fruticose lichens on an exposed syenite tor at around 700 m in N. Scotland (Ben Loyal); very rare, but recently refound in the same locality.

CETRARIA Ach. (1803)

Thallus dorsiventral, either foliose, ± loosely appressed with the lobe-margins often ascending and sometimes forming rosettes, or shrubby and erect, the lobes often channelled, sometimes ± tubular, rarely flat, sometimes with conspicuous spine-like projections, forming tufts; dark brown, olivaceous, occasionally grey-green or yellowish. **Cortex** 1- or 2-layered, particularly the lower cortex, cells

thick-walled; an external layer of thick-walled hyphae mostly overlying a more or less thin layer of periclinally arranged hyphae. **Medulla** white or bright yellow. **Pseudocypbellae** often present on lower surface, or marginal. **Rhizines** absent or sparse on the lower surface. **Soralia** rare. **Photobiont** trebouxoid or chlorococcoid. **Ascomata** apothecia, \pm marginal, often obliquely attached, the margin sometimes crenulate. **Thalline margin** present, often incurved. **Epithecium** red-brown to dark brown. **Hymenium** I+ blue. **Hypothecium** colourless. **Hamathecium** of paraphyses, usually straight, sparsely branched, the apices swollen. **Asci** 8-spored, narrowly clavate; tholus moderately large, with an apical ring structure, ocular chamber conical with a narrow to broad beak; *Lecanora*-type. **Ascospores** colourless, aseptate, ellipsoidal to subglobose. **Conidiomata** pycnidia; ostiole blackened, laminal or at ends of marginal projections; wall two-layered, colourless or black, the outer layer usually thin (*ca* 5 μ m thick) with cortical tissue beneath. **Conidia** colourless, cylindrical, bottle-shaped, crescent-shaped or lemon-shaped. **Chemistry**: β -orcinol depsidones (fumarprotocetraric, norstictic, gyrophoric, hiascinic acids) and fatty acids (lichesterinic, protolichesterinic acids), usnic acid and pulvinic acid derivatives in some species. **Ecology**: corticolous, saxicolous (non-calcareous), soil.

Separated from other cetrarioid genera mainly on tholus structure (small apical body and ring structure) and on the oblong lemon-shaped conidia. *Tuckermannopsis* lacks rhizines and pseudocypbellae and *Cornicularia* differs in being firmly attached to its substratum, being erect, sparsely branched and usually with abundant apical apothecia.

Divakar *et al.* (2017) considered that *Cetrariella* and *Vulpicida* should be placed into synonymy with *Cetraria*, primarily on the basis of evolutionary age but also supported by conidial and ascospore characters. However, the genera involved are morphologically distinguishable and monophyletic, and Lücking (2019) argued against the strict application of temporal phylogenetics to define genera. Thell & Divakar (2022) argued that the broad generic circumscription of *Cetraria* should be accepted as the alternative is a division into further new genera in a group with an already narrow genus concept. As several of the species are of conservation concern in our region, there is an argument for maintaining their accepted names as before, for pragmatic reasons. Species of all three genera are included in the key below.

Cetrariella species can be distinguished from *Cetraria* by their C+ red medulla in edition 2 of this publication, although that is only true for *C. delisei* and then the reaction is sometimes weak. *Vulpicida* has a yellow thallus, especially the medulla, a strong amyloid reaction of the tholus, and \pm globose ascospores.

Literature:

Divakar *et al.* (2017), Duke & Purvis (2009b), Gilbert (2009b, c), Kärnefelt (1979), Kärnefelt *et al.* (1993), Lücking (2019), Lutsak *et al.* (2017, 2020), Thell *et al.* (2011), Thell & Divakar (2022), Thell & Kärnefelt (2011a, b).

- | | | |
|------|---|-----------------------------|
| 1 | Thallus \pm bright yellow, especially the medulla (<i>Vulpicida</i>)..... | 2 |
| | Thallus brown to olivaceous, the medulla white | 3 |
| 2(1) | Bright yellow soralia present on margins; pycnidia rare; apothecia absent | <i>Vulpicida pinastri</i> |
| | Soralia absent; black, stalked pycnidia frequent on margins; apothecia frequent | <i>Vulpicida juniperina</i> |
| 3(1) | Medulla C+ red, branches >3 mm diam. with spinulose margins, distinctly flattened; stems erect, often reddish below | <i>Cetrariella delisei</i> |
| | Medulla C-..... | 4 |
| 4(3) | Thallus \pm foliose (sometimes minutely so), spreading; lobes horizontal, apices and margins ascending; base persistent, firmly attached; apothecia usually abundant; on bark, wood or rock | 5 |
| | Thallus \pm shrubby, ascending; lobes erect, intertwined, loosely attached and dying from the base; apothecia very rare; terricolous | 6 |

- 5(4) Epiphytic; thallus \pm foliose, spreading, irregular; with prominent apothecia, which appear terminal but are in fact laminal *sepincola*
On rock; thallus lobes elongate and \pm channelled; black globose pycnidia sometimes prominent, on margins of lobes and apothecia *Cetrariella commixta*
- 6(5) Thallus dorsiventrally flattened, margins often strongly incurved, becoming subtubular; more than 1 mm wide 7
Thallus terete, or flattened in the older branches, 0.5–1 mm diam. 9
- 7(6) Laminal pseudocyphellae usually distinct; lobes flattened, usually 4–10 mm wide *islandica* subsp. *islandica*
Laminal pseudocyphellae rare and indistinct; lobes \pm subtubular, with incurved margins, usually 1–5 mm wide 8
- 8(7) Medulla Pd+ red; surface ridged and pitted; marginal pseudocyphellae \pm absent *islandica* subsp. *crispiformis*
Medulla Pd–; surface \pm smooth; pseudocyphellae in marginal lines *ericetorum*
- 9(6) In tufts to 4 cm high; main branches becoming \pm flattened, branching open and coarse; pseudocyphellae concave-elongate, often in pits *aculeata*
In tufts to 3 cm high; main branches rounded, even, delicate, branching compact, branches \pm densely spinulose; pseudocyphellae flattened, rounded *muricata*

***Cetraria aculeata* (Schreb.) Fr. (1826)**

Thallus forming shrubby tufts 2–4 cm high of open coarse spinulose lobes, matt to glossy brown; main branches to 1 mm diam., \pm flattened, uneven, furrowed, pitted, the minor branches more rounded and even; pseudocyphellae concave, excavate and elongate, usually present in pits on the main branches; soredia very rare, present only in damaged material. Apothecia scarce; disc 2–5 mm diam. when mature; paraphyses 45–60 \times 1–2 μ m. Asci 45–55 \times 10–13 μ m. Ascospores 5.5–6.5 \times 2.5–3.5 μ m. Cortical tissue present beneath pycnidia. Thallus C–, K–, Pd– (lichesterinic and protolichesterinic acids). **BLS 0430**.

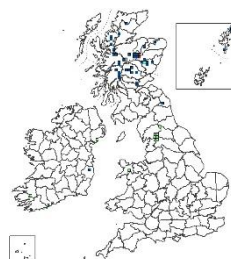
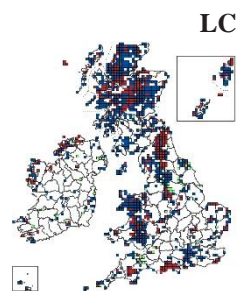
Characteristic of acid soil amongst *Calluna* and of industrial spoil heaps. Widespread and common on heaths, often forming \pm extensive patches, from sea-level to 1000 m. Locally frequent on coastal sand-dunes and stabilized shingle, also mossy scree slopes; rare on mossy rocks, tree-trunks and stumps. Throughout Britain and Ireland, but less common and declining in the south and east.

Intergrades with *Cetraria muricata* (see below), and both species are polyphyletic according to Lutsak *et al.* (2017, 2020).

Abnormal morphs of *Cetraria aculeata* with gross, efflorescent pale ‘soralia’ are occasionally encountered; this malformation is the result of infection by the lichenicolous hyphomycete, *Taeniolella rolfii* Diederich & Zhurb. (1997). Also host to *Lichenocodium erodens*, *L. usneae*, and the facultatively lichenicolous *Eonema pyriforme* (M.P. Christ) Redhead *et al.* (2009).

***Cetraria ericetorum* Opiz (1852)**

Thallus shrubby, erect or decumbent; lobes 0.5–1 mm wide, strongly channelled, strongly incurved, appearing \pm tubular, dark grey-brown, red-brown or grey-green, usually greener in shaded conditions; with marginal projections; with linear pseudocyphellae on margins of the lower surface, particularly distinct near the lobe ends. Apothecia rare; paraphyses 40–45 \times 0.5–1 μ m. Asci 35–45 \times ca 10 μ m. Ascospores 5–9 \times 2.5–4 μ m. Pycnidia at ends of marginal projections, dark brown; cortical tissue present beneath pycnidia. Medulla and pseudocyphellae C–, K–, KC–, Pd–, UV– (protolichesterinic acid). **BLS 0331**.



On lichen-rich heaths in montane situations above 900 m; rare. C. & N. Scotland, with a single record from the Cheviot Hills, formerly in the northern Pennines and N. Wales; a very few records from Ireland.

Cetraria islandica differs in the Pd+ orange medulla and broader, less incurved lobes.

Cetraria islandica* (L.) Ach. (1803) subsp. *islandica

Thallus 2–6 cm tall, shrubby, erect or decumbent, forming tufts; lobes 1–10 (–30) mm wide, ± channelled, wider lobes flatter with a distinct marginal edge, moderately branched; upper surface dark grey-brown, red-brown or grey-green, basal parts often reddish, smooth or sometimes pitted, shiny or dull; marginal projections 0.1–1 mm in length, often frequent, rarely absent; lower surface usually concolorous or paler with numerous, conspicuous white pseudocyphellae, also present on margins. Apothecia rare, on the lower surface of wide lobe ends; disc 2–20 mm diam., dark brown; thalline margin often crenulate; paraphyses *ca* 50 × 1 µm. Asci *ca* 50 × 10 µm. Ascospores 6–10 × 3.5–5 µm. Pycnidia at ends of marginal projections, dark brown. Medulla and pseudocyphellae C–, K–, KC–, Pd+ orange-red, UV– (fumarprotocetraric, and sometimes also protocetraric and protolichesterinic acids). **BLS 0333.**

On lichen-rich heaths, especially in hilly and montane districts; locally dominant. Throughout Britain above a line from the Wash to S. Wales, but now infrequent and declining to the south, scattered throughout western Ireland.

Cetraria ericetorum is Pd–. *C. islandica* is separated from *Cetrariella delisei* by the infrequent branching in the upper parts of the thallus, the absence of numerous short, marginal outgrowths towards the apices, the paler base of the thallus and the Pd+ orange reaction of the medulla.

Host to *Lichenocmium erodens* and *Lichenopeltella cetrariicola* (Nyl.) R. Sant. (1989).

***Cetraria islandica* subsp. *crispiformis* (Räsänen) Kärnefelt (1979)** **NE**

Distinguished from subsp. *islandica* by the very small, indistinct laminal pseudocyphellae, the often rather narrower lobes (1–15 mm wide) which often become ± tubular and which lack a distinct marginal edge, the few, short lateral branches and the more pitted and ridged surface. **BLS 0334.**

On acid soils and peat, montane (Scottish Highlands).

***Cetraria muricata* (Ach.) Eckfeldt (1895)**

Like *C. aculeata* and often treated as an ecological morph or subspecies of that species from generally acid habitats. It is separated by the smaller (1–3 cm high), often darker, more delicate, densely and evenly branched lobes with numerous small lateral spinules and more rounded, even branches with flat circular pseudocyphellae. Differences are especially apparent where the two species grow together. **BLS 0431.**

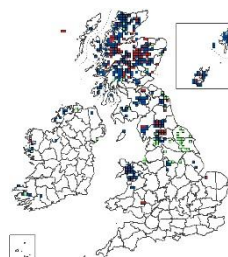
On the ground, scattered on acid heaths from sea-level to 600 m., often with *C. aculeata* but generally less abundant, occasionally on mossy rocks, old tree-trunks and mossy scree-slopes.

Throughout Britain and Ireland, particularly in upland areas. According to Lutsak *et al.* (2017, 2020) the species is polyphyletic, with many populations nesting within *Cetraria aculeata* s.l. There does appear to be a distinct clade containing *C. muricata* morphotypes, but the status of British and Irish collections has not been established.

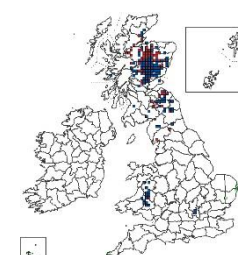
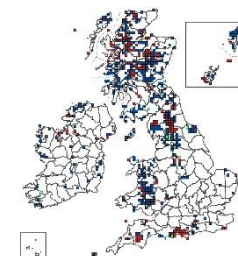
***Cetraria sepincola* (Ehrh.) Ach. (1803)**

Thallus 1–2 cm diam., 0.5–1 cm tall, foliose, forming neat round cushion-like tufts, ± monophyllous, irregularly incised-lobate; upper surface dark grey-green, brownish or olive-brown, matt, ± wrinkled; lower surface white or pale brown, weakly veined or wrinkled; rhizines pale, unbranched or branched, scattered. Apothecia abundant, often covering the entire thallus, at the ends of short lobes; disc 1–4 mm diam., red-brown, smooth, flat or ± convex with a thin thalline margin. Ascospores 6–9.5 × 3.5–5 µm. Medulla C–, K–, KC–, Pd–, UV– (protolichesterinic acid). **BLS 0338.**

LC



LC



On twigs, predominantly of *Betula*, more rarely *Salix* and *Juniperus*, often with *Tuckermannopsis chlorophylla* and *Melanohalea septentrionalis* in well-lit situations, rarely on fence-posts. Locally abundant in Scotland (Highlands, mainly C. & E.), extending to and rare in N. England, C. Wales.

Distinguished from *Tuckermannopsis chlorophylla* by the abundant apothecia, the darker thallus and absence of soredia. *Cetraria sepincola* superficially resembles *Parmelia* s. lat. but is characterized by the marginal, almost always inclined, apothecia and the pycnidia which are never sunken in the thallus but are on marginal projections.

There is a single report of both anamorph and teleomorph of *Abrothallus* cf. *bertianus* De Not. (1849) on this host. Also reported are *Lichenocodium erodens*, *Lichenostigma maureri* and *Spirographa fusisporella* s. lat.

CETRARIELLA Kärnefelt & Thell (1993)

Thallus foliose, erect or flat with upturned margins, dark to pale brown; lobes channelled to sub-tubular, narrow. **Pseudocyphellae** marginal or laminal on the lower surface, though not always well-developed. **Cortex** composed of 1-3 layers of thick-walled rather large isodiametric cells. **Photobiont** trebouxoid. **Apothecia** terminal on lobe tips. **Hamathecium** of paraphyses, straight, sparsely branched with swollen tips. **Asci** broadly clavate, ca 40 × 15 µm, 8-spored, tholus moderately small, lacking an amyloid ring, ocular chamber short and broad, axial body broad (ca 5 µm diam.), maximal tholus thickness ca 3 µm. **Ascospores** ellipsoidal, small. **Conidiomata** marginal, sessile or on tips of projections, 1- to 2-layered, non-pigmented. **Conidia** bacilliform to narrowly bottle-shaped. **Chemistry**: gyrophoric and hiascinic acids or none. **Ecology**: terricolous.

Distinguished from other brown, erect cetrarioid genera by the generally bottle-shaped conidia and broad, clavate asci lacking the amyloid ring structure, and from brown parmelioid genera by the marginal apothecia and pycnidia. The genus has been merged with *Cetraria* by several authors, and the two British species are included in the key to *Cetraria* s.l. above.

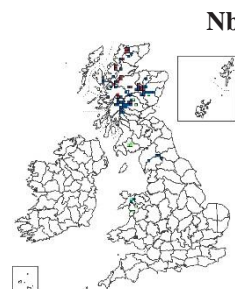
Literature:

Divakar *et al.* (2017), Gilbert (2009d), Thell (1995), Thell & Kärnefelt (2011b).

Cetrariella commixta (Nyl.) A. Thell & Kärnefelt (2004)

Cetraria commixta (Nyl.) Th. Fr. (1871)

Thallus 1–5 (–15) cm, often forming mat-like rosettes; lobes elongate and heavily, irregularly divided, 5–20 mm long, 1–2 mm wide, ± channelled, often overlapping; margins often upturned and superficially appearing isidiate at the margins, often with globose pycnidia at lobe apices; the axils angular or rounded; upper surface dark brown-black, ± shiny, pseudocyphellae reported but not seen in British/Irish specimens but they may appear only as slightly roughened lobe edges and are more apparent on the margin of the apothecia; lower surface pale brown, yellowish brown towards the margin, sparsely rhizinate; rhizines coarse, to 2 mm long, whitish brown, unbranched or branched, scattered. Apothecia 1–5 (–8) mm, frequent; disc concolorous with the thallus; thalline margin often crenate. Pycnidia ca 0.1 mm diam., frequent, black, ± globose, sessile, on margins of lobes and apothecial margins, rarely occurring on the upper surface; conidia 3.5–5 × ca 1 µm, bacilliform. Lichen substances not detected by TLC in British material. **BLS 0328**.



On siliceous rocks in exposed, montane and hilly situations. N. & S.W. England (Lake District, Pennines, Dartmoor), Wales (Snowdonia, Brecknockshire), more common in Scotland (Highlands), not reported from Ireland.

Differs from *Melanelia stygia* by the flat to concave lobes, the pale underside and the predominantly marginal apothecia and pycnidia. *M. hepatizon* differs in the Pd+ orange reaction, dark brown to black underside and its more strongly channelled lobes. Thell (1995) described three different chemotypes: (1) with α -collatolic acid, (2) with alectronic acid and (3) lacking secondary compounds. British specimens appear to belong to this third race.

Cetrariella delisei (Bory ex Schaer.) Kärnefelt & A. Thell (1993)

Cetraria delisei (Bory ex Schaer.) Nyl (1866)

Thallus 2–4 (–5) cm tall, shrubby, erect, forming rigid, spiky tufts; lobes narrow, 2–5 mm wide, often channelled, smooth, \pm matt, richly branched and dissected towards the apices with abundant short fimbriate prolongations to 0.5 mm in length, with stalked pycnidia along the margins; upper surface dark brown-black, paler olive- to yellow-brown towards base; lower surface concolorous or paler; pseudocyphellae frequent, white, elongate, laminal and marginal. Apothecia unknown in British material. Conidia $3.5\text{--}7 \times ca\ 0.5\ \mu\text{m}$. Medulla and pseudocyphellae C+ pink-red, K–, KC+ pink-red, Pd–, UV– (hiascinic and sometimes also gyrophoric acids). **BLS 0330**.

In small wet grit-lined depressions with moderate winter snow-lie, usually above 900 m; rare, but locally frequent. Only in N.E. Scotland (Cairngorm Mtns).

Separated from *Cetraria islandica* by the greater degree of branching in the upper parts of the thallus, the tendency to develop numerous short marginal projections towards the apices, the paler base of the thallus, and the C+ pink-red, KC+ pink-red, Pd– medulla.

NT



CETRELIA W.L. Culb. & C.F. Culb. (1968)

Thallus foliose, with large loosely attached rounded lobes, without marginal rhizines. **Upper surface** with punctiform pseudocyphellae and marginal soredia. **Lower surface** black, with sparse rhizines and a broad bare zone around the margin. **Cortex** composed of intertwined hyphae. **Medulla** I–. **Photobiont** *Trebouxia*. **Ascomata** apothecia, laminal, occasionally marginal, usually perforate. **Thalline margin** persistent. **Hymenium** colourless. **Asci** *Parmelia*-type, 8-spored. **Ascospores** ellipsoidal, aseptate, colourless. **Conidiomata** pycnidia, marginal. **Conidia** bacilliform, colourless, aseptate. **Chemistry**: atranorin (K+ yellow) in cortex; medulla with a range of orcinol depsides and depsidones. Several chemical races with differing KC and C reactions are recognized, four of these occur in Britain. **Ecology**: on trees, moss, rock.

Cetrelia is superficially similar to large parmelioid lichens. It is distinguished from *Parmotrema* and *Platismatia* by the presence of very small, scattered, fleck-like laminal pseudocyphellae and the absence of rhizines and cilia. *Punctelia* has larger, laminal pseudocyphellae which often become sorediate and the pycnidia are laminal, although they may be concentrated towards the margin, the lobes are smaller (3–10 mm broad) and the lower surface has numerous rhizines. The four British species can only be distinguished reliably by chemistry.

British and Irish populations of *Cetrelia olivetorum* have been divided into four segregate species, based on differing chemical syndromes. The distribution of these chemotypes is poorly known and mapping numbers are provided to encourage reporting of each type.

Literature:

Gilbert & Purvis (2009b), Kukwa *et al.* (2012), Mark *et al.* (2019), Thell & Kärnefelt (2011c).

Cetrelia olivetorum (Nyl.) W.L. Culb. & C.F. Culb. (1968) *sensu lato***LC**

Thallus to 10 cm diam., foliose, forming wavy, wide-spreading patches; lobes 0.5–2 cm broad, contiguous, often overlapping, rounded at the apices and with wavy crisped raised margins; upper surface glaucous-grey, sometimes tinged brown, dotted with minute scattered white punctiform pseudocyphellae ($\times 10$ lens); older parts of lobes with half-moon-shaped to \pm continuously sorediate margins; lower surface black, somewhat wrinkled; rhizines scattered, unbranched, with a wide and often paler rhizine-free zone towards the margin; marginal cilia absent. Apothecia not seen in British material, not perforate; hymenium 60–110 μm tall. Ascospores 12–15 \times 7–10 μm . Pycnidia unknown. **BLS 0339** [*C. olivetorum s. lat.*], **BLS 2352** [*C. olivetorum s. str.*].

Amongst mosses on broad-leaved trees or, less frequently, rocks in well-lit but moist or boggy, sheltered, often long-established woodlands and *Salix* carr. Western Britain and Ireland.

Host to *Clypeococcum cladonema* (Wedd.) D. Hawksw. (1977), forming black ‘shot-holes’ in the thallus, as well as *Lichenocodium* spp.

The *C. olivetorum* aggregate is characterized by the large, loosely attached lobes with small scattered white laminal pseudocyphellae and pale ‘frilly’ marginal soralia. Some correlation between chemistry and morphology, especially pseudocyphella shape and position, has been observed on foreign material, suggesting that several separate species are involved. *Punctelia subrudecta* has more obvious pseudocyphellae on the upper surface, the thallus is much smaller (< 6 cm diam.) and the lobes are 5–10 mm broad. *C. olivetorum s.l.* differs from *Platismatia glauca* in having pseudocyphellae, \pm continuously rounded margins, a smoother surface to the lobes, an I– medulla and a distinctive chemistry. It may also be mistaken for large *Parmotrema* species (e.g. *P. arnoldii*, *P. perlatum*, *P. robustum*).

Spot tests & fluorescence of the segregate species (all are K– & Pd–).

Species	C	KC	UV	Acids	Status
<i>C. cetrarioides</i>	–	–	Bright blue-white	Perlatolic acid	Common
<i>C. chicitae</i>	–	KC+ pink to red	White (paler)	α -collatolic and alectoronic acids	Very rare
<i>C. monachorum</i>	–	–	–	Imbricatic acid	Very rare
<i>C. olivetorum s. str.</i>	Pink to reddish	KC+ red	–	Olivetoric acid	Rare

The segregate species are as follows:

Cetrelia cetrarioides (Delise ex Duby) W.L. Culb. & C.F. Culb. (1968)**NE**

Distinguished from *Cetrelia olivetorum s. str.* by chemistry: thallus C–, K–, KC–, Pd–, UV+ bright blue-white (perlatolic acid). As with *C. olivetorum*, thalli have labriform soralia and fine soredia. **BLS 2353**.

Widely distributed in W. Scotland, Cumbria, N. Wales and S.W. England, with scattered records in Ireland.

C. cetrarioides appears to be much more common than any of the other species in our region, and appears itself to be a species aggregate according to Mark *et al.* (2019). The very bright UV fluorescence combined with the KC– spot test makes this a distinctive taxon.

Cetrelia chicitae W.L. Culb. (1965)**NE**

Thallus medium to large, 10–16 cm broad, lobes 0.7–1.7 cm broad, light grey or ashy (brown or tan in old preserved specimens); smooth, often pruinose at the tips, the margins erupting with moderately coarse soredia; pseudocyphellae small, rarely exceeding 1 mm in diam. Lower surface jet black, the margins brown or concolorous with the upper surface and in some specimens wrinkled. Cortex K+ yellow, medulla C–, K–, KC+ pink to red, Pd–, UV+ white (α -collatolic and alectoronic acids). **BLS 2354**.

Differs from *Cetrelia olivetorum* by the coarser soredia, and distinct chemistry (medulla C–, versus C+ pink to reddish, with α -collatolic and alectoronic acids rather than olivetoric acid). The description has been largely abstracted from the original description (Culberson 1965).

Considered to be very rare in Britain and Ireland, but recently detected in N. Wales. It is also polyphyletic according to Mark *et al.* (2019), and the identity of British material needs further investigation. The UV fluorescence is noticeable weaker than that seen in *C. cetrarioides*, which is a good field indication that this is not that species and the identity can be confirmed by the KC+ pink to red spot test.

***Cetrelia monachorum* (Zahlbr.) W.L. Culb. & C.F. Culb. (1977)**

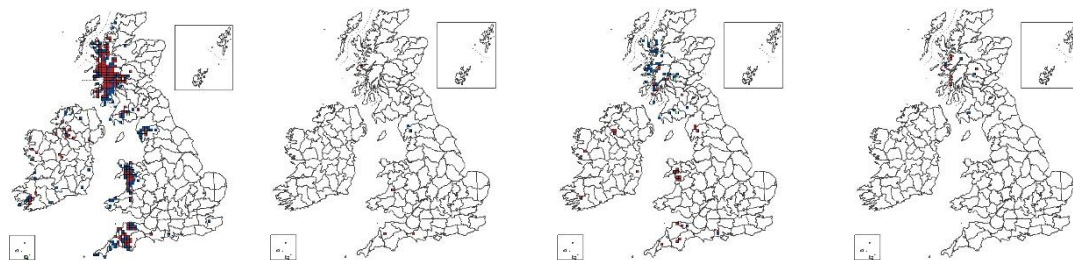
Distinguished from *Cetrelia olivetorum* s. str. by chemistry: thallus C–, K–, KC–, Pd–, UV– (imbricatic acid). There do not appear to be any morphological traits that can separate the two taxa, but they are phylogenetically distinct. **BLS 2355.**

Recorded from various sites in western Scotland, also from Cumbria, Somerset and N. Ireland (Co. Derry). Can be detected in the field by the lack of any UV fluorescence and the negative spot tests.

Cetrelia olivetorum* (Nyl.) W.L. Culb. & C.F. Culb. (1968) *sensu stricto

Distinguished from the other segregates by the chemistry: thallus C+ pink to reddish, K–, KC+ red, Pd–, UV– (olivetoric acid). **BLS 2352.**

C. olivetorum appears rare but with scattered records from Dorset to Argyll. The lack of UV fluorescence is a good field indication, with a C+ reddish and KC+ red spot tests confirming the identity.



Distribution maps, from left to right: *Cetrelia olivetorum* s. lat., *C. olivetorum* s. str., *C. cetrarioides*, *C. monachorum*. No map can be generated for British and Irish records of *C. chicitae*.

CORNICULARIA (Schreb.) Hoffm. (1792)

As this is a monotypic genus the description below (*C. normoerica*) constitutes the generic description.

Differs from *Cetraria* in being firmly attached to its substratum, erect and sparsely branched, with usually abundant apical apothecia. It occupies a phylogenetic clade that is sister to that including *Usnea*.

Literature:

Kärnefelt (1986), Seaward & Purvis (2009a), Thell & Kärnefelt (2011d).

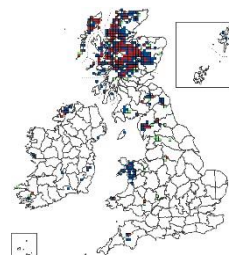
***Cornicularia normoerica* (Gunn.) Du Rietz (1926)**

LC

Thallus to 2 cm tall, shrubby, forming \pm erect tufts, firmly attached; main branches 0.3–0.6 mm broad, stiff, tough, solid, \pm flattened, bilaterally symmetrical, sparingly branched, tapering abruptly towards the apices, arising from a proliferating holdfast; surface black-brown, \pm shiny; cortex thick, of massive, periclinial hyphae; photobiont *Trebouxia*. Ascomata apothecia, 1–5 (–8) mm diam., frequent, apical or subapical; disc black and

shiny, usually with a few short cylindrical extensions. Asci elongate-clavate, with thickened blunt apex, *Lecanora*-type, 8-spored. Ascospores $5\text{--}6 \times 3\text{--}4 \mu\text{m}$, aseptate, colourless, ellipsoidal. Conidiomata pycnidia, black, globose, half sunken, mostly at the apices of branches; conidia $6.5\text{--}7.5 \times 0.5\text{--}0.8 \mu\text{m}$, dumb-bell-shaped. Lichen products not detected by TLC. **BLS 0472.**

Widespread and locally frequent on well-lit coarse-grained siliceous rocks in wind-swept, usually montane situations. N. & W. Britain, but rare and localized on hills in Ireland.



EVERNIA Ach. (1809)

Thallus fruticose or shrubby-foliose, pendent or prostrate when on the ground, somewhat soft and flaccid, attached by a spreading basal holdfast; lobes numerous, angular and ridged or (in *E. prunastri*) dorsiventral, flattened, strap-shaped, corticate on both sides, the lower surface paler than the upper, upper side lacunose, medulla soft and loosely woven. **Photobiont** chlorococcoid. **Ascomata** apothecia, \pm stoutly and shortly stalked, marginal. Disc red-brown. **Thalline margin** irregular, crenate. **Asci** 8-spored, *Lecanora*-type. **Ascospores** colourless, ellipsoidal, aseptate. **Conidiomata** pycnidia, laminal and marginal, immersed, rounded, blackened around the ostiole, rare. **Conidia** needle-shaped. **Chemistry**: cortex K⁺ yellow (atranorin, sometimes also usnic acid); medulla with evernic acid or (in non-British species) divaricatic acid. **Ecology**: corticolous and lignicolous, occasionally saxicolous or terricolous.

Evernia prunastri resembles *Ramalina* but the thallus is dorsiventral, with the photobiont cells mainly confined to the upper side thus accounting for the grey-green upper and white lower surfaces; *Ramalina* species are not dorsiventral, are whitish to grey-green both above and below, the cortex is usually stiff and cartilaginous, and the ascospores are 1-septate. *Pseudevernia* has a grey upper and \pm blackened lower surface. The remaining, non-British species of *Evernia* have angular or ridged lobes, without distinct upper and lower surfaces. In particular, *E. divaricata* (L.) Ach. is widespread in Scandinavia on conifer bark; it could possibly occur also in the Scottish Highlands. It differs by long narrow pendulous thalli with \pm terete rather than flattened lobes, and lacking soralia.

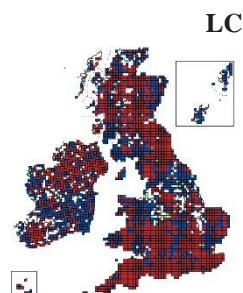
Literature:

Fletcher & Purvis (2009), Moberg & Thell (2011b).

Evernia prunastri (L.) Ach. (1810)

Thallus (1–) 2–6 (–10) cm long, 2–4 (–6) mm broad, about 1 mm thick, foliose; lobes rather soft, numerous, strap-shaped, \pm palmately branched, often twisted and pendulous; upper surface green-grey to pale green-yellow, often with an incomplete network of elongate ridges spreading towards the margins and delimiting hollows; lower surface white, almost lacking photobiont but occasionally dotted green especially towards the tips; soralia marginal and/or laminal, at first rounded and often confined to eroded surfaces of ridges and/or lobe margins, later becoming confluent, paler or concolorous with the upper surface. Apothecia rare in Britain, 2–5 mm diam. Ascospores $7\text{--}11 \times 4\text{--}6 \mu\text{m}$. Pycnidia ca 0.3 mm diam.; conidia $6\text{--}7 \times \text{ca } 0.5 \mu\text{m}$. Medulla C⁻, K⁻, KC⁻, Pd⁻, UV⁻ (usnic and evernic acids, atranorin). **BLS 0511.**

Widespread and often abundant with a wide ecological amplitude, principally on sunny, often windswept, neutral to acid barked trunks or the canopy of wayside and parkland trees and in hedgerows; also on fence-posts,



LC

old stems of *Calluna* or on the ground on heathland and dunes, more rarely in sheltered woodland and boggy sites; sometimes on nutrient-rich siliceous rocks, gravestones, stabilized shingle, short turf and brick walls.

Throughout Britain and Ireland. It returned rapidly since 1980 to the English Midlands and urban areas as SO₂ levels declined, and is now almost ubiquitous, but sensitive to high levels of ammonia pollution.

The 'oak moss' of the perfume industry. Material from shaded habitats usually has fewer, paler, often more elongate lobes. Specimens from polluted sites are often reduced in size with contorted or downturned lobes which can be markedly eroded and sorediate. Here they can be confused with *Ramalina farinacea* which has a cartilaginous cortex and twisted, rope-like structure. A grey race, deficient in usnic acid, has been called *E. prunastri* f. *herinii* (Duvign.) D. Hawksw. (1980), and can grow with the yellow-green f. *prunastri*, where it retains its identity. The presence of both atranorin and usnic acid is demonstrated on TLC plates by the purple coloration produced on charring where the spots of the two substances overlap.

Sometimes confused with *Pseudevernia furfuracea* which has a grey upper side, often with isidia and a lower side that becomes dark grey to black in the older parts.

Host to numerous lichenicolous fungi: *Athelia arachnoidea* (Berk.) Jülich (1972), *Briancoppinsia cytospora* (Vouaux) Diederich *et al.* (2012), *Everniicola flexispora* D. Hawksw. (1982), *Illosporiopsis christiansenii* (B.L. Brady & D. Hawksw.) D. Hawksw. (2001), *Lichenocodium erodens*, *Lichenodiplis lecanorae* (Vouaux) Dyko & D. Hawksw. (1979), *Lichenostigma maureri*, *Marchandiomyces corallinus* (Roberge) Diederich & D. Hawksw. (1990), *Phaeospora everniae* Etayo & van den Boom (2014), *Phoma everniae* D. Hawksw. (1994), *Spirographa* spp. (as the anamorphs *Cornutispora ciliata* Kalb (1993) and *C. lichenicola* D. Hawksw. & B. Sutton (1976)) and *Unguiculariopsis lettaui* (Grumann) Coppins (1990), as well as two unidentified species of *Abrothallus* and *Endococcus*.

FLAVOCETRARIA Kärnefelt & Thell (1994)

Thallus of erect foliose dichotomously branched lobes, weakly to strongly channelled, the upper surface pale sulphur-yellow, the lower surface with pseudocyphellae. Cortex one-layered, of gelatinized hyphae. **Photobiont** trebouxoid. **Ascomata** apothecia (rare), brown, marginal, at the lobe ends. **Thalline margin** two-layered, strongly gelatinized. **Asci** narrowly clavate, axial body small, with a distinct K/I+ blue ring structure in the rather large tholus, *Cetraria*-type. **Paraphyses** broadest at the tips. **Ascospores** 8 per ascus, ellipsoidal, colourless, aseptate. **Conidiomata** pycnidia; black, marginal. **Conidia** slightly dumbbell-shaped, *ca* 6 × 1 μm. **Chemistry**: upper cortex with usnic acid, medulla sometimes with lichesterinic and protolichesterinic acids, lower part of thallus sometimes with anthraquinones. **Ecology**: terricolous among mosses and low vegetation.

Cetrarioid lichens are primarily recognized by an erect foliose habit and marginal or submarginal position of apothecia and pycnidia (Thell *et al.* 2005). *Flavocetraria*, along with *Nephromopsis* and *Tuckermannopsis* and a further seven genera, comprises one of two major cetrarioid clades of the Parmeliaceae (Thell *et al.* 2002, 2005, 2009, 2012). The group is characterized in morphological terms largely by dumb-bell shaped conidia with two apical or subapical swellings, in contrast to the other major clade in which they are usually ovoid or lemon-shaped. The constituent taxa have been treated as separate genera by most recent authors, but they form a monophyletic clade that is comparable in evolutionary age to other Parmeliaceae groups treated as single genera (Divakar *et al.* 2017). Lücking (2019) argued against a strict application of data on evolutionary age to define genera, and *Flavocetraria* in its traditional circumscription is morphologically distinguishable from *Nephromopsis* s.l. However, it is not monophyletic, and the British species *F. nivalis* should not be regarded as congeneric with the type *F. cucullata*. Nevertheless, *F. nivalis* is a well-known species in Scotland and is the subject of substantial interest in its conservation, and is retained here for practical reasons.

Literature

Divakar *et al.* (2017), Geml *et al.* (2010), Gilbert (2009e), Kärnefelt *et al.* (1993, 1994), Lücking (2019), Randlane & Thell (2011), Thell *et al.* (2002, 2005, 2009, 2012).

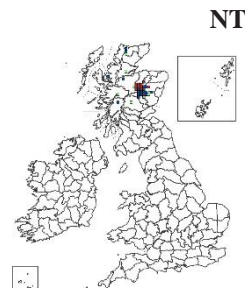
Flavocetraria nivalis (L.) Kärnefelt & A. Thell (1994)

Nephromopsis nivalis (L.) Divakar, A. Crespo & Lumbsch (2017)

Thallus 2–4 (–6) cm tall, shrubby, erect, rigid, forming tufts; branches to 1 cm broad, flat or weakly channelled, irregularly branched, with truncate, deeply indented apices; upper and lower surfaces pale sulphur-yellow to yellow-grey, often deep yellow-orange at the base; surface with depressions, ridged and wrinkled, often slightly channelled, lower surface with pseudocyphellae, without rhizines. Apothecia not seen in British material. Pycnidia black, marginal, slightly protruding. Conidia slightly dumbbell-shaped, *ca* 6 × 1 µm. Medulla C–, K–, KC–, Pd–, UV–, usnic acid abundant in the cortex. **BLS 0336.**

Characteristic of lichen-moss heaths particularly in exposed wind-pruned *Calluna* heath and more sheltered *Calluna-Vaccinium uliginosum-Empetrum-Salix herbacea* communities with some winter snow lie, but avoiding patches with late snow-lie, usually above 900 m. Scotland (Cairngorms), extending locally to N. & W. Scotland.

Flavocetraria cucullata (Bellardi) Kärnefelt & A. Thell (1994), not yet reliably recorded from Britain and Ireland, has a strongly inrolled, subtubular thallus, the basal parts of which are often red-violet (anthraquinones), and has lichesterinic and protolichesterinic acids in the medulla (TLC).

**FLAVOPARMELIA** Hale (1986)

Thallus foliose, loosely to closely appressed, dorsiventral, often very large, corticate on both sides. **Lobes** irregular, roughly rounded and lacking cilia. **Upper surface** yellow-green to green (usnic acid), ± sorediate; soredia superficial or formed in pustules or with isidia (species in Britain and Ireland are sorediate only), lacking pseudocyphellae. **Upper cortex** of brick-like cells with a thin, pored epicortex. **Cell walls** containing isolichenan. **Medulla** white. **Lower surface** black, rhizinate, with a narrow brown region lacking rhizines along the margins; rhizines sparse to moderately abundant, unbranched, black but often paler towards the lobe apices. **Ascomata** apothecial, laminal, sessile or semi-stalked, to *ca* 10 mm diam.; disc red-brown. **Ascospores** ellipsoidal, 8 per ascus, aseptate, colourless. **Conidiomata** pycnidial, laminal, immersed, the ostiole black. **Conidia** typically fusiform, 4–12 × *ca* 1 µm. **Chemistry**: cortex: usnic acid, atranorin (sometimes); medulla: orcinol depsides, β-orcinol depsides, β-orcinol depsidones, aliphatic acids, anthraquinones, secalonic acids, amino acid derivatives. **Ecology**: on rock, bark, dead wood and old fence posts.

Separated from the morphologically similar *Parmotrema* by presence of usnic acid, the smaller spores (to 22 µm compared with to 37 µm in length) and by the fusiform rather than filiform conidia. In phylogenetic terms, *Flavoparmelia* constitutes a sister group to *Parmotrema*.

Literature:

Del Prado *et al.* (2013), Hale (1986b), Louwhoff (2009a), Moberg *et al.* (2011).

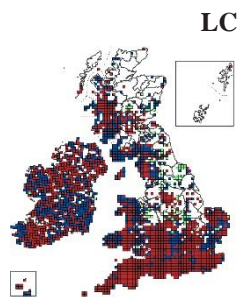
- 1 Soralia pustular, soredia coarse and granular; medulla K– or K+ dirty yellow
 (protocolic acid).....*capitata*
 Soralia not pustular, soredia fine and farinose; medulla K+ yellow→red (salazinic acid)*soredians*

Flavoparmelia caperata (L.) Hale (1986)

Thallus to 20 cm diam., often forming conspicuous, extensive patches, \pm closely appressed but becoming somewhat detached towards the centre; lobes 5–13 mm broad, wavy, rounded at the apices, \pm separate at tips but overlapping at the centre; margins often indented; upper surface pale yellow-green, occasionally grey-green (in shade), often coarsely corrugate, especially towards the centre, pustulate-sorediate; pustules laminal, initially punctiform and intact, eventually coalescing to form more extensive erose spreading areas; soredia coarse and granular, occasionally adhering and then forming gnarled lumps; lower surface black, brown towards the apices; rhizines absent from a narrow (*ca* 1 mm wide) zone along the margin. Apothecia rare, to 8 mm diam.; disc red-brown; thalline exciple \pm sorediate. Ascospores 15–19 (–22) \times (8–) 9–10 μ m, ellipsoidal. Pycnidia not seen. Cortex K–; medulla C–, K– or K+ dirty yellow, KC+ red or KC–, P+ orange-red, UV– (usnic, protocetraric and caperatic acids). **BLS 0987**.

On well-lit \pm acid-barked broad-leaved trees, a major species of the *Parmelietum revolutae*, also on conifers, fences, siliceous rocks, memorials, roofing tiles, coastal turf and *Calluna* heath; common. At one time restricted in distribution due to SO₂ pollution, but now almost ubiquitous except in the northern highlands. It is however suppressed by high ammonia pollution..

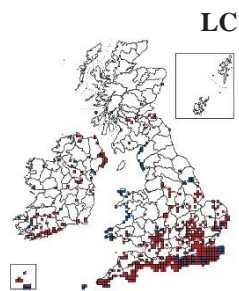
Host to the lichenicolous fungus *Abrothallus microspermus* Tul. (1852), sometimes as its *Vouauxiomyces* anamorph; also *Briancoppinsia cytospora*, *Lichenoconium erodens*, *Marchandiomyces corallinus* and *Spirographa* sp. (as *Cornutispora lichenicola*).

**Flavoparmelia soredians** (Nyl.) Hale (1986)

Like *F. caperata* but with a generally smaller thallus in neat rosettes to *ca* 5 cm diam. (rarely to 10 cm diam.), usually more closely appressed, lobes narrower (to 7 mm broad), becoming congested centrally, soralia not arising from pustules, inconspicuous at first, fusing to form finely sorediate patches; soredia farinose. Apothecia rare, when present usually with mature spores; *ca* 17–18 \times 7–8 μ m, ellipsoidal, spore wall *ca* 1 μ m thick. Cortex K–; medulla C–, K+ yellow→red, KC+ red, P+ orange, UV– (usnic and salazinic acids). **BLS 1018**.

On dry, neutral or \pm acid-barked broad-leaved trees, normally somewhat nutrient-enriched, weathered fences, walls and monuments, siliceous rocks in sunny exposed sites, originally restricted near the southern coast, but now also along inland urban roadsides, usually within the *Parmelietum revolutae*. Locally common; southern and central England, S. & W. Wales, extending locally to central and E. Scotland, throughout Ireland, currently rapidly increasing in range, especially in England.

Lichenostigma maureri is so far the only reported lichenicolous fungus.

**HYPOGYMNIA** (Nyl.) Nyl. (1896)

Thallus foliose, attached by adhesive discs below, or rarely by most of the lower cortex. **Lobes** \pm inflated, often tubular, solid or \pm hollow. **Upper surface** corticate, grey or suffused brown, often with soredia or pustules, lacking isidia and pseudocyphellae. **Photobiont** chlorococcoid. **Medulla** white, solid or hollow, the hyphae loosely woven or arachnoid. **Lower surface** black, corticate, shiny, wrinkled, without rhizines, sometimes with gaping perforations. **Ascomata** apothecia, sessile to prominently stalked; disc shining, concave to flat, red- to yellow-brown; thalline margin well-developed, persistent, concolorous, becoming torn. **Ascospores** aseptate, colourless, globose to shortly ellipsoidal, 8 per ascus. **Conidiomata** pycnidial, common and often conspicuous, minute and punctiform, immersed and blackened around the ostiole. **Conidia** weakly bifusiform to cylindrical or fusiform. **Chemistry**: cortex: atranorin and usnic acid in some species; medulla: β -orcinol depsides

and orcinol and β -orcinol depsidones. **Ecology:** on bark, twigs, dead wood and rocks, less frequently on soil and in grassland.

The genus *Cavernularia* Degel. (1938) is now included within *Hypogymnia*, following phylogenetic studies by Miadlikowska *et al.* (2011) and Divakar *et al.* (2017). The phylogeny of *Hypogymnia* has been studied by Divakar *et al.* (2019) since the publication of edition 2 of this volume. This investigation highlighted incongruence between the phylogeny and phenotypic characters to circumscribe species, suggesting re-evaluation of species boundaries especially in widespread taxa.

Allantoparmelia has a brown upper surface without atranorin and a \pm convex but solid thallus. *Menegazzia* has rounded perforations in the upper surface of the thallus. An account and key to lichenicolous fungi associated with *Hypogymnia* species has been provided by Zhurbenko (2020).

Literature:

Divakar *et al.* (2017, 2019), Gilbert & Purvis (2009c), Goward *et al.* (2012), Louwhoff (2009b), Miadlikowska *et al.* (2011), Wei *et al.* (2016), Westberg *et al.* (2011), Zhurbenko (2020).

- | | | |
|------|---|------------------|
| 1 | Lower surface of lobes with pores or depressions..... | 2 |
| | Lower surface of lobes \pm smooth, without pores or depressions..... | 3 |
| 2(1) | Thallus grey (grey-green when wet); lobes solid, the undersurface with numerous, almost coalescent depressions | <i>hultenii</i> |
| | Thallus with a distinct brown hue; lobes \pm hollow, undersurface of most lobes with a single large pore | <i>vittata</i> |
| 3(1) | Soralia discrete, confined to the ends of lobes | 4 |
| | Soralia diffuse, laminal, irregularly spreading | <i>farinacea</i> |
| 4(3) | Soralia capitate on ends of lobes; thallus lobes \pm tubular, often ascending at the lobe tips; medulla Pd – | <i>tubulosa</i> |
| | Soralia lip-shaped on ends of lobes; lobes \pm flattened, usually not strongly ascending except at the tip; medulla Pd+ orange to red | <i>physodes</i> |

Hypogymnia farinacea Zopf (1907)

Thallus to 5 cm diam., closely appressed, \pm forming rosettes or irregularly spreading; lobes 1–3 mm broad, hollow, \pm convex but flattened towards the ends, contiguous and overlapping, sometimes intricately convoluted at the centre, often \pm discrete towards the margins; upper surface grey, wrinkled; soralia spreading, laminal; lower surface black. Apothecia not observed in British material. Cortex K+ yellow; medulla C–, K–, KC+ red, Pd–, UV+ pale violet-blue (chloroatranorin, atranorin, physodic and 3-hydroxyphysodic acids, and some unknowns). **BLS 0580.**

On trunks of *Pinus* and *Alnus* in relict Caledonian forests with outlying occurrences on boulders; rare. Scottish Highlands, S.E. Scotland & N. England, N. Ireland (Fermanagh).

Distinguished by the diffuse, laminal, Pd– soralia; this species may be a recent arrival to Britain and seems to be starting to spread.



Hypogymnia hultenii (Degel.) Krog (1951)

Nb IR

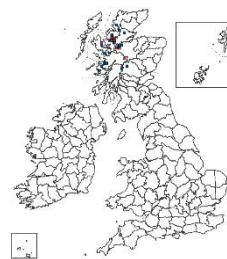
Cavernularia hultenii Degel. (1938)

Thallus small, to 2 cm diam., forming \pm orbicular or fragmented rosettes; lobes solid, to 1 mm broad, \pm palmate, radiating, contiguous or overlapping towards the centre, \pm discrete and horizontally spreading; upper surface somewhat roughened, grey, becoming green-grey when wet; soralia frequent, on or near lobe-ends, convex, occasionally becoming confluent; soredia finely granular, pale greenish white; lower surface dark brown-black, without rhizines, with numerous, almost contiguous depressions 0.1–0.2 mm diam. Apothecia very rare,

immature, shortly stalked, with a uniformly thick thalline margin; disc brown. Cortex K+ yellow or K- (atranorin); medulla C-, K-, KC+ red, Pd- (physodic acid). **BLS 0326**.

Markedly oceanic, on *Pinus sylvestris*, *Betula*, *Calluna*, *Sorbus aucuparia* and *Ilex*, mostly in moist, sheltered areas of relict Caledonian pine and birch forests and ravines; rather rare but locally frequent. N.W. Scotland.

Distinguished from other species of *Hypogymnia* by the abundant perforation-like depressions on the lower surface, and by its generally smaller size. *H. lophyrea* (Ach.) Krog (1951), a non-sorediate, fertile counterpart, is confined to N.W. America. The superficially rather similar *Imshaugia aleurites* and *Parmeliopsis hyperopta* have rhizines and lack pore-like depressions on the lower surface.



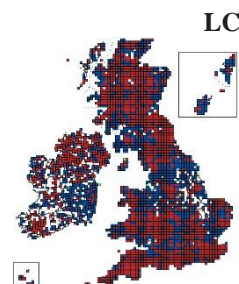
Hypogymnia physodes (L.) Nyl. (1896)

Thallus to 10 cm diam., ± loosely attached, forming rosettes or irregularly spreading, often forming large patches; lobes 2–3 mm broad, ± hollow, often ascending somewhat towards the tips; upper surface grey, smooth, ± shining; soralia lip-shaped, developing from the rupture of the underside tips of the lobes, becoming upturned and fan-like; lower surface black, pale brown towards the margin, wrinkled. Apothecia rather rare, with short, thick stalks; disc red-brown; thalline margin thin, persistent. Ascospores not seen. Pycnidia common, with carbonized ostioles visible in a zone just subtending the lobe tips. Cortex K+ yellow; medulla and soralia C-, K-, KC+ red, Pd+ orange to red, UV+ pale violet-blue (atranorin, chloroatranorin, physodic acid, physodalic acid, sometimes also 3-hydroxyphysodic acid and/or protocetraric acid). **BLS 0582**.

On siliceous rocks, trees, *Calluna* stems and other acidic (ca pH 4.5) substrata, supralittoral to montane; abundant. One of the most widespread macrolichens in Britain and Ireland, but absent in heavily urban areas and now rural areas with high ammonia pollution and probably declining in many localities.

A polymorphic species, ranging from contorted, plate-like thalli with coarse, overlapping and swollen lobes to thin, finely finger-like thalli with discrete lobes; the latter is often characteristic of moist sheltered habitats, e.g. amongst *Calluna*. Separated from *H. vittata* by the Pd+ orange to red reaction, and the presence of spreading, upturned lip-shaped and fan-like rather than gnarled soralia at the ends of lobes. In addition, the apices of most lobes of *H. vittata* have a large pore on the underside, unlike *H. physodes*. *H. tubulosa* is separated by the rounded soralia that occupy most of the lobe tip and do not become ruptured. *Menegazzia terebrata* and *M. subsimilis* resemble *Hypogymnia physodes* in colour and in their inflated lobes, but are distinguished by the scattered, round perforations on the upper surface, and the Pd+ yellow to orange and UV- medulla.

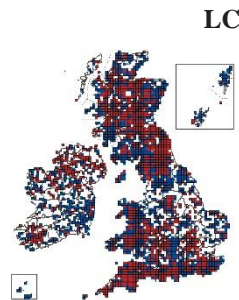
Lichenicolous fungi include the black, sessile *Abrothallus prodiens* (Harm.) Diederich & Hafellner (1998), the pink *Pronectria anisospora* (Lowen) Lowen (1990) and the gall-forming *Tremella hypogymniae* Diederich & M.S. Christ. (1996). Others are *Briancoppinsia cytospora*, *Lichenocodium erodens*, *Marchandiomyces corallinus*, *Nesolechia oxyspora* (Tul.) A. Massal. (q.v.) and *Spirographa* sp. (as *Cornutispora lichenicola*).



Hypogymnia tubulosa (Schaer.) Hav. (1918)

Like *H. physodes*, but medulla and soralia Pd-. The lobes are more tubular and ascending and the upper surface more roughened, matt; the soralia are rounded, not ruptured or lip-shaped, capitate, each involving the entire tip of the lobe. Cortex K+ yellow; medulla and soralia C-, K-, KC+ red, Pd-, UV+ pale violet-blue (atranorin, physodic acid and 3-hydroxyphysodic acid). **BLS 0583**.

On similar substrata as *H. physodes*, and often with it, but rarely as frequent; most frequent on twigs. Throughout Britain and Ireland. Lichenicolous fungi reported are *Abrothallus prodiens*, *Briancoppinsia cytospora*, *Lichenocodium erodens*, *Lichenodiplis lecanorae*, *Marchandiomyces corallinus*, *Nesolechia oxyspora*, *Spirographa* sp. (as *Cornutispora lichenicola*) and *Tremella tubulosae* Diederich *et al.* (2020). In addition an undescribed *Pronectria* with disarticulating spores and a *Roselliniella* with 8-spored asci and spores 17–22 × 7.5–10 µm have been found.



Hypogymnia vittata (Ach.) Parrique (1898)**VU(D2) NR**

Like *H. physodes* but Pd–, with browner coloration of the thallus and irregular, gnarled, lip-shaped soralia. Apices of most lobes have a large pore on the underside. Cortex K+ yellow; medulla C–, K–, KC+ red, Pd–, UV+ pale violet-blue (atranorin, physodic acid, 3-hydroxyphysodic acid and vittatolic acid). **BLS 0638**.

In short, coastal turf, mostly alongside tracks. Reported from a single site in N.E. Scotland (East Sutherland) where it is locally abundant, not found elsewhere in Britain and Ireland.

**HYPOTRACHYNA** (Vain.) Hale 1974

Thallus foliose, loosely to tightly attached, often large. **Lobes** broad, sometimes radiating and elongate, with ± truncate ± incised apices; axils sinuous or V-shaped; margins sometimes ciliate. **Upper surface** white-grey or grey-green (atranorin and chloroatranorin) or yellow-green (usnic acid), without pseudocyphellae, with or without maculae, soredia, pustules or isidia. **Upper cortex** composed of angular cells with a pored epicortex. **Cell walls** containing isolichenan. **Photobiont** trebouxoid. **Medulla** white or occasionally yellow. **Lower surface** ivory white to black (only black in British material), sometimes paler towards the lobe apices and margins; rhizines sparsely to richly dichotomously branched, rarely squarrosely branched in part, sometimes projecting beyond the lobe margins. **Ascomata** apothecia, laminal, sessile to semi-stalked; disc sometimes radially split with age, pale to dark brown. Asci 8-spored, *Lecanora*-type. **Ascospores** colourless, ellipsoidal, sometimes thick-walled. **Conidiomata** pycnidia, immersed, laminal. **Conidia** bacillar or bifusiform. **Chemistry**: cortex: atranorin, lichexanthone, usnic acid; medulla: orcinol depsides and depsidones, β-orcinol and depsidones, aliphatic acids, triterpenes (rare), anthraquinones, xanthenes and dibenzofurans. **Ecology**: corticolous or saxicolous.

Hypotrachyna is distinguished by the dichotomously branched rhizines, commonly sinuous lobe axils, (usually) bifusiform conidia and ± truncate lobe apices. Although these characters usually distinguish members of this genus clearly in Britain and Ireland, some confusion may arise over *H. revoluta* (see under taxonomic notes for this species).

Parmelinopsis has been demonstrated to nest within the large genus *Hypotrachyna* by Divakar *et al.* (2013, 2017) and Lendemer & Allen (2020). The two were distinguished by the presence of isidia, simple (unbranched) cilia and mostly unbranched rhizines in *Parmelinopsis*, with *Hypotrachyna* species having thallus margins without cilia, mainly dichotomously branched rhizines, and either with soralia or without either form of vegetative reproduction.

Literature:

Divakar *et al.* (2006, 2013, 2017), Elix (1993), Hawksworth *et al.* (2008), Kirika *et al.* (2019), Lendemer & Allen (2020), Louwhoff (2009c, d), Powell & Cannon (2013).

1	Thallus sorediate	2
	Thallus lacking soredia	7
2(1)	Thallus yellow-green (usnic acid); medulla K+ yellow→red (salazinic acid)	<i>sinuosa</i>
	Thallus grey-white, grey-green (atranorin); medulla K– (salazinic acid absent)	3

- 3(2) Medulla pale yellow; upper surface dull grey *endochlora*
 Medulla white; upper surface grey-green or glaucous to bluish grey-white 4
- 4(3) Medulla C+ orange (barbatic acid); rhizines dense, often projecting mat-like beyond the
 lobe margin *laevigata*
 Medulla C+ red (gyrophoric acid); rhizines sparse, not projecting beyond the lobe margin 5
- 5(4) Lobes narrow (1–4 mm wide), parallel-sided with narrow tips, frequently dichotomously
 branched; soralia neatly pustulate and sometimes coalescing; usually saxicolous *britannica*
 Lobes wider (2–8 mm wide), divergently widening to revolute tips, little-branched; soralia
 pustulate or not, or soon irregularly spreading and coalescing; usually corticolous 6
- 6(5) Soredia small, farinose, marginal on raised thallus lobes *revoluta*
 Soredia small to medium, granular, arising as pustules and coalescing into soralia *afrorevoluta*
- 7(1) Thallus without isidia or soredia, not ciliate *taylorensis*
 Thallus with isidia, ciliate at least at the edge 8
- 8(7) Isidia ciliate and flattened when mature; medulla C– (gyrophoric acid minor only) *horrescens*
 Isidia not ciliate and always cylindrical; medulla C+ pink (gyrophoric acid major) *minarum*

Hypotrachyna afrorevoluta auct. br., *non* (Krog & Swinscow) Krog & Swinscow (1987)

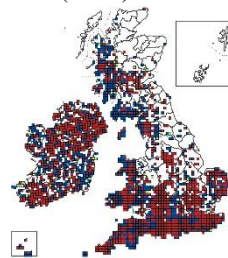
LC

Similar to *Hypotrachyna revoluta* (see below) but with marginal lobes that are not raised, and with pustulate soralia derived from break-up of the upper cortex. The soredia can be concolorous with the thallus but are variable and range to greenish to brown, and are larger and more granular than those in *H. revoluta*. The undersurface is black as in *H. revoluta* and, as it lacks distinct lobes there are no large pale areas on the undersurface. The rhizines may be somewhat more strongly pigmented. **BLS 2468.**

Common on bark of wayside and woodland trees and shrubs, more rarely on weakly acidic rocks and walls in inland and maritime situations.

This taxon has not been distinguished from *H. revoluta* until quite recently and they are often found together. As defined here, *H. afrorevoluta* auct. br. tends to be more common in oceanic areas and on rock, and *H. revoluta* on trees in eastern districts with higher nitrogen deposition. Both *H. afrorevoluta* and *H. revoluta* have been demonstrated to be polyphyletic (Lendemer & Allen 2020), and European material identified as *H. afrorevoluta* occupies a different clade to tropical collections that may be assumed to be *H. afrorevoluta* s. str. A full revision of the species complex is needed.

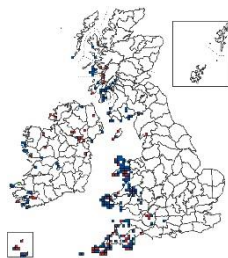
Host to *Cladophialophora parmeliae* (Etayo & Diederich) Diederich & Untereiner (2013), *Nigromacula uniseptata* (D. Hawksw.) D. Hawksw. (2003) and an unidentified *Didymocyrtis* with spores 8–9 × 4–5 μm.



Hypotrachyna britannica (D. Hawksw. & P. James) Coppins (2002)

LC

Thallus moderately adnate to appressed, (1–) 4–10 cm diam.; lobes becoming crowded and imbricate with age, parallel-sided, subdichotomously to irregularly branched, 1–2.5 (–4) mm broad; margins entire or crenate, sometimes irregularly incised; apices truncate to subrotund, often revolute; upper surface grey to bluish-grey, becoming brownish at the apices, shiny to matt, maculate particularly at the lobe tips, developing cracks with age, pustulate; pustules submarginal and laminal, becoming coarsely sorediate, sometimes coalescing but not extensively; soredia pale greenish grey to blue-black, the colour darker when well-illuminated, ultimately eroding away and revealing the blackened lower cortex; medulla white; lower surface dark brown to black, with a pale brown margin, rugulose, moderately rhizinate; rhizines unbranched or sparsely to occasionally moderately dichotomously branched, continuing up to the lobe apices or not, rarely projecting beyond lobe margins and appearing cilia-like. Apothecia not seen. Pycnidia rare; conidia not seen. Cortex K+ yellow, medulla C+ red, K–, KC+ red, Pd–, UV– (atranorin, gyrophoric acid [major], lecanoric acid [trace]). **BLS 0986.**



On siliceous outcrops, boulders, memorials and stone walls in \pm sheltered but well-lit sites, usually on or near the coast, rarely on the ground or on old *Calluna* stems and *Ulex*; local. W. Britain, Ireland and the Channel Isles; probably over-recorded in the past because of reliance on the colour of the soralia.

Distinguished by the extended, \pm ascending parallel-sided pustulate lobes, and by the largely coastal rock habitat. Separated from the similar *H. revoluta* by the narrow dichotomously branching lobes, and by the presence of pustules more resembling those of *H. afrorevoluta* that typically develop blue-black eroding soredia when well-lit, but can be much paler. The colour of the soredia is not diagnostic and dark soredia on well-lit specimens are shared by well-illuminated thalli of *H. afrorevoluta* and *H. revoluta*.

Host to the plurivorous *Marchandiomyces corallinus*.

Hypotrachyna endochlora (Leight.) Hale (1975)

Thallus moderately to loosely adnate, (3–) 6–13 cm diam.; lobes \pm imbricate, sublinear, 1–4 (–6) mm broad; subirregularly branched with a thin black margin, sinuous in axils, apices truncate or sometimes pointed; margins entire or rarely lobulate or lacinate-incised; upper surface pale mineral grey or yellow-grey, smooth or occasionally finely foveolate, sometimes pruinose, white-maculate, sorediate; soralia \pm pustulate at the apices or \pm capitate with diffuse soredia, occasionally extending laminally; soredia coarsely granular, rarely becoming lobulate; cortex \pm becoming blackened and eroded and sometimes fragile and flaking. Medulla pale lemon yellow or almost lime green; lower cortex black, shiny, smooth to rugulose, with a brown marginal zone, moderate to densely rhizinate; rhizines densely dichotomously or rarely squarrosely branched, growing horizontally from the margins, more rarely projecting as a dense mat. Apothecia rare, 3–14 mm diam., with ascospores $18\text{--}22 \times 9\text{--}14 \mu\text{m}$. Pycnidia subterminal and laminal; conidia bifusiform, $5\text{--}6.5 \times ca 1 \mu\text{m}$. Cortex K+ yellow; medulla C+ orange, K–, KC+ orange, Pd– [atranorin, obtusatic acid (major), chloroatranorin, barbatic, secalonin A, and norobtusatic acids (minor/trace)].

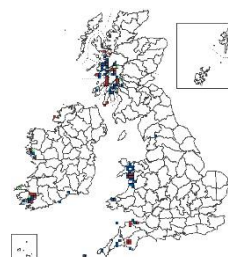
BLS 0994.

On trees (*Quercus*, *Betula*, etc) in woodlands with well-lit leached very acid bark (pH 3.5–4.0); also in *Salix* carr, on mossy rocks and in coastal cliff-top *Armeria* heaths, in areas of very high rainfall. W. & S.W. Britain and Ireland.

Characterized by the sublinear, mineral grey to yellowish/grey lobes, the \pm terminal, diffuse \pm pustulate soredia and by the lemon-yellow or lime-green medulla (due to presence of the pigment secalonin A). The latter character, especially, distinguishes it from *H. laevigata*. The upper surface sometimes becomes densely lobulate centrally, especially so for Scottish specimens.

Phylogenetic study has shown that this is not a monophyletic species, and additional research is needed to clarify the species boundary (Kirika *et al.* 2019).

Nb IR



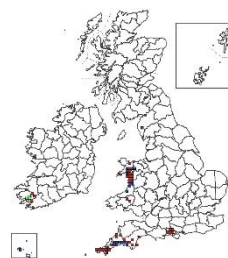
Hypotrachyna horrescens (Taylor) Krog & Swinscow (1987)

Parmelinopsis horrescens (Taylor) Elix & Hale (1987)

Thallus tightly appressed, 2–7 cm diam., \pm irregular or forming small rosettes; lobes crowded, to 3 mm broad with subtruncate apices; margins frequently irregularly incised, often becoming lobulate, with abundant, mostly unbranched cilia; upper surface grey-white, matt or partly shiny, isidiate; isidia laminal, dense and \pm obscuring the thallus, cylindrical or flattened when well-developed and becoming \pm lobulate-coralloid, often dark-tipped with cilia growing from base or tips of isidia; lower surface black, \pm brown towards the apices; rhizines unbranched or rarely squarrose or dichotomously branched. Apothecia very rare, sessile, 2–4 mm diam.; disc concave, split at maturity, dark brown to red-brown; thalline margin irregularly incised and ciliate-isidiate. Ascospores broadly ellipsoidal, $12\text{--}15 \times 9\text{--}11 \mu\text{m}$. Pycnidia not reported for British specimens. Cortex K+ yellow; medulla C–, K–, KC+ rose-red, Pd–, UV– (atranorin, sometimes also gyrophoric acid and a complex of medullary substances). **BLS 0999.**

On strongly acid bark of old broad-leaved trees in ancient (sheltered, humid) woodlands and on sheltered sides of rock outcrops; localized. S. & S.W. England (New Forest, Devon, Cornwall), C. & N. Wales, Lake District & S.W. Ireland.

NT IR



H. minarum lacks the laminal cilia associated with isidia, which are never flattened, and has a C+ pink medulla (gyrophoric acid major). *Parmotrema crinitum* also has ciliate isidia but is distinguished by the larger thallus, the broad (around 5 mm wide) marginal zone without rhizines on the lower surface and by the K+ yellow medulla (stictic acid).

Hypotrachyna laevigata (Sm.) Hale (1975)

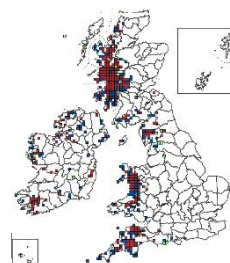
Thallus loosely adnate, to 15 cm diam.; lobes crowded, becoming ± imbricate, linear to sublinear, dichotomously to subdichotomously or rarely irregularly branched, (1–) 2–6 (–8) mm broad, ± subrevolute; margins mostly entire, sometimes irregularly lobulate or lacinate-dissected, not ciliate; apices truncate, sometimes pointed; lobe axils sinuous or V-shaped; upper surface glaucous to bluish grey-white or grey-green, smooth or small-pitted, shiny or matt, maculate, sorediate; soralia terminal to subterminal, rarely cuff-shaped, often globose; soredia granular, grey or blackened; medulla white; lower surface black with a brown margin, shiny, smooth, densely rhizinate; rhizines moderately to densely branched, continuing to lobe margins and often protruding beyond, sometimes as a dense mat. Apothecia rare, laminal, stalked; disc (1–) 3–10 mm diam., dark brown; exciple mostly sorediate, entire, becoming torn on larger apothecia. Ascospores rare, reported as 18–21 × 9–13 µm but measured as 12.5–13.5 × ca 5 µm in British material. Pycnidia subterminal and laminal; conidia bifusiform, 4–6 (–7.5) × ca 1 µm. Cortex K+ yellow, medulla C+ pale orange, K–, KC+ deep orange, Pd–, UV+ bluish-grey or UV– (atranorin, chloroatranorin, barbatic acid [major], 4-*O*-demethylbarbatic acid [submajor], obtusatic acid [trace], norobtusatic acid [trace]). **BLS 1002.**

On well-lit acid-leached bark in damp oak or birch woodland and *Salix* carr, more rarely on mossy rocks and coastal cliffs, requiring high rainfall (in excess of 127 cm p.a. and with over 180 rain days p.a.); local but then often abundant. W. Britain, becoming rarer to the N., absent in C. & E. Britain, scattered in Ireland.

This is a variable species but in general is characterized by the maculate upper surface, globose soralia and a white medulla, the latter clearly separates *H. laevigata* from *H. endochlora*. This also is a polyphyletic species and African populations have been assigned to a separate species, *H. nyandaruaensis* (Kirika *et al.* 2019). This provides some indication that *H. laevigata* populations growing in disjunct geographic areas may correspond to distinct lineages.

Main host to the lichenicolous fungus *Nigromacula uniseptata* (D. Hawksw.) D. Hawksw. (2003). Also recorded are: *Briancoppinsia cytospora*, *Lichenocodium erodens*, *Nectriopsis rubefaciens* (Ellis & Everh.) M.S. Cole & D. Hawksw. (2002) and *Spirographa* sp. (as *Cornutispora lichenicola*).

LC



Hypotrachyna minarum (Vain.) Krog & Swinscow (1987)

Parmelinopsis minarum (Vain.) Elix & Hale (1987)

Thallus moderately to tightly attached, 2–5 (–7) cm diam., forming small, irregular patches; lobes ± crowded, sublinear, to 1–3 (–5) mm broad with apices more rounded than subtruncate; margins frequently irregularly incised, with abundant, mostly unbranched, ± unevenly dispersed cilia; upper surface grey-white, matt or partly shiny, isidiate; isidia laminal, dense and ± obscuring the thallus, cylindrical and becoming coralloid-branched, brown-tipped when mature. Lower surface black, ± brown towards the apices; rhizines unbranched or rarely forked. Apothecia very rare in British material, 1–4 mm diam. with a dark brown disk and isidiate thalline margin. Ascospores ellipsoidal, 12–17 × 8–10 µm. Pycnidia not seen on British specimens. Cortex K+ yellow; medulla C+ rose-red, K–, KC+ red, Pd–, UV– (atranorin, gyrophoric acid (major) and a complex of medullary substances). **BLS 1004.**

On old trees, often *Fagus*, but also found on *Quercus*, *Alnus*, *Betula*, *Salix*, *Quercus cerris*, *Castanea* and on the trunks of *Pinus sylvestris*, also *Ulex* stems, exposed roots and on rocks; rare but very locally frequent. Local along the south coast from the New Forest to Cornwall, most frequent in the far S.W., rare in N. Wales.

H. horrescens has laminal cilia associated with the isidia, which are flattened when mature, and has a C– medulla. The brown tips of the isidia of *H. minarum* give mature thalli a distinctive brownish tinge. Immature thalli before the isidia develop cannot be separated from either *H. afrorevoluta* or *H. revoluta*.

Nb



***Hypotrachyna revoluta* (Flörke) Hale (1975)**

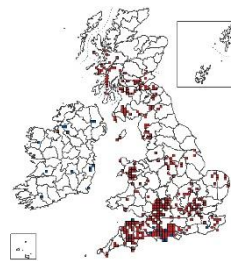
Thallus 1–4 (–6) cm diam., rather compact, sometimes coalescing and forming extensive patches; lobes 2–5 mm broad, appressed, separate but \pm overlapping towards the centre, rounded, often \pm indented, axils rounded but not markedly sinuose, revolute at the tips; upper surface grey or grey-green, smooth, \pm matt; marginal cilia very sparse, usually absent, sorediate; soralia laminal, irregularly spreading, \pm diffuse, mainly on or near lobe ends, \pm concolorous with the thallus or darker in full light; lower surface black, \pm rhizinate to margins, rhizines simple, forked or \pm dichotomously branched. Apothecia rare; disc to 6 mm diam.; thalline margin \pm sorediate. Ascospores 11–16 \times 8–10 μ m, broadly ellipsoidal to almost spherical. Cortex K+ yellow; medulla C+ pink-red, K–, KC+ red, Pd–, UV– (atranorin, gyrophoric acid [major], lecanoric acid [minor] and related accessory substances [including those in the hiassic acid group]). **BLS 2577** [**BLS 1013** is available for *H. revoluta* s. lat.; i.e. specimens or records that cannot be separated from *H. afrorevoluta*].

Common on wayside and woodland trees and shrubs, more rarely on weakly acidic rocks and walls in inland and maritime situations, and widely distributed on bark in a range of conditions from nutrient poor to nutrient enriched. Throughout Britain and Ireland.

See discussion under *H. afrorevoluta*. Unusual for a *Hypotrachyna* in bearing what appear to be marginal cilia and also lacking the distinct dichotomously branched rhizines typical of this genus. *H. britannica* is also similar, with an almost identical chemistry (save from some accessory metabolites), but that species has narrow parallel-sided lobes, is mainly coastal and occurs almost exclusively on rock.

Marchandiomyces corallinus has been reported from *H. revoluta* s. str.

LC



***Hypotrachyna sinuosa* (Sm.) Hale (1975)**

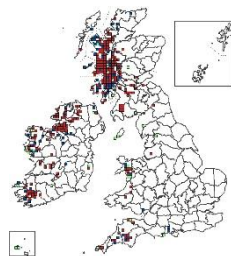
Thallus 1–4 (–6) cm diam., rather compact, sometimes forming extensive patches; lobes (1–) 2–5 mm broad, separate or partly contiguous, overlapping centrally, dichotomously branched with wider, often ascending, truncate apices, axils markedly sinuate; upper surface yellow-grey to yellow-green, smooth, \pm shiny, sorediate; soralia covering apices of ascending lobes, \pm globose; soredia farinose; lower surface jet-black, rhizines dichotomously branched, numerous, often projecting beyond lobe margins. Apothecia and pycnidia not seen (in British material). Cortex K–; medulla C–, K+ yellow \rightarrow red, KC+ red, Pd+ orange, UV– (usnic acid, salazinic acid [major] and traces of related compounds [including norstictic acid]). **BLS 1017**.

On damp siliceous rocks and well-lit acid-barked trees, especially on twigs and young branches in oceanic valley woodland, occasionally on wood and *Calluna* stems; a member of a moist facies of the *Parmelietum laevigatae*, also occasionally in moist *Salix* carr facies of the *Lobarion*; local. W. Britain and Ireland, but with rare and probably casual occurrences further east.

Readily separated from other *Hypotrachyna* species in the British Isles by the yellow-green thallus (usnic acid) and medulla K+ yellow \rightarrow red (salazinic acid). Again, phylogenetic study has shown that this is not a monophyletic species in its traditional circumscription, and East African populations have been accommodated in a separate species, *H. meridionalis* (Kirika *et al.* 2019).

Host to *Nigromacula uniseptata* and with one report of *Clypeococcum cladonema*.

Nb IR

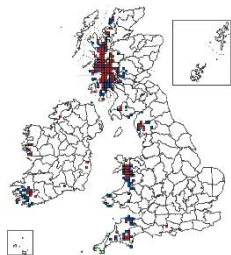


***Hypotrachyna taylorensis* (M.E. Mitch.) Hale (1974)**

Thallus often forming extensive patches, to 15 cm diam., \pm loosely attached; lobes sub-dichotomously to irregularly branched, to 8 mm broad (rarely wider), overlapping, with \pm tightly sinuate axils; margins entire or \pm indented, lobe ends \pm down-turned; upper surface whitish grey, fragile, with occasional irregular white abraded areas caused by peeling of the fragile cortex; soredia and isidia absent; lower surface black, dark brown near margins; rhizines richly dichotomously branched. Apothecia rare; thalline margin coarsely crenulate, without rhizines. Ascospores 9–12 \times 6–10 μ m, almost spherical to broadly ellipsoidal. Conidia 4–4.5 \times ca 1 μ m, bacilliform, with a small swelling near each end. Cortex K+ yellow; medulla C+ carmine-red, K–, KC+ red, Pd–, UV sometimes bluish (atranorin, lecanoric and evernic acids). **BLS 1023**.

Overgrowing mosses on trunks with very acidic bark (pH 3.5–4.0) and rocks in ancient and relict woodlands, occasionally on mosses on rather exposed coastal rocks; local and strongly oceanic. S.W. & W. Britain, N to

Nb IR



Sutherland, mostly upland (also one locality in New Forest), otherwise absent in E. Britain, rare in Ireland except Kerry & W. Cork.

Young specimens may resemble *H. revoluta*, which is always sorediate.

Host to *Didymocyrtis melanelixiae* (Brackel) Diederich *et al.* (2015) [anamorph], *Lichenocmium erodens* and an unidentified *Nectriopsis* with spores $7\text{--}9.5 \times 1.7\text{--}2.3 \mu\text{m}$.

IMSHAUGIA S.L.F. Meyer (1985)

Thallus foliose, closely appressed, dorsiventrally flattened. **Lobes** narrow, linear, without cilia. **Upper surface** mineral grey to grey or grey-green (atranorin and chloroatranorin), without maculae or pseudocyphellae, with isidia or soredia. **Upper cortex** paraplectenchymatous with a pored epicortex. **Cell walls** containing *Cetraria*-type lichenan. **Medulla** white. **Lower surface** whitish to pale brown; rhizines moderate to dense, extending to the margins, simple, \pm tufted, concolorous. **Ascomata** apothecia, mostly laminal, sessile to shortly stalked, disc imperforate. **Ascospores** ellipsoidal, 8 per ascus. **Conidiomata** pycnidial, laminal or marginal, globose, emergent. **Conidia** *Psora*-type, borne terminally from joints of conidiogenous hyphae, bifusiform. **Chemistry**: cortex: atranorin; medulla: orcinol depside (evernic acid) or β -orcinol depside (thamnolic acid). **Ecology**: corticolous.

Imshaugia is similar morphologically to *Parmeliopsis* but is separated from that genus based upon a paler thallus, smaller spores and bifusiform conidia that are much smaller than those of *Parmeliopsis*. According to Divakar *et al.* (2017) it occupies an isolated position within the Parmeliaceae, and appears to be most closely related to *Platismatia*. However, the study of Grewe *et al.* (2020), which used a larger set of genes, indicates that *Imshaugia* and *Parmeliopsis* form sister groups distinct from *Platismatia*.

There is only one British species.

Literature:

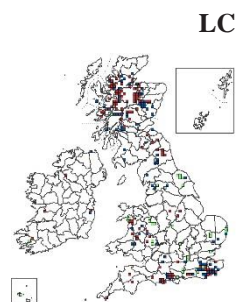
Divakar *et al.* (2017), Grewe *et al.* (2020), Louwhoff & Purvis (2009), Meyer (1982, 1985).

Imshaugia aleurites (Ach.) S.L.F. Meyer (1985)

Thallus 1–3 (–5) cm diam., often forming rosettes or scattered unorientated lobes, closely appressed to the substratum, the lobes (0.5–) 1–3 mm wide, linear to sublinear, indented or sometimes branching towards the apices, divergent, contiguous or overlapping; upper surface grey-white, \pm shining, older parts often obscured by a \pm continuous crust of crowded, concolorous or slightly darker cylindrical isidia which may become eroded; lower surface whitish to pale brown with unbranched rhizines. Apothecia infrequent, to 3 mm diam., sessile to semi-stalked; disc red-brown, flat and undulating; thalline margin isidiate and disappearing; paraphyses unbranched, apices not or little enlarged. Ascospores $6\text{--}9 \times 5\text{--}6 \mu\text{m}$. Conidia $3.5\text{--}4.5 \times ca 1 \mu\text{m}$, bifusiform. Cortex K+ yellow; medulla C–, K+ yellow, KC–, Pd+ yellow-orange, UV– (atranorin and thamnolic acids). **BLS 1033**.

On acid bark and wood, especially conifer and *Betula*, rarely directly on peat and siliceous rocks. Formerly restricted to ancient Caledonian pine woodlands in Scotland, but now of scattered occurrence in C. Wales & N. England, and also frequent and spreading in S. England on artificial substrata, e.g. worked oak and softwood fence rails.

At times eroded isidia have been mistaken for the soredia of *Parmeliopsis hyperopta* but this may be distinguished by its truly sorediate upper surface and UV+ glaucous medulla (divaricatic acid). *I. aleurites*



superficially resembles *Physcia clementei* but that species is Pd–, has narrower lobes, and occurs in a different habitat.

Lichenicolous fungi reported are: *Lichenocodium erodens*, *Marchandiomyces corallinus*, *Spirographa* sp. (as *Cornutispora lichenicola*), *Tremella imshaugiae* Diederich *et al.* (2020) and an unidentified *Sphinctrina* from Glen Strathfarrar pinewood.

MELANELIA Essl. (1978)

Thallus foliose, loosely to closely appressed, dorsiventral, large. **Lobes** short and rounded to elongate, margins without cilia. **Upper surface** brown or olive-brown to brown-black (K– and N–), thin or fleshy, not maculate, sometimes with pseudocyphellae or soredia. **Upper cortex** composed of isodiametric cells, with a non-pored epicortex. **Medulla** loosely packed, white. **Lower surface** pale tan to black; rhizines mostly unbranched, rarely furcate or penicillate at the tips, tan to black. **Ascomata** apothecia, laminal, sessile or rarely short-stalked; disc concave to flat, imperforate, red-brown to black-brown. **Ascospores** ellipsoidal, 8 per ascus. **Conidiomata** pycnidia, laminal and immersed or marginal and emergent (sessile). **Conidia** fusiform to weakly bifusiform, or bacilliform. **Chemistry**: unidentified brown pigment(s) which give the lichen its characteristic colour; lacking secondary substances or producing orcinol para-depsides, β -orcinol depsidones or aliphatic acids. **Ecology**: saxicolous or very rarely corticolous in partial shade or open situations.

At first glance *Melanelia* may be confused with some brown species of *Xanthoparmelia*, another parmelioid group with a dark-coloured upper cortex. The two are separated by a different cortical reaction to nitric acid (N), usually blue-green for *Xanthoparmelia* and negative for *Melanelia*. In addition, *Melanelia* has a non-pored rather than a pored epicortex and the cell wall contains a different polysaccharide (isolichenan rather than *Xanthoparmelia*-type). The genus is not closely related to *Melanelixia* and *Melanohalea*, but belongs to the cetrarioid clades.

Melanelia disjuncta was recognized as anomalous for the genus by Hawksworth *et al.* (2008), and was transferred to the new genus *Montanelia* by Divakar *et al.* (2012). *M. disjuncta* is isidiate, in contrast to species of *Melanelia*, and the conidia are not bifusiform.

Literature:

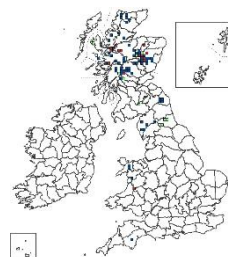
Blanco *et al.* (2004a), Divakar *et al.* (2012, 2017), Elix (1993), Esslinger (1978), Hawksworth *et al.* (2008), Louwhoff & Esslinger (2009a), Lumbsch *et al.* (2008), Otte *et al.* (2005), Thell (1995), Thell *et al.* (2004), Westberg & Thell (2011b), Xu *et al.* (2017).

- | | | |
|---|--|------------------|
| 1 | Pseudocyphellae laminal and marginal, without thickened, raised margins; medulla K+ yellow→red (stictic and norstictic acids) | <i>hepatizon</i> |
| | Pseudocyphellae laminal, with thickened, often darker, raised margins; medulla K– (fumarprotocetraric and protocetraric acids) | <i>stygia</i> |

Melanelia hepatizon (Ach.) A. Thell (1995)

Thallus to 20 cm diam., loosely to tightly appressed; lobes 1–2 mm broad, elongate, ± convex, the margins often slightly thickened and raised; upper surface olivaceous to black, shiny, with small (visible with $\times 10$ handlens) rounded to elongate whitish pseudocyphellae, each with a thick, ± raised, often darker, margin; soredia and isidia absent; lower surface dark brown-black, sometimes paler near the margin; rhizines unbranched or rarely forked, scattered. Apothecia common, to 9 mm diam., usually submarginal, sessile to shortly stalked; disc dark brown; thalline margin grossly

Nb



warted, irregularly crenate and pseudocyphellate. Ascospores $7\text{--}10.5 \times 4.5\text{--}6 \mu\text{m}$. Pycnidia numerous, marginal to submarginal, \pm spherical, sessile or shortly stalked with a constricted base, black; conidia $3.5\text{--}5.5 \times 1\text{--}1.5 \mu\text{m}$, bifusiform. Cortex K $^-$, N $^-$; medulla K $^+$ yellow, KC $^+$ yellow-orange, C $^-$, Pd $^+$ yellow, UV $^-$ (stictic and norstictic acids). **BLS 0332**.

Like *Cetraria commixta* but with marginal and laminal pseudocyphellae, a dark brown to black lower surface with scattered, dark rhizines, conidia which are $3.5\text{--}5.5 \times 1\text{--}1.5 \mu\text{m}$ and bifusiform and a K $^+$ yellow medullary reaction (stictic acid).

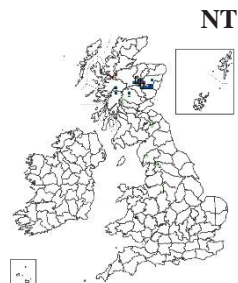
Siliceous rocks in uplands; very local. S.W. England (Devon, Dartmoor), N. Wales, Cumbria and N. Pennines, Scotland (Highlands).

Melanelia stygia (L.) Essl. (1978)

Thallus 2–6 (–8) cm diam., firmly but not tightly appressed, fleshy; lobes 0.5–2 mm broad, sublinear-elongate, very variable, fleshy-looking and \pm convex, marginal lobes irregularly branching in all directions, overlapping or entangled; margins irregularly nodulose, occasionally severely so and then losing their dorsiventral nature; upper surface dark brown-black, shiny, with small (visible with $\times 10$ handlens) dark-brown laminal punctiform pseudocyphellae, each with a thick \pm raised, often darker margin; soredia and isidia absent; lower surface dark brown-black, wrinkled; rhizines coarse, unbranched or rarely forked, scattered. Apothecia common, to 5 mm diam., sessile, sometimes becoming obscured by overlapping lobes; disc dark brown, concave when immature, becoming flat and undulating or convex when mature, shiny; thalline margin grossly warted, irregularly crenate and pseudocyphellate. Ascospores $7\text{--}10 \times 4.5\text{--}6 \mu\text{m}$. Pycnidia numerous, immersed, black, sometimes confluent, rounded or elliptical in outline (may be confused with pseudocyphellae at first glance); conidia $3.5\text{--}5.5 \times ca 1 \mu\text{m}$, bacilliform. Cortex K $^-$, N $^-$; medulla C $^-$, K $^-$, KC $^-$, Pd $^+$ orange-red or Pd $^-$, UV $^-$ (fumarprotocetraric and protocetraric acids). **BLS 1019**.

On siliceous rocks, montane; very local. N. Scotland (Highlands), very rare in the Lake District and C. Wales (Radnor).

M. hepatizon has marginal apothecia, marginal and markedly emergent pycnidia, mostly marginal pseudocyphellae and its medulla is K $^+$ yellow (stictic and norstictic acids). *Allantoparmelia alpicola* has a matt surface, without pseudocyphellae, lacks rhizines and a Pd $^+$ pale yellow, C $^+$ pink medulla (alectorialic and barbatolic acids).



MELANELIXIA O. Blanco *et al.* (2004)

Thallus foliose, loosely to moderately adnate, dorsiventral, large. **Lobes** flat to concave, short, apices rounded, margins without cilia. **Upper surface** olive-green to dark brown, smooth to rugose, maculate or not, lacking pseudocyphellae, with or without isidia, soredia or cortical hairs. **Upper cortex** composed of isodiametric cells covered with a pored epicortex (dispersed pored or fenestrations). **Medulla** loosely packed, white to pale yellow or occasionally orange in lower parts. **Lower surface** flat, smooth, dark brown to black; rhizines unbranched, sometimes with white tips. **Ascomata** apothecia, laminal, sessile or slightly stalked; disc concave to flat, imperforate, pale to dark brown, thalline margin commonly maculate and with an abundantly fenestrated or pored epicortex. **Asci** elongate, clavate, *Lecanora*-type, apically thickened, without an internal apical beak, 8-spored. **Ascospores** ellipsoidal to ovoid, colourless, thin-walled, aseptate. **Conidiomata** pycnidia, laminal, immersed. **Conidia** cylindrical to fusiform, aseptate, colourless. **Chemistry**: cortex with a brown coloured pigment but no other compounds; medulla containing depsides (lecanoric and sometimes 5-methoxylecanoric acids), sometimes with rhodophyscin. **Ecology**: occurring on bark or wood, or saxicolous.

At first glance *Melanelixia* may be confused with some of the brown *Xanthoparmelia* species, previously assigned to *Neofuscelia*. The two genera are separated by a different cortical reaction to nitric acid (N); usually blue-green for the brown *Xanthoparmelia* species and absent for *Melanelixia*. In addition, *Melanelixia* has cell walls composed of a different polysaccharide (isolichenan rather than *Xanthoparmelia*-type [lichenin]). *Pleurosticta* resembles *Melanelixia* but has broader lobes, reticulated epicortical pores, a pigment that is K⁺ and N⁺ violet, and by the presence of depsidones instead of depsides in the medulla. Both *Melanelixia* and *Melanohalea* are distinguished by a non-pored epicortex and pseudocyphellae. *Melanelixia* and *Melanohalea* are closely related, but *Melanelixia* belongs to a quite different clade of the Parmeliaceae.

Literature:

Arup & Sandler Berlin (2011), Blanco *et al.* (2004a, b), Divakar *et al.* (2012, 2017), Esslinger (1977), Hawksworth *et al.* (2008), Laundon (2006), Leavitt *et al.* (2012b, 2016), Louwhoff & Esslinger (2009b), Otte *et al.* (2005), Westberg & Thell (2011c).

- 1 Thallus with unbranched or branched isidia, never associated with soredia; thallus surface glossy2
 Thallus with a mixture of soredia and ± secondarily corticate isidia; thallus surface matt3
- 2(1) Thallus black-brown; usually on siliceous rocks *fuliginosa*
 Thallus green to light olive brown; usually on bark or wood *glabratula* [and *hawksworthii*]
- 3(1) Sorediate-isidiate areas pale yellow when abraded, thallus ± closely appressed, pale cortical hairs at ends of lobes absent (×20 lens) *subaurifera*
 Sorediate-isidiate areas white when abraded, thallus often ascending at the margins, pale cortical hairs present on lobe ends (×20 lens) *subargentifera*

Melanelixia fuliginosa (Fr. ex Duby) O. Blanco *et al.* (2004)

Thallus to 10 (–15) cm diam., thin, closely appressed centrally but often free at the margins, rosette-forming or irregular; lobes 1–2 mm broad, flat or occasionally with the apices ± upturned, elongate, contiguous or overlapping; margins crenate or irregularly incised; upper surface dark brown to blackish, glossy especially towards lobe ends, isidiate; isidia cylindrical, smooth, becoming branched-coralloid, leaving a white area when abraded, usually numerous and often obscuring the centre of the thallus; medulla white, orange pigment (K⁺ purple [rhodophyscin]) sometimes present, especially in the lower part; lower surface black; rhizines pale brown, unbranched. Apothecia occasional, to 6 mm diam., sessile or very shortly stalked; disc red-brown, shiny; thalline margin often becoming isidiate. Ascospores 10–14 × 5.5–9.5 μm. Pycnidia sparse. Conidia ± swollen towards each end, 6–7.5 × ca 1 μm. Cortex K[–], N[–]; medulla C⁺ red, K⁺ purple or K[–], KC⁺ red, Pd[–], UV[–] (lecanoric and 5-methoxylecanoric acids, rhodophyscin, unknowns). **BLS 0998.**

Primarily on siliceous rocks, tiles (slate) and memorials (granite), pebbles of fixed shingle beaches and only occasionally on acid-barked trees in exposed conditions. Widespread and common in Britain and Ireland, perhaps less so in C. Ireland.

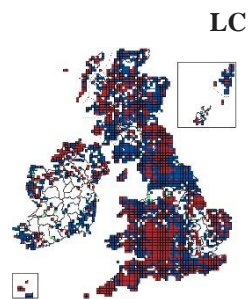
Differs from *Melanelixia glabratula* in the consistently dark brown to black-brown colour of the upper surface, usually being more exuberantly isidiate, and by being primarily saxicolous. *M. glabratula* and *M. fuliginosa* are both phylogenetically divergent species, and further cryptic speciation may be uncovered in the future.

Host to *Brianccoppinsia cytospora*, *Lichenocodium erodens*, *L. usneae* and *Marchandiomyces corallinus*.

Melanelixia glabratula (Lamy) Sandler & Arup (2011)

Melanelixia fuliginosa subsp. *glabratula* (Lamy) J.R. Laundon (2006)

Thallus 1–5 (–10) cm diam., thin, closely appressed centrally but often free at the margins, rosette-forming or irregular; lobes (2–) 3 (–4.5) mm wide, flat or occasionally with the apices ± upturned, elongate, contiguous or overlapping; margins crenate or irregularly incised; upper surface green to olive brown, sometimes with a reddish tinge, glossy especially towards the lobe ends, isidiate; isidia cylindrical, arising singly, smooth, becoming



LC

branched-coralloid, leaving a white area when abraded, usually numerous and often obscuring the centre of the thallus; medulla white, orange pigment (K+ purple [rhodophyscin]) sometimes present, especially in the lower part; lower surface black, often with a brown marginal zone; rhizines pale brown, unbranched. Apothecia occasional, to 5 mm diam., very shortly stalked; disc red-brown, shiny; thalline exciple often becoming isidiate. Ascospores $10\text{--}14 \times 5.5\text{--}8 \mu\text{m}$. Conidia \pm swollen towards each end. Cortex K-, N-; medulla C+ red, K+ purple or K-, KC+ red, Pd-, UV- (lecanoric and 5-methoxylecanoric acids, rhodophyscin, unknowns). **BLS 0997**.

On bark of many species of broad-leaved trees, rarely on conifers or on lignin, also not uncommonly on siliceous stone (as on gravestones) and basic rocks. Throughout Britain and Ireland, except parts of N. Midlands & S. Pennines.

The K+ purple reaction from the pigment rhodophyscin can often also be obtained in squash preparations of the black lower cortex and rhizines. *Melanelixia subaurifera* has isidia that arise from partially corticate soredia which are fragile and easily abraded (as when lightly rubbed with a finger), revealing a pale yellow (K-) eroded patch and it never contains the K+ purple pigment in the medulla and lower cortex. See also *Melanohalea elegantula*.

Host to the lichenicolous fungus *Abrothallus bertianus* De Not. (1849) **BLS 2001** (black, \pm faintly green-pruinose, convex apothecia); also *Crittendenia coppinsii* (P. Roberts) Diederich *et al.* (2021) and *Paranectria oropensis* (Ces.) D. Hawksw. & Piroz. (1977).

Melanelixia hawksworthii S.D. Leav., Essl., Divakar, A. Crespo & Lumbsch (2016) **NE**

Apparently indistinguishable in morphological terms from *Melanelixia glabrata*, but occupying a phylogenetic clade sister to *M. subaurifera* (see Leavitt *et al.* 2012b, 2016). **BLS 2848**.

Known from two collections from oceanic areas of Scotland (on bark of *Fagus*, Wester Ross and on unidentified bark, Skye).

Melanelixia subargentifera (Nyl.) O. Blanco *et al.* (2004)

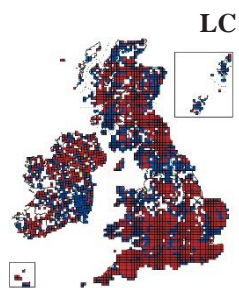
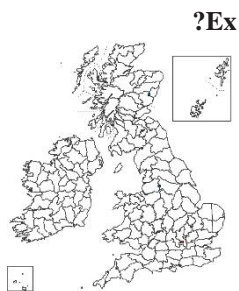
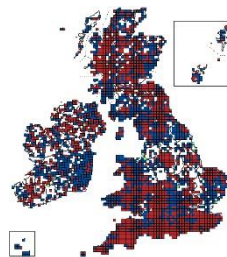
Thallus ca 5 cm diam., loosely appressed, margins usually ascending; lobes to 3 mm broad, flat; upper surface pale olive-brown to dark brown, often with a reddish or yellowish tinge, \pm matt, usually pruinose, colourless cortical hairs present towards the lobe ends ($\times 20$ lens); soralia laminal or marginal, usually confluent towards the centre of the thallus; soredia coarsely granular or isidioid. Cortex K-, N-; medulla and soralia C+ red, K-, KC+ red, Pd-, UV- (lecanoric acid). **BLS 1570**.

On nutrient-rich tree trunks, in *Xanthorion* communities. Known on a single *Juglans* trunk in E. Scotland (Kincardineshire) from 1983 to 1996, but not seen on the tree in 2004. Perhaps a recent range extension that did not become established. Records from England (S. Lancashire and Buckinghamshire) are almost certainly errors.

Distinguished from *Melanelixia subaurifera* and *M. glabrata* by the loosely attached thallus with \pm reflexed lobes, the granular to isidioid, partially corticated soredia, the lack of true isidia and by the presence of tiny cortical hairs towards the lobe margins and ends. North American populations previously identified as *M. subargentifera* have been assigned to a separate species, *M. ahtii* (see Leavitt *et al.* 2016).

Melanelixia subaurifera (Nyl.) O. Blanco *et al.* (2004)

Thallus 0.5–5 (–10) cm diam., often rosette-forming, thin, closely appressed centrally but often free at the margins; lobes to 5 mm broad, flat or occasionally with the apices \pm upturned, irregular, radiating, contiguous, sometimes overlapping; margins often crenate or irregularly incised; upper surface brown to green-brown, rarely with a reddish tinge, matt or rarely shiny in parts (particularly towards the lobe apices), faintly to extensively pitted or ridged, isidiate-sorediate; isidia globose, cylindrical or irregular, soft, secondarily derived from soredia by partial cortication, arising in clusters and often leaving white patches (rarely yellow: subauriferin) where abraded (could be mistaken for pseudocypellae); medulla white; lower surface dark brown to black; rhizines concolorous, unbranched. Apothecia rare, to 2 mm diam., thalline margin sorediate. Ascospores



9–12 × 5.5–7 µm. Conidia 5.5–7 × ca 1 µm. Cortex K–, N–; medulla and soredia C+ red, K–, KC+ red, Pd–, UV– (lecanoric acid and subauriferin). **BLS 1020**.

On smooth bark of neutral to acid-barked trees, especially horizontal branches and twigs, less frequently on trunks, less commonly on rocks; moderately pollution-tolerant; frequent. Widespread throughout Britain and Ireland and now almost ubiquitous.

Melanelixia glabratula lacks soredia and has branched, true isidia, a more shiny upper surface and a K+ purple, orange medullary pigment (rhodophyscin). Immature or poorly developed specimens can be definitively distinguished from *M. subaurifera* by the presence of 5-methoxylecanoric acid.

Host to *Abrothallus bertianus*, *Crittendenia coppinsii*, *Erythricium aurantiacum* (Lasch) D. Hawksw. & A. Henrici (2015), *Illosporopsis christiansenii* and *Lichenostigma maureri*.

MELANOHALEA O. Blanco *et al.* (2004)

Thallus foliose, large, loosely to ± closely appressed, dorsiventral. **Lobes** flat to concave, flat, short, the apices rounded, margins without cilia. **Upper surface** olive-green to dark brown, smooth to rugose, not maculate, with or without isidia or soredia, commonly pseudocyphellate on warts or on tips of isidia. **Upper cortex** composed of isodiametric cells, with a non-pored epicortex. **Medulla** loosely packed, white. **Lower surface** flat, smooth, pale brown to black; rhizines unbranched. **Ascomata** apothecia, laminal, sessile to shortly stalked; disc imperforate, concave to convex, brown, thalline margin with pseudocyphellate papillae, not maculate. **Asci** elongate, clavate, *Lecanora*-type, apically thickened, without an internal apical beak. **Ascospores** globose to ovoid or ellipsoidal, thin-walled, colourless, 8–32 per ascus. **Conidiomata** pycnidia, laminal, immersed. **Conidia** cylindrical to fusiform, aseptate, colourless. **Chemistry:** cortex with a brown coloured pigment but no other compounds; medulla containing depsidones (fumarprotocetraric or norstictic acids), or lacking secondary metabolites. **Ecology:** occurring on bark or wood, rarely on rocks.

Melanohalea may be confused with some of the brown *Xanthoparmelia* species, previously known as *Neofusclia*. The two are separated by a different cortical reaction to nitric acid (N), usually blue-green for the brown *Xanthoparmelia* species and negative for *Melanohalea*. In addition, *Melanohalea* contains a cell wall composed of a different polysaccharide (isolichenan rather than *Xanthoparmelia*-type [lichenan]). *Pleurosticta* resembles *Melanohalea* but has broader lobes, reticulated epicortical pores and a pigment that is K+ and N+ violet. *Melanelixia* is distinguished by a pored epicortex and lacks pseudocyphellae. *Melanelia* has flat and effigurate rather than raised pseudocyphellae; all British species have a C+ red medulla.

Literature:

Blanco *et al.* (2004a, b), Divakar *et al.* (2017), Esslinger (1977), Leavitt *et al.* (2012a, 2013, 2016), Louwhoff & Esslinger (2009c), Otte *et al.* (2005), Westberg & Thell (2011d).

1	Isidia or papillae present	2
	Isidia or papillae absent	4
2(1)	With distinctly even-topped, ± evenly spaced papillae; isidia absent; apothecia frequent	<i>exasperata</i>
	With scattered to abundant, randomly distributed isidia; apothecia very rare	3
3(2)	Isidia becoming ± branched, mostly erect, solid; lobes appressed	<i>elegantula</i>
	Isidia remaining unbranched, often ± decumbent, hollow, clavate or spatulate; lobes ascending	<i>exasperatula</i>

- 4(1) Thallus of numerous overlapping squamule-like lobes, marginal lobes absent or poorly developed, pseudocyphellae absent; apothecia unknown; medulla Pd- *laciniatula*
 Thallus rosette-forming, pseudocyphellae present on upper surface; apothecia common; medulla Pd+ rust-red *septentrionalis*

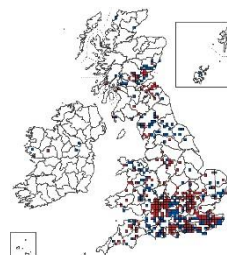
Melanohalea elegantula (Zahlbr.) O. Blanco *et al.* (2004)

Thallus to 5 cm diam., ± closely appressed, thin; lobes to 2 mm broad, ± flat, contiguous, ± overlapping at the centre; upper surface brown to green-brown, dark olive-green when wet, mostly smooth or occasionally undulating and slightly pitted, matt or occasionally shiny towards the margins, lacking pseudocyphellae, densely isidiate; isidia laminal and marginal, intact and not becoming soresiate, cylindrical, becoming branched-coralloid, not inflated, ± smothering older parts of the thallus, initials on newer lobes discrete, ± evenly spaced; lower surface pale brown; rhizines unbranched, pale, scattered. Apothecia very rare, 2–3 mm diam.; thalline margin densely isidiate. Ascospores 8–11 × 4.5–6.5 µm, ellipsoidal. Pycnidia not seen. Lichen products not detected by TLC. **BLS 0993.**

On ± nutrient-rich, acid-barked trees, more rarely on rocks including memorials, increasing in relatively polluted areas, frequently with *M. laciniatula*. An open parkland species. S. and S.E. England, E. & N. Wales (where it is still rare), extending locally to C., N. & S.E. Scotland, recently found in W. Ireland (rare).

Melanelixia fuliginosa and *M. glabrata* have a dark lower surface, C+ red medulla (lecanoric acid) and a tendency for the young initials of the isidia to be more randomly distributed. *Melanohalea exasperatula* also lacks secondary compounds but has coarser ± spathulate and ± decumbent, hollow isidia.

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Melanohalea exasperata (De Not.) O. Blanco *et al.* (2004)

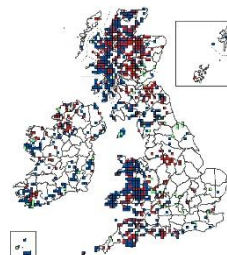
Thallus to 2–3 (–6) cm diam., closely appressed, thin; lobes irregular to sublinear, 1–4 (–6) mm broad, discrete or commonly contiguous or somewhat overlapping; upper surface colour variable, red-brown, olive or black-brown, ± green-brown when wet, commonly undulating and pitted centrally, matt, densely papillate; papillae appearing like stumpy isidia (with hand lens), evenly scattered, conical with a distinctly flattened top and rim, 50–100 µm diam., with a pseudocyphella at the apex (best seen using dissecting microscope); lower surface black with a pale tan to cream margin; rhizines unbranched, brown centrally and pale tan to white at the margins, sometimes seen projecting beyond lobe margins. Apothecia common, 1–4 (–5) mm diam., sessile or semi-stalked; disc red- to olive-brown, flat and undulating or concave; thalline margin papillate. Ascospores 9–12 × 5–6 µm. Conidia 7–8 × ca 1 µm, bacilliform. Lichen substances not detected by TLC. **BLS 0995.**

On acid-barked, smooth twigs and branchlets of broad-leaved trees but very rarely on trunks, rarely on fence posts and (exceptionally) rocks, in well-lit but sheltered sites, localized and dispersed; possibly still decreasing in S.E. & S. England. Most common in W. & N. Britain and Ireland; presumed sensitive to SO₂ pollution.

Readily distinguished by the presence of evenly dispersed, flat-topped, pseudocyphella-tipped papillae on the upper surface and thalline margin.

Commonly host to *Abrothallus cf. bertianus*; also recorded are *Lichenocodium erodens* and *Roselliniella atlantica* Matzer & Hafellner (1990).

LC



Melanohalea exasperatula (Nyl.) O. Blanco *et al.* (2004)

Thallus to 5 cm diam., ± closely appressed in the centre, thin, often with raised, wavy marginal lobes to 5 mm broad with irregularly incised margins; upper surface pale olive-green to dark olive-brown or red-brown, semi-transparent when wet, isidiate; isidia unbranched, inflated, hollow, becoming clavate or ± spathulate and eventually developing into divided lobules, often decumbent and then orientated in all directions, very dense towards the centre of the thallus; lower surface pale tan to pale brown or concolorous with the upper surface, dark brown centrally; rhizines scattered, pale. Apothecia very rare, 2–3 mm diam.; disc concave, pale red brown; thalline margin ± uneven, isidiate. Ascospores 8–10 × 3.5–8 µm, ellipsoidal. Pycnidia not seen in British specimens. Lichen products not detected by TLC. **BLS 0996.**

LC

On trunks and branches of nutrient-rich wayside broad-leaved trees (especially *Acer pseudoplatanus*) or on open hillsides, occasionally saxicolous, especially on walls and wooden fence rails under trees, often in relatively polluted areas and increasing, also directly foliicolous with young lobules establishing on spruce needles; possibly with high nitrogen or phosphate requirements. Scattered throughout Britain and Ireland, less common in S.E. and E. England and in lowland areas further north.

Readily distinguished by the presence of distinctive, \pm decumbent isidia, which are inflated and hollow and become clavate or \pm spatulate in shape.

Melanohalea laciniatula (Flagey ex H. Olivier) O. Blanco *et al.* (2004)

Thallus to 5 cm diam., the thalli sometimes coalescing to form large patches to 15 cm diam., thin, usually composed of numerous conspicuous small thin overlapping flat or suberect folioles; occasionally with distinct well-developed closely appressed thin marginal lobes that are short and irregular, separate or overlapping, with irregularly incised margins; upper surface grey-brown to olive-brown, olive-green when wet, lacking pseudocyphellae; lower surface pale tan or cream; rhizines unbranched, scattered, concolorous with the lower surface. Apothecia and pycnidia unknown. Lichen products not detected by TLC. **BLS 1001.**

On well-lit, nutrient-rich trunks and especially overhanging branches of acid-barked broad-leaved trees, particularly in parklands or woodland edges, occasionally on conifers, siliceous rocks and walls, increasing in relatively air-polluted sites; locally frequent. Southern England, also throughout much of Cumbria, E. Highlands and C. Scotland at low to moderate altitudes, scattered in Wales and Ireland.

Readily distinguished by the usually poorly developed marginal lobes and a thallus almost entirely composed of numerous conspicuous small thin overlapping flat to suberect folioles.

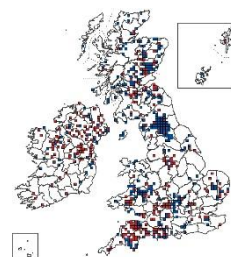
Recorded as host to *Erythricium aurantiacum*, *Lichenocodium erodens* and *Marchandiomyces corallinus*.

Melanohalea septentrionalis (Lynge) O. Blanco *et al.* (2004)

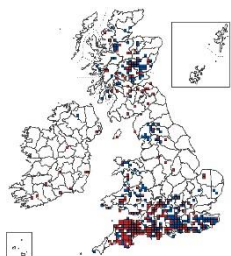
Thallus forming small rosettes, 1–3 (–5) cm diam., closely appressed, occasionally with upturned lobe apices, thin; lobes 1–3 (–5) mm broad, flat to somewhat convex, discrete to overlapping with \pm wavy margins; upper surface red- or dark brown, frequently pitted, shiny at the margins; pseudocyphellae small, dot-like, appearing like scattered white dots (with hand lens); lower surface pale to dark brown; rhizines unbranched, scattered, pale to dark brown. Apothecia abundant, often crowded and overlapping, covering most of the thallus apart from the extreme margin, 0.5–3 (–5) mm diam.; disc red-brown, concave when immature, becoming flat and undulating; thalline margin thin, smooth with many pseudocyphellae. Ascospores 9–13 \times 5–8 μ m, ellipsoidal. Conidia 5–6.5 \times ca 1 μ m, bacilliform. Cortex K–, N–; medulla C–, K–, KC–, Pd+ orange-red, UV– (fumarprotocetraric and protocetraric acids). **BLS 1016.**

Mainly on twigs of *Betula* in well-lit open situations, especially margins of woods, often with *Cetraria sepicola* and *Tuckermannopsis chlorophylla*; very local. N.E. Scotland (Cairngorm region).

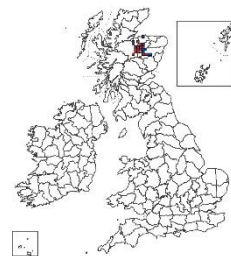
Forms small, neat, richly fertile thalli. The occurrence on *Betula* in Britain is unusual as it is normally reported on *Alnus incana* and *Salix* abroad. *Melanelia olivacea* (L.) Ach. (1803), unknown in Britain, has a more wrinkled, matt thallus, a broader more distinct marginal zone without apothecia and a crenulate thalline exciple. It has been incorrectly reported from Scotland.



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MENEGAZZIA A. Massal. (1854)

Thallus foliose, dorsiventral, lobate, \pm radiate, often forming rosettes or spreading irregularly, rather closely attached throughout; lobes \pm inflated, tubular, hollow. **Upper surface** smooth, with rounded

perforations, sometimes pruinose. **Lower surface** corticate, uneven, blackened, without rhizines or perforations; walls of internal medullary cavity white or rarely pigmented above, black at the base. **Photobiont** trebouxoid. **Soredia** and, rarely, isidia present in some species. **Ascomata** apothecia, laminal, rounded, cup-shaped, sessile to ± stalked. **Thalline margin** well-developed, persistent, thin. **Disc** concave, ± shining. **Epithecium** brown, non-granular. **Hymenium** colourless, I+ blue. Hypothecium of thick-walled, conglutinated hyphae. **Hamathecium** of paraphyses, richly branched and anastomosed, apical cells not capitate, ± pigmented. **Asci** 2-spored (some 8-spored spp. in S. Hemisphere). **Ascospores** colourless, aseptate, ellipsoidal, thick-walled. **Conidiomata** pycnidia, immersed, punctiform, laminal; the apex pigmented. **Conidia** bacilliform. **Chemistry**: atranorin in the cortex and various depsides, depsidones or fatty acids in the medulla. **Ecology**: on acid bark and siliceous rocks in oceanic woodlands.

Resembles *Hypogymnia*, but that genus lacks perforations on the upper surface (though they may be present underneath), contains physodic acid and has smaller, thinner-walled ascospores. However, *Menegazzia* and *Hypogymnia* are distantly related in phylogenetic terms, and the former genus shares a common ancestor with *Usnea*, *Cornicularia* and *Coelopogon* (Divakar *et al.* 2017).

A key to lichenicolous fungi is provided by Berger & Zimmermann (2022).

Literature:

Berger & Zimmermann (2022), Divakar *et al.* (2017), James (2009), Kantvilas (2012, 2019), Miadlikowska *et al.* (2011), Westberg & Thell (2011).

- 1 Soralia lip-shaped, ± lacerate, perforate, often ascending, ± forming nodulose-branched, finger-like extensions *subsimilis*
Soralia usually scattered, ± convex, non-perforate, rounded to ring-shaped *terebrata*

Menegazzia subsimilis (H. Magn.) R. Sant. (1942)

Differs from *M. terebrata* in the form of the soralia which, when at the lobe ends, are lip-shaped, ± lacerate, often markedly ascending, ± with nodulose-branched ± ascending finger-like extensions which when mature are perforate, connecting with the lobe cavities of the main thallus; laminal soralia erupt from ± vertically uplifted lobules or protuberances, 0.5–1.5 mm tall; thallus perforations <1 mm diam. Apothecia very rare, unknown Britain and Ireland, the thalline margin ± sorediate. Ascospores ellipsoidal, 36–44 × 17–22 µm. Chemistry as in *M. terebrata*. **BLS 2447**.

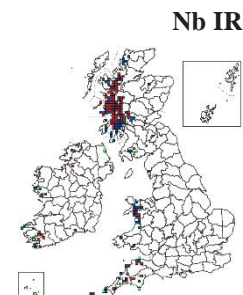
On *Betula* and *Fraxinus*, as well as shaded mossy rocks, in humid woodland. Widespread in W. Scotland, appears rare in Ireland, N. Wales and N.W. England (Lake District).

The perforate soralia with ascending, ± proliferating margins are diagnostic. There is a single report of *Lichenocmium ?erodens* on this host.



Menegazzia terebrata (Hoffm.) A. Massal. (1854)

Thallus to 5 (–10) cm diam., often forming neat closely appressed rosettes or sometimes spreading irregularly; lobes 0.5–1.5 mm broad, ± rounded at the apices, indented, branched, radiating, contiguous for most of their length, more rarely partially discrete, sometimes ± overlapping in older parts of the thallus; upper surface grey or green-grey, often with brownish margins, smooth, shiny, with scattered, round perforations >1 mm diam.; soralia laminal, scattered or sometimes contiguous, rather regular, ± even, not markedly proliferating, non-perforate; lower surface black, wrinkled, without rhizines. Apothecia very rare; disc pale or red-brown. Ascospores 50–68 × 30–36 µm, ellipsoidal; wall ca 5 µm thick. Pycnidia black, rare; conidia 4–5 × ca 1 µm, bacilliform. Cortex K+ yellow (atranorin), medulla C–, K+ yellow, KC–, Pd+ yellow-orange, UV– (stictic, constictic, menegazziaic, sometimes with norstictic acids). **BLS 0869**.



On leached acid bark of broad-leaved trees such as *Betula*, *Alnus* and *Quercus*, more rarely conifers, also on mossy siliceous rocks in humid woodlands, rarely in humid coastal sites; locally frequent. W. Scotland, much more localised and potentially declining in W. Ireland, N. Wales, N.W. & S.W. England.

Resembles *Hypogymnia physodes* in colour and inflated lobes, but may be distinguished easily by the scattered perforations on the upper surface and laminal soralia. The UV– medulla is a useful character for separating poorly grown material from *H. physodes*, which has a UV+ pale violet-blue medulla.

Host to *Lichenonium erodens* and *L. lecanorae* (Jaap) D. Hawksw. (1979).

MONTANELIA Divakar, A. Crespo, Wedin & Essl. (2012)

Thallus foliose, adpressed or sometimes pulvinate, loosely to moderately adnate. **Lobes** sublinear, short, narrow, 0.4–3 mm broad, flat to convex, margins not ciliate. **Upper surface** usually dark brown to blackish, smooth to rugulose, not maculate, often with pseudocyphellae. **Pseudocyphellae** flat, effigurate. **Upper cortex** with a nonpored epicortex. **Medulla** white. **Lower surface** smooth to rugulose, black, dark brown at the edges, moderately rhizinate. **Rhizines** short, unbranched, concolorous with the lower surface. **Apothecia** laminal, sessile to subpedicellate; discs imperforate, concave and becoming convex with age, brown, apothecial margin pseudocyphellate. **Asci** *Lecanora*-type, 8-spored. **Ascospores** aseptate, colourless, ellipsoidal or rarely ovoid, thin-walled. **Conidiomata** pycnidial, immersed, laminal. **Conidia** cylindrical to fusiform. **Ecology**: on siliceous rocks, very rarely on wood.

Montanelia was characterized by Divakar *et al.* (2012) by having short, narrow lobes with flat to convex margins, a nonpored epicortex, flat, effigurate pseudocyphellae on the upper surface, cylindrical to fusiform conidia, and a medulla containing orcinol depsides. There is only one British species.

Literature

Divakar *et al.* (2012), Esslinger (1977, 1978).

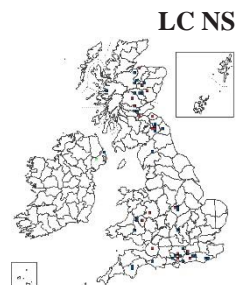
Montanelia disjuncta (Erichsen) Divakar, A. Crespo, Wedin & Essl. (2012)

Melanelia disjuncta (Erichsen) Essl. (1978)

Thallus to 5 cm diam., closely appressed, fleshy; lobes 0.5–1.5 mm broad, flat or slightly convex, short, compact and clustered centrally, often broadened towards the tips, bearing rounded sub-marginal white pseudocyphellae (×10 lens); upper surface dark brown-black, ± irregularly pitted, matt, shiny towards the margins, isidiate; isidia very small, dark grey to black, peg-like, eroding into coarse soralia, scattered or aggregated into conspicuous granulose or wart-like clusters; lower surface black, with scattered unbranched black rhizines. Apothecia and pycnidia not seen. Cortex K–, N–; medulla C–, K–, KC+ fleeting pink or KC–, Pd–, UV+ white (perlatolic and stenosporic acids). **BLS 0992**.

On hard sunny siliceous, commonly volcanic rocks, mainly upland, on steep-sloping S.W.- to S.-facing rocks, rarely on the coast; very rare and scattered in Britain (C. & W., rarely in the S.E. on granite memorials), E. Scottish Highlands & Ireland.

Melanelixia subaurifera has isidia developing from ± corticate soredia, not from wart-like clusters and *M. subargentifera* has hyaline cortical hairs present towards the lobe ends (×20 lens). The brown *Xanthoparmelia* species previously known as *Neofuscelia*: *X. verruculifera*, *X. pulla* and *X. delisei*, are all primarily coastal. *M. disjuncta* can be separated from these *Xanthoparmelia* species by the proportionally smaller thallus and the N–cortical reaction. *Melanelixia fuliginosa* has a shining upper surface with narrower isidia and a strong C+ red medullary reaction. These latter two isidiate species differ from *X. verruculifera* in their chemistry. *X. perrugata* has a similar chemistry but lacks isidia.



NESOLECHIA A. Massal. (1855)

Thallus absent (lichenicolous), often causing galls. **Ascomata** apothecia, circular to irregular, scattered or in clusters, immersed to sessile, the margin usually indistinct. **Exciple** colourless to dark brown, often reduced and difficult to distinguish. **Hypothecium** colourless to blackish brown, in some species I+ violet. **Hymenium** colourless or pale brown, hymenial gel I– or faintly I+ blue. **Epithecium** pale brown, to olivaceous, with an outer colourless gelatinous layer. **Hamathecium** of septate paraphyses, ± anastomosing, the apices irregularly swollen with dark brown-pigmented caps. **Asci** broadly clavate, 8-spored, *Lecanora*-type. **Ascospores** colourless, aseptate, ovoid to fusiform or lemon-shaped, often inaequilateral, smooth, the wall occasionally thickened at the ends. **Conidiomata** pycnidia, immersed in the host thallus. **Conidia** bacilliform.

Considered by most authors to incite gall formation in infected host tissues, although Diederich *et al.* (2018) suggested that species may develop subspherical to lobate or foliose gall-like structures that can be regarded independent lichenized thalli.

Formerly combined with *Phacopsis* Tul., but differs by a poorly-developed exciple and fusiform, often inaequilateral ascospores, and the separation was confirmed by Peršoh & Rambold (2002) and Divakar *et al.* (2015) using molecular data. *Raesaenia* (q.v.) differs by its ± cylindrical ascospores with thickened apices.

Using a time-banding phylogenetic approach, Divakar *et al.* (2017) concluded that the sequence difference between *Nesolechia*, *Canoparmelia* and *Punctelia* was insufficient to justify recognition of three separate genera, and accordingly transferred *N. oxyspora* to the lichenized genus *Punctelia*. However, all three genera are monophyletic in their existing circumscription, and the synonymy has not been accepted for practical reasons.

Only one confirmed species of *Nesolechia* is present in Britain and Ireland.

Literature

Diederich *et al.* (2018), Divakar *et al.* (2015), Peršoh & Rambold (2002), Triebel *et al.* (1995).

Nesolechia oxyspora (Tul.) A. Massal. (1856)

Punctelia oxyspora (Tul.) Divakar, A. Crespo & Lumbsch (2017)

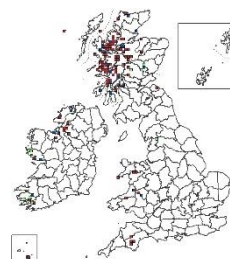
Thallus absent. Apothecia initially immersed, becoming erumpent, 0.2–0.3 (–0.45) mm diam., round, in clusters and sometimes confluent; disc flat to convex, dark brown, matt or glossy, the margin indistinct; exciple thin, colourless or pale brown, composed of ± isodiametric cells; hypothecium colourless to brownish, usually I+ violet; subhymenium colourless; hymenium colourless or pale brown; paraphyses sparsely branched and anastomosed, the apical cells 3–5 µm diam. with small dark brown caps; epithecium brown. Asci clavate, 43–55 × 14–19 µm, 8-spored. Ascospores fusiform-ellipsoidal to narrowly lemon-shaped, the ends mostly attenuated, (13–) 16–18 (–21) × (5–) 5.5–6.5 (–7) µm, thin-walled, smooth. Pycnidia 90–100 µm, globose, immersed in the host thallus; wall brown, paler below. Conidia bacilliform, 5.5–6 × 0.5–1 µm [description largely adapted from Triebel *et al.* 1995]. **BLS 2139.**

On living and moribund thalli of species of *Hypogymnia*, *Parmelia*, *Platismatia* and *Xanthoparmelia*; England (Devon), Wales, Scottish Highlands and islands and W. Ireland.

The host specificity of this species is uncertain. Collections on *Hypogymnia* and *Xanthoparmelia* were referred to *Nesolechia oxyspora* var. *fusca* by Triebel *et al.* (1995) and Diederich *et al.* (2018), which has a dark brown hypothecium that does not react with iodine. The phylogenetic significance of this distinction needs further examination.

Abrothallus parmiliarum is sometimes associated with *Nesolechia* galls on *Parmelia saxatilis* and *P. sulcata*, and has been observed by Diederich (2011); the ecological significance of this three-way parasitism needs further study.

NE



PARMELIA Ach. (1803)

Thallus foliose, loosely attached to closely appressed, dorsiventral, 2–30 (–60) cm diam., corticate on both sides. **Lobes** sublinear to subirregular, 1–25 mm broad, with roughly rounded, often variously incised, margins that lack cilia. **Upper surface** grey to grey-green or dark brownish grey, with or without soredia, pustules or isidia (species from Britain and Ireland are sorediate or isidiate only), with a linear network of pale coarse effigurate pseudocyphellae. **Upper cortex** of intertwined hyphae with a non-pored epicortex. **Cell walls** containing isolichenan. **Medulla** white. **Lower surface** black, uniformly rhizinate; rhizines extending to the margins, mostly unbranched or sometimes squarrosely branched, black. **Ascomata** apothecial, laminal, sessile or shortly stalked, often large; disc rarely perforate, pale to dark brown; thalline margin often incised. **Ascospores** ellipsoidal, aseptate, 8 per ascus. **Conidiomata** pycnidial, laminal, immersed, the ostiole black. **Conidia** cylindrical or bacilliform to bifusiform (latter shape not seen in British species). **Chemistry**: cortex: atranorin and chloroatranorin; medulla: orcinol depsides, orcinol depsidones, β -orcinol depsidones, aliphatic acids. **Ecology**: on bark, wood, rock and, less commonly, soil.

There has been intensive research recently on phylogeny and speciation in the genus *Parmelia*, and a number of cryptic and semi-cryptic species have been recognized (e.g. Crespo *et al.* 2020, Divakar *et al.*, 2016, Molina *et al.* 2017). Most require DNA analysis for confirmation (e.g. Corsie *et al.* 2019), and there have been few British and Irish collections sequenced to date.

British and Irish species formerly included in this genus are now placed in *Arctoparmelia*, *Flavoparmelia*, *Hypotrachyna*, *Melanelia*, *Melanelixia*, *Melanohalea*, *Montanelia*, *Parmelina*, *Parmelinopsis*, *Parmotrema*, *Pleurosticta*, *Punctelia* and *Xanthoparmelia*. *Parmelia* in its current circumscription has a Eurasian and North American distribution; segregates from Eastern Asia and Japan (*Nipponoparmelia*) and Australasia (*Notoparmelia*) have been described (see Divakar *et al.* 2017).

Literature:

Corsie *et al.* (2019), Crespo *et al.* (2002, 2020), Divakar *et al.* (2005, 2016, 2017), Hale (1987), Louwhoff *et al.* (2009a), Molina *et al.* (2004, 2011, 2017), Ossowk *et al.* (2018, 2019, 2021), Thell *et al.* (2008, 2011).

- | | | |
|------|---|-------------------|
| 1 | Upper surface dark brown (or \pm grey-brown in shade), lacking isidia and soredia | 2 |
| | Upper surface grey-white or grey-green, isidiate and/or sorediate | 3 |
| 2(1) | Pseudocyphellae distinct and becoming raised; medulla K+ yellow-red | <i>omphalodes</i> |
| | Pseudocyphellae indistinct, not becoming raised; medulla K– | <i>discordans</i> |
| 3(1) | Thallus isidiate only | <i>saxatilis</i> |
| | (see also <i>ernstiae</i> and <i>serrana</i>) | |
| | Thallus sorediate or with isidia developing from soredia | 4 |
| 4(3) | Thallus with true soredia only, lobes not subpendulous | <i>sulcata</i> |
| | (see also <i>encryptata</i>) | |
| | Thallus with isidium-like soredia, most lobes \pm subpendulous | <i>submontana</i> |

***Parmelia discordans* Nyl. (1886)**

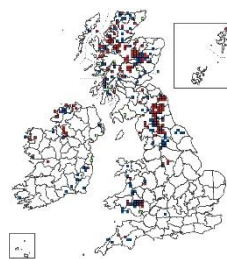
LC

Thallus 5–10 cm diam., moderately loosely attached; lobes to 3 mm broad but mostly not exceeding 1 mm, somewhat brittle, sublinear to subirregular, consistently overlapping and markedly crowded; margins often \pm upturned centrally; upper surface uniformly dark brown, glossy, mostly flat and smooth, with faint scattered white linear pseudocyphellae; lower surface black, rugose, with mostly unbranched or sometimes forked rhizines. Apothecia very rare; disc to 10 mm diam., dark red-brown, for a long time cup-shaped; thalline margin thin,

roughened, paler. Ascospores $10\text{--}15 \times 7\text{--}9 \mu\text{m}$, ellipsoidal. Conidia $5.5\text{--}6.5 \times ca 1 \mu\text{m}$, bacilliform. Cortex K+ yellow; medulla C-, K-, KC+ violet or K-, Pd+ rust-red, UV sometimes glaucous, often faintly so (atranorin, protocetraric and lobaric acids). **BLS 0991.**

On nutrient-poor siliceous rocks in moorland and montane sites, also on very acidic bark in montane areas. Rare in S.W. England, locally frequent in the uplands of Wales, N. England & Scotland, apparently rare in Ireland; likely to be under-recorded due to similarities with *P. omphalodes*.

P. discordans is separated from *P. omphalodes* by its smaller thallus, having pseudocyphellae that are less frequent, not as distinct and do not become raised, by the uniformly dark-brown upper surface and by the K-, not K+ yellow-red reaction of the medulla. The two taxa are considered as subspecies by Thell *et al.* (2011), but preliminary data suggests that they may be distinct in molecular terms (Molina *et al.* 2017).



Parmelia omphalodes (L.) Ach. (1803)

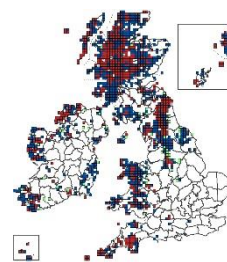
Thallus to 20 cm diam., often forming extended patches, \pm loosely attached; lobes 2–4 mm broad, somewhat brittle, sublinear, discrete, contiguous or markedly crowded and overlapping, apices markedly truncated; upper surface shiny, flat or \pm honeycombed, dark brown, partly greyish (in shade), with oval or elongate pseudocyphellae which frequently fuse to form a coarse \pm complete raised white network; lower surface black, rugose, with numerous unbranched or forked rhizines. Apothecia infrequent; disc to 10 mm diam., dark red-brown, for a long time cup-shaped; thalline margin thin, roughened, paler. Ascospores $10\text{--}15 \times 7\text{--}9 \mu\text{m}$, ellipsoidal. Conidia $5.5\text{--}6.5 \times ca 1 \mu\text{m}$, bacilliform. Cortex K+ yellow; medulla C-, K+ yellow-red, KC+ orange, Pd+ orange, UV sometimes glaucous (atranorin, salazinic and lobaric acids). **BLS 1006.**

On hard acid siliceous rocks, especially granite and sandstone, in moorland and montane sites, rarely on acid bark; widespread. W. & N. British Isles, especially in the upland areas of the Highland zone, rare in the S.E., in Ireland largely confined to the peripheral uplands.

See also *P. discordans*. Distinguished from *P. saxatilis* and *P. sulcata* in thallus colour and the absence of isidia and soredia; shade specimens, which can be greyish, need to be checked carefully. *P. pinnatifida* Kurok. (1976) could occur in northern areas; this has narrower repeatedly branched lobes (<1 mm broad) and pseudocyphellae that are mostly marginal.

Host to the lichenicolous fungi *Abrothallus parmeliarum* (Sommerf.) Arnold (1874), *Homostegia piggottii* (Berk. & Broome) P. Karst. (1873), *Marchandiomyces corallinus* and *Nesolechia oxyspora* (q.v.).

LC

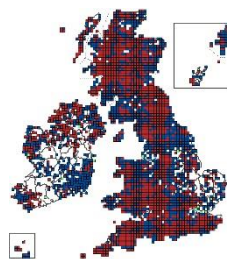


Parmelia saxatilis (L.) Ach. (1803)

Thallus 3–6 (–20) cm diam., often forming complete or partial rosettes, \pm loosely attached; lobes to 3 mm broad, slightly broadened and truncate at the apices, discrete or contiguous and overlapping; upper surface grey-white to grey-green, sometimes tinged brownish towards the lobe ends or if stored for many years, with oval to elongate \pm raised scattered white pseudocyphellae which may fuse to form a \pm complete coarse network, isidiate; isidia concolorous or with the tips tinged brown, cylindrical, initially unbranched but becoming coralloid, at first arising from pseudocyphellae, later from the rest of upper cortex, rather sparse or becoming numerous and obscuring the thallus; lower surface black, brownish towards the margin; rhizines dense, unbranched or occasionally forked. Apothecia occasional, to 1 cm diam.; disc red-brown to dark brown; thalline margin often isidiate at the margin. Ascospores $16\text{--}18 \times 9\text{--}11 \mu\text{m}$. Conidia $6\text{--}7 \times ca 1 \mu\text{m}$, cylindrical or bacilliform. Cortex K+ yellow; medulla C-, K+ orange, KC+ orange, Pd+ orange, UV+ violet-blue or UV- (atranorin, salazinic, sometimes also galbinic, consalazinic, lobaric and protocetraric acids; fatty acids not present). **BLS 1015.**

On acid-barked trees and shrubs, *Calluna* stems, siliceous rocks, walls, memorials, roofing tiles, more rarely on the ground in shady to exposed situations, from the coast to mountain summits; often abundant. Relatively insensitive to SO₂ pollution (<70 $\mu\text{g}/\text{m}^3$), not found on nutrient-enriched substrata and notably decreasing in nutrient-enriched sites. Widespread and common throughout Britain and Ireland, except in parts of East Anglia.

LC



Very variable. The morphologically and chemically similar *P. sulcata* has linear soralia and *P. omphalodes* is usually darker brown and lacks both soredia and isidia.

P. ernstiae and *P. serrana* (see below) are not reliably distinguished from *P. saxatilis* in morphological terms and DNA sequence analysis is needed to identify these species.

Host to the lichenicolous fungi *Abrothallus parmeliarum*, *Erythricium aurantiacum*, *Homostegia piggotii*, *Lichenocodium erodens*, *Lichenopuccinia poeltii* D. Hawksw. & Hafellner (1984), *Nectriopsis rubefaciens*, *Nectriopsis* sp. (spores 9–12 × 1.8–2.3 µm) and *Nesolechia oxyspora* (q.v.).

Parmelia ernstiae Feuerer & A. Thell (2002)

NE

A cryptic species belonging to the *P. saxatilis* complex. Closely similar to *P. saxatilis* but with most samples studied containing lobaric acid, with galbanic acid and the fatty acids lichesterinic and protolichesterinic acids occasionally present.. **BLS 2412.**

More frequent in wetter, western environments in Scotland. Field identification is not advisable, and DNA analysis is necessary. *P. ernstiae* has been characterized in the past by strongly pruinose thalli and isidia, but two recent studies have demonstrated that these are not distinctive features. Partial diagnostic characters identified by Ossowska *et al.* (2018), i.e. relatively broad lobes with narrow marginal lobules and isidia predominantly in the central part of the thallus, were also not confirmed for Scottish material by Corsie *et al.* (2019).

Parmelia serrana A. Crespo, M.C. Molina & D. Hawksw. (2004)

NE

A cryptic species belonging to the *P. saxatilis* complex, usually with pale and rounded lobe tips. Field identification is not advisable, and DNA analysis is necessary. **BLS 2678.**

More frequent in wetter, western environments in Scotland. Attempts to distinguish it from *P. saxatilis sensu stricto* using morphological and chemical methods are inconsistent and appear to differ according to region of study; in our area thalli lack galbanic acid but may contain fatty acids. Molina *et al.* (2004) observed that the thallus tends to be paler and less strongly adnate to the substratum, with lobes that tend to be overlapping, broader and more rounded. Thell *et al.* (2011) observed that the isidia of *P. serrana* are common along thallus margins and often clustered on ridges, in contrast to those of *P. saxatilis* which are mostly laminal and concentrated in the central part. Ossowska *et al.* (2018) agreed with Molina *et al.* that thallus lobes tend to overlap but did not find differences in position of isidia, and indicated that the presence of fatty acids is the most reliable method to distinguish *P. serrana* from *P. saxatilis*. Corsie *et al.* (2019) found that thalli of *P. serrana* occurred more frequently on branches compared with trunks, mostly had rounded rather than truncate lobe tips, and that lobaric acid (UV+) was present only in about one quarter of samples but fatty acids occurred frequently.



Parmelia submontana Nádv. ex Hale (1987)

Nb

Resembles a loosely attached *P. sulcata*, but has small ± orbicular laminal soralia with granular to isidioid soredia on strap-shaped ± pendent little-branched lobes with raised apices and down-rolled margins; rhizines unbranched or rarely forked. Not yet seen fertile in Britain. Cortex K+ yellow turning red; medulla and soralia C–, K+ orange, KC+ orange, Pd+ orange, UV– (atranorin and salazinic acid). **BLS 1785.**

Corticolous on *Acer* and *Fagus* in exposed wayside situations or open woodland glades, also on tops of siliceous gravestones and wooden garden tubs; very local. First recorded for Britain in 1992, with single sites in Lanarkshire, Dumfries, Carmarthen and Devon. The species could well be overlooked.



Parmelia sulcata Taylor (1836)

LC

Thallus 5–10 (–20) cm diam., often forming complete rosettes or randomly intricate, ± loosely attached lobes to 5 mm broad, the apices incised, discrete or contiguous and overlapping, especially at the centre of the thallus; upper surface grey-white to grey-green, sometimes partly white-pruinose, flat to weakly pitted, with scattered oval or elongate white pseudocyphellae that frequently fuse to form a conspicuous coarse incomplete network; soralia elongate, laminal and marginal, derived from breakdown of the cortex above the pseudocyphellae; soredia

granular, eroding; lower surface black, brown towards the margin; rhizines squarrosely branched. Apothecia occasional; disc red-brown to dark brown; thalline margin partially sorediate. Ascospores $11\text{--}14$ (-15) \times $6\text{--}8$ μm . Conidia $5\text{--}8$ \times *ca* 1 μm , cylindrical to bacilliform. Upper cortex K+ yellow, C-, KC-, P+ yellow; medulla K+ yellow turning deep red, C-, KC-, P+ orange (atranorin and salazinic acid). **BLS 1022**.

On trees and any firm siliceous rock, occasionally on ground in shingle, acid dunes, lignum, heather, etc., from coastal regions to exposed mountain summits, more tolerant of less acidic and nutrient-enriched sites than *P. saxatilis* but only moderately tolerant of high levels of SO₂; very common. Throughout Britain and Ireland.

Varies considerably in the size and degree of separation of the lobes, also in the extent of soralium development. Collections with unbranched or forked rhizines might belong to the cryptic segregate *P. barroanae* (Divakar *et al.* 2005, Molina *et al.* 2011), not yet recorded from Britain and Ireland. *P. saxatilis* differs in being isidiate, and *P. submontana* by the more ascending, strap-like lobes, nature of the soredia, and unbranched or forked rhizines.

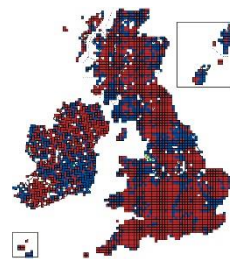
Host to the lichenicolous fungi *Abrothallus parmeliarum*, *Arthophacopsis parmeliarum* Hafellner (1998), *Briancoppinsia cytospora*, *Clypeococcum cladonema*, *Erythricium aurantiacum*, *Homostegia piggottii*, *Illosporiotopsis christiansenii*, *Lichenocodium erodens*, *L. lecanorae*, *Lichenopuccinia poeltii* D. Hawksw. & Hafellner (1984), *Nectriopsis rubefaciens*, *Nesolechia oxyspora* (q.v.), *Perigrapta superveniens* (Nyl.) Hafellner (1996), *Spirographa* sp. (as *Cornutispora lichenicola*) and *Xenonectriella subimperspicua* (Speg.) Etayo (2017).

Parmelia encryptata A. Crespo, Divakar & M.C. Molina (2011)

NE

A cryptic species segregated from *Parmelia sulcata* based on molecular data; see Molina *et al.* (2011, 2017) for more information. Sequenced samples have been reported from Ireland (Killarney) and Wales (Cardiganshire, Merioneth) but may be more widespread. **BLS 2852**.

P. encryptata can easily be distinguished by gel electrophoresis without need of sequencing as it has 800 base pairs in PCR products due to presence of group I introns. Moreover, two distinct ascospore size lengths have been reported in the *P. sulcata* complex (Molina *et al.* 2011) and an examination of fertile material of this species may find a distinctive phenotypic feature.



PARMELINA Hale (1974)

Thallus foliose, tightly appressed, dorsiventral, 2–10 cm diam. **Lobes** contiguous, flat, sublinear or somewhat irregular, 0.5–2 (–5) mm broad, rounded at the apices; margins incised, with sparse unbranched cilia mainly restricted to lobe axils, the axils characteristically rounded. **Upper surface** grey to grey-green or with a yellowish tinge (atranorin), lacking pseudocyphellae, maculate, with or without isidia, soredia or pustules. **Upper cortex** composed of angular cells, with a pored epicortex. **Cell walls** containing isolichenan. **Medulla** white or lower medulla yellow-orange (British and Irish species white only). **Lower surface** very dark brown to black, brownish towards the lobe apices; rhizines mostly unbranched, very rarely squarrose. **Ascomata** apothecia, laminal, sessile or shortly stalked, to 5 mm diam.; disc imperforate, pale to dark brown; thalline margin smooth. **Asci** 8-spored, lecanorine. **Ascospores** broadly ellipsoidal or subglobose. **Conidiomata** pycnidia, laminal, immersed, punctiform. **Conidia** cylindrical or bacilliform to weakly fusiform. **Chemistry**: cortex: atranorin; medulla: orcinol depsides and aliphatic acids. **Ecology**: corticolous, rarely saxicolous.

Hypotrachyna differs from *Parmelina* primarily in the absence of marginal cilia, dichotomously-branched instead of simple or squarrose rhizines (*H. revoluta* is an exception) and by \pm truncate rather than rounded lobe apices. The species of *Hypotrachyna* formerly placed in *Parmelinopsis* are

separated by the smaller, non-maculate thallus and finer apically truncate lobes with \pm abundant cilia that are evenly dispersed along the margins.

The genus has been the subject of several monographic treatments in Europe, but there is confusion about some differential characters which makes identification problematic. It occupies a clade that is sister to that containing the primarily eastern Asian genus *Myelochroa* (Núñez-Zapata *et al.* 2017).

Literature:

Aguirre-Hudson (2021), Alors *et al.* (2019), Argüello *et al.* (2007), Clerc & Truong (2008), Crespo *et al.* (2010), Elix (1993), Hale (1976), Louwhoff *et al.* (2009b), Núñez-Zapata *et al.* (2011, 2015, 2017), Thell (2011a).

- | | | |
|------|---|----------------------|
| 1 | Thallus lacking isidia; apothecia frequent | 2 |
| | Thallus isidiate; apothecia very rare | 3 |
| 2(1) | Conidia 8–9.5 μm long; thallus usually strongly maculate (at least when old) | <i>carporrhizans</i> |
| | Conidia 9.5–11 μm long; thallus not strongly maculate | <i>quercina</i> |
| 3(1) | Isidia almost sessile, \pm rounded, \pm flattened or button-like, tips blue-black | <i>pastillifera</i> |
| | Isidia cylindrical to clavate or coralloid, tips pale- to grey-brown | <i>tiliacea</i> |

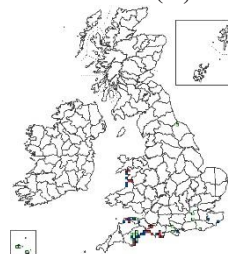
***Parmelina carporrhizans* (Taylor) Poelt & Vězda (1977)**

Thallus 2–5 (–15) cm diam., closely appressed, rosette-forming; lobes to 10 mm broad, slightly irregular, rounded at the apices, \pm overlapping and becoming crowded at the centre, not down-turned; margins crenate with cilia mainly restricted to axils; upper surface blue-grey or grey, mostly smooth and often shiny, faintly to distinctly maculate at least when old, the maculae at times developing into cracks; lower surface dark brown to black, paler brown towards the lobe ends, rhizines unbranched. Apothecia frequent, to 7 mm diam., sessile; disc initially imperforate but becoming perforate, red-brown; thalline margin intact or small-incised, \pm densely black rhizinate at or towards the point of attachment. Ascospores almost spherical to broadly ellipsoidal, (8–) 9–11 \times 6–8.5 μm . Pycnidia common, laminal; conidia 8–9.5 \times ca 1 μm , bacilliform, straight. Cortex K+ yellow; medulla C+ carmine-red, K–, KC+ red, Pd–, UV– (atranorin, lecanoric acid). **BLS 1010.**

On well-lit nutrient-rich hedgerow and parkland broad-leaved trees, frequently on \pm horizontal boughs, especially where receiving periodic sea-spray, coastal; rare and very local. S. & S.W. England, extending to mid-W. Wales, rare in Ireland, not reported for Scotland.

Very similar to *P. quercina* and sometimes confused with that species; conidial length and degree of maculation of the thallus surface appear to be the only robust distinguishing characters, although the mean ascospore length is slightly shorter in *P. carporrhizans*, the thallus tends to be less strongly adnate to the substratum, and the rhizines are longer. The conidial length for this species given in Edition 2 of this publication is 4.5–6.5 \times (0.5–) 1 μm , which suggests that there is confusion as to the identity of some collections. It and *P. quercina* have been confirmed as phylogenetically distinct (Núñez-Zapata *et al.* 2017).

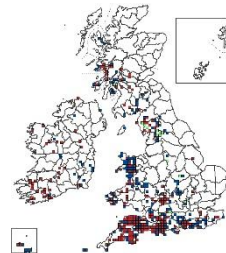
VU(A, C1)



***Parmelina pastillifera* (Harm.) Hale (1976)**

Thallus 4–8 (–15) cm diam., closely appressed, rosette-forming; lobes 3–7 (–10) mm broad, sublinear, contiguous or slightly overlapping, somewhat undulating centrally; margins broadly rounded but irregularly indented, short-ciliate in axils; upper surface mineral grey with blue tinge, faintly maculate, often pruinose towards the apices, isidiate; isidia blue-black, scattered or densely covering central lobes, laminal, short and initially flat-topped, tips developing a raised margin (button-like) and becoming knob-like and contorted, at times becoming confluent; lower surface black, brown towards the lobe margins; rhizines continuing up to the lobe margins, unbranched. Apothecia and pycnidia not seen on British specimens but apothecia are reportedly the same as for *P. carporrhizans*. Cortex K+ yellow; medulla C+ carmine-red, K–, KC+ red, Pd–, UV– (atranorin, lecanoric acid). **BLS 1007.**

LC



On nutrient-rich or -enriched, well-lit bark, especially on branches of *Fraxinus* and *Acer*, also on siliceous rocks, roofing tiles and memorials in well-lit situations. Widespread and increasing, especially in S. & W. Britain and Ireland, probably more widespread than recorded due to possible confusion with *P. tiliacea*.

Distinguished by the blue-black, flat- or button-topped knob-like isidia, which readily separate it from *P. tiliacea*. However, molecular phylogenetic study does not separate it from that species as currently circumscribed (Núñez-Zapata *et al.* 2017).

Host to *Marchandiomyces corallinus*.

Parmelina quercina (Willd.) Hale (1974)

NE

Similar to *P. carporrhizans*, but the thallus is weakly or non-maculate and tightly appressed to the substratum, the rhizines are mat-like, shorter and broader (0.5-1 mm long versus 0.8-1.5 mm in *P. carporrhizans*), the conidia are longer (9.5-11 µm versus 8-9.5 µm in *P. carporrhizans*) and the mean ascospore length is slightly greater.

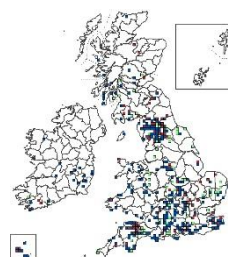
BLS 2618.

Known from Southern Britain (Hampshire, Surrey, Sussex), but the only records are historical and the species may well be extinct in Great Britain and Ireland.

Parmelina tiliacea (Hoffm.) Hale (1974)

LC

Thallus 4–8 (–20) cm diam., loosely to moderately attached; lobes 5–10 mm broad, radiating, contiguous but often overlapping along margins and centrally, undulating towards the centre; margins broadly rounded but irregularly indented, sparsely short-ciliate in axils; upper surface mineral grey to grey, ± faintly pruinose towards the apices, faintly pale-maculate, isidiate; isidia pale brown to grey-brown, laminal, scattered or densely covering the central lobes, cylindrical to clavate, unbranched or coralloid, often crowded and forming a ± continuous crust; lower surface black, brown towards lobe margins; rhizines continuing up to the lobe margins, mostly unbranched. Apothecia rare, sessile, to 7 mm diam.; disk red-brown, perforate or not; thalline margin intact or small-incised, reportedly ± densely rhizinate at or towards the point of attachment. Ascospores 9–10 × 6–9 µm., almost spherical to broadly ellipsoidal. Pycnidia rare; conidia *ca* 4.5 × 1 µm, bacilliform, straight or slightly curved. Cortex K+ yellow; medulla C+ carmine-red, K–, KC+ red, Pd–, UV– (atranorin, lecanoric acid). **BLS 1024.**



On ± nutrient-rich bark of broad-leaved trees and siliceous rocks, roofing tiles and macadamized paths in sunny situations; widespread. England and Wales but with distinct continental tendencies, largely lowland, rare in Scotland and scattered in Ireland.

Distinguished in morphological terms from *P. pastillifera* by the colour and shape of the isidia and by the slightly larger thallus with a bluish tinge. *P. tiliacea* appears to be phylogenetically diverse, with *P. pastillifera* nested within it (Núñez-Zapata *et al.* 2011, 2017).

Host to *Marchandiomyces corallinus* and an unidentified *Abrothallus*.

PARMELIOPSIS (Nyl.) Nyl. (1866)

Thallus foliose, very closely appressed, small, rosette-forming, corticate on both sides. **Lobes** ± radiating, discrete or contiguous and overlapping, sublinear and narrow, lacking cilia, apices incised. **Upper surface** yellow-green (usnic acid) or grey (atranorin), lacking maculae, pseudocyphellae and isidia, sorediate. **Upper cortex** composed of angular cells with a pored epicortex. **Cell walls** containing isolichenan. **Photobiont** chlorococcoid. **Medulla** white. **Lower surface** pale to dark brown or black, less frequently whitish (pale to dark brown in British species); rhizines moderately dense, unbranched or sparsely branched. **Ascomata** apothecia, rare, sessile to shortly stalked, the disc

becoming flat, imperforate, pale to dark brown; thalline margin concolorous with the thallus. Ascospores reniform to ellipsoidal, with one end more pointed, 8 per ascus. **Conidiomata** pycnidia, laminal and marginal, emergent, black. **Conidia** sickle-shaped, filiform. **Chemistry**: cortex: atranorin or usnic acid; medulla: orcinol and β -orcinol depsides. **Ecology**: corticolous and lignicolous, rarely saxicolous.

A recent study (Grewe *et al.* 2020) found that *Parmeliopsis* and *Imshaugia* occupy sister clades, distinct from other members of the major parmelioid clade within the Parmeliaceae.

Literature:

Ahti *et al.* (2011), Divakar *et al.* (2017), Grewe *et al.* (2020), Louwhoff (2009e), Tehler & Källersjö (2011).

- 1 Thallus greenish yellow to yellow-grey*ambigua*
 Thallus light to dark grey*hyperopta*

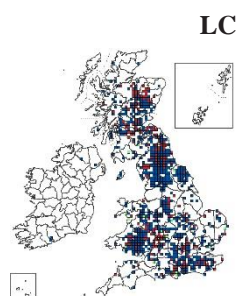
Parmeliopsis ambigua (Wulfen) Nyl. (1866)

Thallus 1–3 (–4) cm diam., closely appressed, often forming neat rosettes, or of scattered, \pm unoriented lobes, often contiguous with adjacent thalli and forming extensive patches; lobes 0.5–1 mm broad, sometimes much reduced, \pm elongate, often radiating, flat or concave, contiguous or partly overlapping centrally; margins sparingly indented; upper surface bright to dull yellowish green or yellowish grey, \pm brown-speckled towards the apices, matt; soralia frequent, laminal, yellow, flat or convex, rarely pustular and concave, paler or concolorous with the thallus, sometimes contiguous to form a \pm continuous sorediate crust in older parts of the thallus; lower surface pale brown to dark brown; rhizines scattered, concolorous with white tips. Apothecia rare, to 2 mm diam. Ascospores 7–11 \times 2.5–3 μ m. Pycnidia rare. Conidia 12–18 (–22) \times 0.5–1 μ m. Cortex K+ faintly yellow; medulla C–, K–, KC–, Pd–, UV+ glaucous-white (atranorin, usnic and divaricatic acids). **BLS 1034**.

On acid-barked, wayside and parkland broad-leaved trees, rarely on worked timber or siliceous rocks (mainly sandstone) in moderately polluted areas. Throughout N., central & S.E. England and S. and central Highland Scotland, rare in oceanic areas and Ireland.

P. ambigua appears to have spread south with SO₂ pollution and was widespread but is now retreating and becoming rarer in C. & S.E. England, due to the decrease in SO₂ pollution and increased nutrient enrichment.

Mainly distinguished from *P. hyperopta* by the colour of the upper surface, which in the past has led to the suggestion that it is simply a chemotype. However, recent molecular studies support *P. ambigua* at the species level (Tehler & Källersjö 2001, Divakar *et al.* 2017). Saxicolous morphs sometimes resemble *Xanthoparmelia mougeotii*, which differs in the K+ yellow medullary reaction (stictic acid). *Arctoparmelia incurva* differs in being consistently rhizinate, having convex lobes, globose soralia restricted to lobe tips and a KC+ pink and UV+ blue-white medulla.

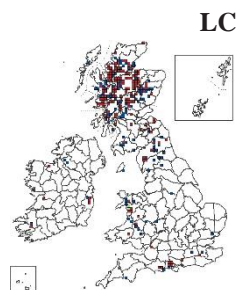


Parmeliopsis hyperopta (Ach.) Arnold (1880)

Like *P. ambigua* but thallus grey or blue-grey, the upper surface with scattered to contiguous laminal white to blue-grey-white pustular soralia, bursting open like little cauliflowers; soredia granular. Cortex K+ weakly yellow; medulla C–, K–, KC–, Pd–, UV+ glaucous-white (atranorin and divaricatic acid). **BLS 1035**.

Mainly restricted to bark of old conifers, also occasionally on acid-barked, broad-leaved trees (e.g. *Betula*, *Quercus*), natural acid lignum and wood palings in open, dry woodlands; local. Declining due to atmospheric ammonia pollution. N. England, Scotland (Highlands), Wales, extending locally to S. England, very rare in Ireland.

Thalli of *Imshaugia aleurites* with damaged and eroded isidia could be confused with *Parmeliopsis hyperopta*, that species is most easily separated by the presence of isidia instead of pustular soredia and the UV– medulla, and it also has a paler thallus, ellipsoidal ascospores, shorter and partly swollen conidia and a K+ orange and Pd+ orange medullary reaction (thamnolic acid). *P. hyperopta* has not shown the same recent, rapid spread that occurred in *P. ambigua* in response to changes in



SO₂ pollution levels, and was long present in the south as a possibly relict species in old growth woodland and on wooden palings in deer parks. *Physcia clementei* has a white lower surface and soredia that arise from isidia rather than pustules.

There is a single report of *Lichenodiplis lecanorae* on this host.

PARMOTREMA A. Massal. (1860)

Thallus foliose, moderately to loosely attached, large, to 30 cm diam., corticated on both sides. **Lobes** broad, often wavy and overlapping, rounded at the apices, 2–30 mm broad; margins entire or variously incised or ornamented, sometimes with cilia. **Upper surface** grey to grey-green (atranorin), with or without maculae, soredia, isidia or pustules, lacking pseudocyphellae. **Upper cortex** composed of angular tissue with a well-developed pored epicortex. **Cell walls** containing *Cetraria*-type lichenan. **Medulla** white- or yellow-pigmented (the latter not detected in British and Irish species). **Lower surface** mostly black with a broad (5–10 mm wide) brown marginal zone lacking rhizines; rhizines mostly unbranched. **Ascomata** apothecial, laminal, commonly stalked, sometimes shortly so; disk perforate or not; thalline margin entire or not, ± maculate. **Asci** 8-spored. **Ascospores** ellipsoidal, large and thick-walled. **Conidiomata** pycnidia, common, laminal, immersed. **Conidia** sublageniform, filiform or cylindrical. British and Irish material with filiform conidia only. **Chemistry**: cortex: atranorin, rarely usnic acid (not found in British and Irish species); medulla: orcinol depsides, orcinol depsidones, β-orcinol depsides, xanthonones, β-orcinol depsidones, aliphatic acids, pulvinic acid derivatives, anthraquinones. **Ecology**: corticolous and saxicolous, in moist, forested areas, from coastal to montane habitats.

Cetrelia is distinguished from *Parmotrema* by the presence of scattered fleck-like laminal pseudocyphellae and the absence of rhizines and marginal cilia. *Flavoparmelia* is readily separated by the yellow colour of the thallus (usnic acid), smaller ascospores (to 22 μm *cf.* to 37 μm in length) and by the fusiform rather than filiform conidia. *Platismatia* does not have cilia and generally lacks depsides and depsidones in the medulla; apothecia and pycnidia are rare and marginal or submarginal.

In phylogenetic terms, *Parmotrema* has a sister-group relationship with *Flavoparmelia* and *Crespoa* (the last not known to occur in Britain and Ireland).

Literature:

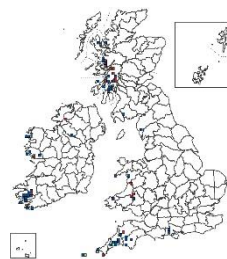
Aptroot *et al.* (2008), Del Prado *et al.* (2011, 2016, 2019), Divakar *et al.* (2005), Elix & Thell (2011a), Lendemer *et al.* (2015), Louwhoff (2009f), Spielmann & Marcelli (2020), Stelate *et al.* (2022).

- | | | |
|------|---|--------------------------|
| 1 | Upper surface with a faint, close network of white lines, ± developing into an intricate mosaic of hair-line cracks (×20); medulla K+ red | 2 |
| | Upper surface smooth, not reticulately-cracked; medulla K– or yellow | 3 |
| 2(1) | Thallus undersurface with a broad marginal zone free of rhizines; thallus often with a thickened margin | <i>pseudoreticulatum</i> |
| | Rhizines extending to the edge of the thallus undersurface, which is not thickened | <i>reticulatum</i> |
| 3(1) | Thallus isidiate, isidia often with laminal, black cilia | <i>crinitum</i> |
| | Thallus sorediate, cilia absent or marginal | 4 |
| 4(3) | Medulla KC+ pink-red, UV+ ice-blue | <i>arnoldii</i> |
| | Medulla KC–, UV– | 5 |
| 5(4) | Lobe margins sparingly ciliate; medulla K+ dirty yellow-brown or K–; Pd+ rust-red | <i>robustum</i> |
| | Lobe margins abundantly ciliate; medulla K+ bright yellow-orange, Pd+ orange | <i>perlatum</i> |

Parmotrema arnoldii (Du Rietz) Hale (1974)

NT

Thallus loosely attached, 5–15 (–20) cm diam.; lobes sublinear to subirregular, 5–12 (–20) mm wide, broadly rounded at the apices, often overlapping; margins often ascending, wavy and indented or irregularly incised; marginal cilia conspicuous, evenly dispersed, black, to 5 mm long; upper surface grey, ± faintly maculate, smooth or small-pitted or roughened towards the centre, sorediate; soralia marginal on apices of incised lobes or submarginal, soredia fine, coalescing and forming globose clusters; lower surface entirely black or brown towards the margins, rugulose, with a broad marginal zone lacking rhizines; rhizines unbranched. Apothecia unknown in British or Irish material. Pycnidia submarginal; conidia 10–12 (–14) × 0.5–1 μm, filiform. Cortex K+ yellow; medulla C–, K–, KC+ pink-red, Pd–, UV+ ice-blue (atranorin, alectoronic and α-collatolic acids). **BLS 0984**.



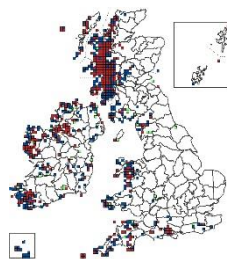
Amongst mosses, especially on horizontal branches of trees and old shrubs in ± well-lit mild and humid undisturbed woodlands, rarely on old *Calluna* heath in windswept, coastal situations. Rare and oceanic; W. British Isles (from Cornwall and Devon to Skye with a few outlying sites in New Forest) and S.W. Ireland.

Separated from the other sorediate, marginally ciliate species (*P. robustum* and *P. perlatum*) by the KC+ pink-red, UV+ ice-blue medulla (alectoronic acid and α-collatolic acids). Some populations of *P. perlatum* have a UV+ blue medulla also, but the KC test is diagnostic.

Parmotrema crinitum (Ach.) M. Choisy (1952)

LC

Thallus loosely attached, large, 5–15 (–20) cm diam., often forming extensive patches; lobes sublinear to subirregular, 5–10 (–15) mm wide, broadly rounded at the apices, contiguous but often overlapping and becoming crowded centrally; margins often ascending, wavy and often incised, irregularly lobulate or isidiate; marginal cilia usually associated with incisions; upper surface grey or grey-green, matt, ± faintly maculate, smooth or small-pitted towards the centre; isidia fragile, marginal and laminal, cylindrical or lobulate, becoming coralloid-branched, brown-tipped and frequently with accompanying black cilia, sometimes forming very dense clusters centrally; lower surface black with a broad, brown marginal zone lacking rhizines; rhizines dense, unbranched. Apothecia very rare, submarginal, stalked, 3–8 mm diam.; disk imperforate, thalline margin isidiate. Ascospores 21–31 × 11–15 μm. Pycnidia rare, not reported for British or Irish material. Cortex K+ yellow; medulla C–, K+ yellow, KC+ yellow-orange, Pd+ yellow-orange, UV– [atranorin, stictic (major), constictic acids (minor) and a range of accessory compounds including menegazziaic acid]. **BLS 0989**.



On ± mossy bark of mature or old broad-leaved trees and mossy siliceous rock outcrops in sheltered ancient woodland and exposed situations. It is characteristic of well-lit acidic habitats and occasionally Lobarion communities in undisturbed sites, also on well-lit rocks, in cliff-top heaths near coasts and on *Calluna* stems in windswept but misty coastal areas. An oceanic species widespread in the western uplands, rare in the south and very rare to absent in E. and C. England, and in E. Scotland. Declining and near-extinct in the southern lowlands except in the New Forest where it is thriving.

Readily distinguished from other *Parmotrema* species by the ciliate isidia. *Hypotrachyna horrescens* also has ciliate isidia but is distinguished by the smaller thallus and the lower surface that is rhizinate to the margins and by the K– yellow medulla (stictic acid).

Stelate *et al.* (2022) found that samples of *P. crinitum* and *P. perlatum* clustered in a single lineage with closely similar ITS sequences, but that phylogenetic relationships among them remained unresolved.

Host to *Abrothallus parmotremae* Diederich (2011).

Parmotrema perlatum (Huds.) M. Choisy (1952)

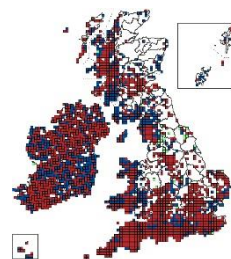
LC

Like *P. arnoldii* but with lobes more closely attached and more distinctly wrinkled centrally, with narrower (3–8 mm broad) and shorter, occasionally forked marginal cilia (1–2 mm long); soralia linear and marginal or sometimes submarginal, causing lobe margins to roll back and appear labriform; soredia fine, rarely spreading laminally as globose clusters. Apothecia rare; thalline margin uneven and partially sorediate. Ascospores 21–28 × 13–15 (–18) μm. Pycnidia scattered, submarginal; conidia not seen. Cortex K+ yellow; medulla C–, K+ yellow, KC+ yellow-orange, Pd+ yellow-orange, UV– or sometimes UV+ ice blue [atranorin, stictic (major), constictic acids (minor) and a range of accessory compounds such as menegazziaic acid]. **BLS 1008**.

On well-lit neutral to somewhat acid-barked broad-leaved trees, also frequently on siliceous rocks and walls, coastal rocks, short coastal turf and shingle beaches, usually where illumination is moderate to good, sensitive to SO₂; locally abundant. Mainly in W. and S. British Isles, spreading into E. & C. England and there recolonising with improving air quality.

Separated from the other sorediate, marginally ciliate species (*P. robustum* and *P. arnoldii*), by the K+ yellow medulla (stictic acid complex). *Platismatia glauca* lacks marginal cilia and has a different chemistry. *Parmotrema reticulatum* is a variable species but readily distinguished from *P. perlatum* by the fine mosaic of hair-line cracks on the upper surface, the soredia at tips of incised lobe margins and by the K+ yellow→orange medulla (salazinic acid).

Host to *Abrothallus parmotrematis* Diederich (2011), *Briancoppinsia cytospora*, *Lichenocodium erodens*, *Marchandiomyces corallinus*, and *Spirographa* sp. (as *Cornutispora lichenicola*).



Parmotrema pseudoreticulatum (Tav.) Hale (1974)

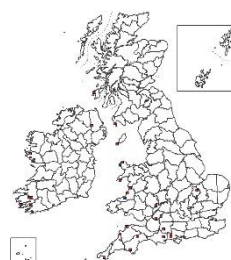
Differs from *P. reticulatum* (see below) by the broad marginal zone without rhizines and generally a thicker thallus with a generally thickened margin and labriform marginal soralia. It never has thin upright lobes with capitate soralia, and the reticulate pattern on the thallus may be reduced in this species to maculae only, especially in young specimens. **BLS 2511**.

The distribution is still poorly known due to confusion with *P. reticulatum*, but *P. pseudoreticulatum* has been recorded from western Britain and Ireland from Islay southwards to Cornwall, with a few outliers in southern England. *P. pseudoreticulatum* has been claimed to be the commoner of the two in Scotland, but database records do not support this hypothesis. A large robust form appears to be spreading on branches in southern England, here this contrasts with *P. reticulatum*, which is mainly found on older trunks and appears to be less mobile.

According to Del Prado *et al.* (2011) both species are polyphyletic, and further segregate taxa may be expected. The less easily visible reticulate pattern (needing a lens to see rather than visible unaided as in *P. reticulatum*) is a useful field indication for this species.

Host to *Tremella parmiliarum* Diederich (1996).

NE



Parmotrema reticulatum (Taylor) M. Choisy (1952)

Thallus to 5–20 (–30) cm diam., often forming extensive patches, loosely attached, appressed; lobes 5–15 mm broad, ± irregular to almost linear, ± rounded at the apices, with margins often irregularly incised or lacinate, with unbranched marginal cilia; upper surface pale grey-green, with a network of fine white lines (maculae) that often form a network of hair-line cracks (×20) with age (i.e. reticulately-cracked); soralia along lobe margins or at tips of laciniae, often causing them to turn upwards, with granular soredia; lower surface black, becoming brown towards the margins, with dense unbranched or squarrosely-branched rhizines centrally, often only papillate towards lobe tips. Apothecia rare, shortly stalked; disc to 8 mm diam., imperforate or eventually becoming perforate, brown; thalline margin often incised and ± sorediate.

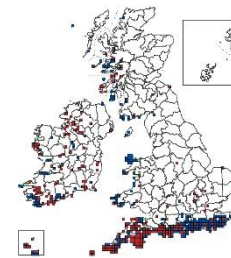
Ascospores 10–16.5 × 7.5–10 μm, ellipsoidal. Pycnidia rare, usually restricted to fertile thalli; conidia filiform, 7.5–12.5 (–16) × ca 1 μm. Cortex: K+ yellow; medulla: C–, K+ yellow→orange, KC+ red or KC–, Pd+ orange-red, UV–; containing atranorin, chloroatranorin, salazinic (major) and consalazinic acids (minor). **BLS 1012**.

On well-lit wayside trees (often in full sun) and woodlands, on trunks of broad-leaved trees, also on exposed, sunny rocks on western coasts. Common throughout S. and S.W. England, more occasional in W. Wales, largely absent from C., E. & N. England, less common in W. Scotland and Ireland.

A variable species but readily distinguished from *P. perlatum* by the network of hair-line cracks on the upper surface (×20), the soredia at tips of incised lobe margins and by the K+ yellow→orange medulla (salazinic acid). Del Prado *et al.* (2016) identified seven potential cryptic species in the *P. reticulatum* complex.

Host to *Abrothallus parmotrematis*, *Briancoppinsia cytospora* and *Marchandiomyces corallinus*.

LC



Parmotrema robustum (Degel.) Hale (1974)

Like *P. perlatum* but with larger (5–15 mm broad), ± elaborately incised and inrolled, sparingly marginally ciliate lobes; soralia sparse, rounded and often clustered on small extensions of the incised lobe margins. Cortex: K+ yellow; medulla: C–, K+ dirty yellow or K–, Pd+ deep orange- to rust-red, UV– [atranorin, protocetraric acid (major), sometimes also fatty acids (minor)]. **BLS 1014**.

On *Prunus spinosa* and mossy rocks on heathland near coast and in rocky oceanic sessile oak woodland; W. Wales, Cornwall (Lizard) and S.W. Ireland (Cork, Baltimore); very rare. *P. robustum* may have been overlooked elsewhere in W. and S.W. Britain as a robust form of *P. perlatum*, but is quite distinctive when well-developed.

Most similar to *P. perlatum* but separated from it by the broader lobes, more elaborate-incised, sorediate and sparingly ciliate lobe margins and by the Pd+ deep orange-red medulla (protocetraric acid). See also *P. arnoldii*.

CR(D)

**PLATISMATIA** W.L. Culb. & C.F. Culb. (1968)

Thallus foliose, rosette-forming or wide-spreading, dorsiventral, lobe margins often ascending, wavy, sometimes crisped. **Lower surface** pale to black with a few scattered rhizines. **Isidia** or **soredia** on margins and sometimes on the upper surface. **Cortex** often I+ blue. **Photobiont** trebouxoid. **Ascomata** apothecia, very rare, marginal or submarginal. **Disc** brown, often perforate. **Thalline margin** persistent. **Hymenium** I+ blue. **Hypothecium** thin, I+ blue, usually lacking algae below. **Asci** 8-spored, *Lecanora*-type. **Ascospores** small, subglobose-ellipsoidal, aseptate, colourless. **Conidiomata** pycnidia, marginal, immersed. **Conidia** cylindrical, not swollen at the apices. **Chemistry**: β-orcinol depsides and fatty acids (particularly caperatic acid). **Ecology**: corticolous.

Platismatia occupies an isolated and somewhat uncertain position within the Parmeliaceae (Divakar *et al.* 2017, Grewe *et al.* 2020). *Parmotrema* differs in often having marginal cilia and depsides and depsidones in the medulla while *Cetraria* differs in the absence of caperatic acid, thin I+ blue hymenium, smaller ascospores and conidia type. See also *Cetrelia*.

Literature:

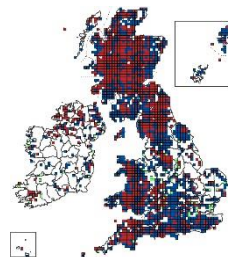
Asher *et al.* (2023), Divakar *et al.* (2017), Duke & Purvis (2009c), Grewe *et al.* (2020), Thell (2011b).

- 1 Upper surface with a continuous coarse network of sharply angled ridges; summits of ridges and lobe margins isidiate, sometimes becoming granular-sorediate*norvegica*
 Upper surface smooth, rugose or with a few low rounded ridges in an incomplete network; margins predominantly dissected or with simple or coralloid isidia, sometimes also granular-sorediate; isidia, if present, on the upper surface, not confined to ridges*glauca*

Platismatia glauca (L.) W.L. Culb. & C.F. Culb. (1968)

LC

Thallus 1–6 (–15) cm diam, often forming extensive patches, rather thin; lobes to 1.5 cm broad, wavy, irregularly indented, margins ascending, entire or sub-lobulate, often with marginal clusters of simple to coralloid, much branched isidia or (in part) granular soredia; upper surface pale to dull grey, often with a brown tinge or totally tinged brownish in exposed sites, ± unchanged in colour when wet, smooth to wrinkled or slightly ridged, without pseudocypbellae; lower surface entirely black (brown or white in shade), especially towards the margin, with few to many scattered unbranched or branched rhizines. Apothecia very rare, 5–9 mm diam., marginal; disc red-brown;



thalline margin thin, \pm excluded at maturity. Ascospores $3.5\text{--}8.5 \times 3\text{--}5 \mu\text{m}$. Cortex K+ yellow (atranorin), medulla C-, K-, KC-, Pd-, UV- (caperatic acid). **BLS 1145**.

On trees, rocks and soil, especially acidic, leached habitats; very common. Throughout Britain and Ireland, but sharply declining to extinct in areas with high ammonia pollution.

A very variable species; the lobes may be elongate, \pm entirely erect with much dissected, coralloid-lobulate-isidiate margins or \pm closely adpressed with only the margins upturned with granular-soresidiate isidia. The isidia or soredia are mainly confined to the margins but, on occasion, may also occur in small patches or widely dispersed on the upper surface. *Tuckermannopsis chlorophylla* has brown lobes turning olive-green when wet. *Cetrelia olivetorum* has scattered, dot-like pseudocyphellae on the upper surface ($\times 10$), a C+ pink medulla and finely soresidiate margins.

Phylogenetic analysis of *Platismatia glauca* sequences reveals two major clades, both of which are represented in our region (Asher *et al.* 2023). However, these could not be correlated with morphological, chemical or ecological features, and they concluded that recognition of cryptic species was premature.

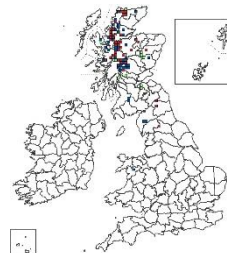
Infection by *Tremella coppinsii* Diederich & G. Marson (1988) results in a red discoloration on the thallus. Sometimes with galls caused by *Nesolechia oxyspora* (Tul.) A. Massal. (1856), often also secondarily infected with *Abrothallus cetrariae* Kotte (1909). Other lichenicolous fungi reported are *Briancoppinsia cytospora*, *Everniicola flexispora*, *Licheniconium erodens*, *Marchandiomyces corallinus*, *Spirographa* sp. (as *Cornutispora lichenicola*) and an unidentified species of *Endococcus* (spores $7.6\text{--}9 \times ca\ 3.5 \mu\text{m}$; asci $40\text{--}56 \times ca\ 10 \mu\text{m}$).

Platismatia norvegica (Lynge) W.L. Culb. & C.F. Culb. (1968) **Nb IR**

Like *P. glauca*, but with broader, more rounded lobes (to 2.5 cm broad), with rounded, sparingly indented margins; upper surface dull pale grey, not or sometimes tinged brownish, with a very pronounced network of low, sharp ridges with indistinct pseudocyphellae and simple or clustered isidia. Apothecia not seen. **BLS 1146**.

Mainly in moss-lichen montane heaths, as well as on exposed, siliceous rocks and on well-lit leached acidic bark, especially of *Pinus*, *Betula*, *Salix* and *Quercus* in relict Caledonian forests; local and rare. N. and N.W. Scotland (Highlands), England (Northumberland, Cumbria), N. Wales.

Host to *Nesolechia oxyspora* (q.v.).



PLEUROSTICTA Petrak (1931)

Thallus foliose, loosely appressed, dorsiventral, large. **Lobes** irregular and broadly rounded at the apices; margins wavy and \pm ascending and often torn, not ciliate. **Upper surface** grey-green to brown-grey (K-, N+ violet), thin, without pseudocyphellae, isidia or soredia. **Upper cortex** composed of isodiametric cells, with a pored epicortex. **Cell walls** containing isolichenan. **Medulla** loosely packed, white. **Lower surface** black; rhizines unbranched. **Ascomata** apothecia, laminal, sessile or rarely shortly-stalked; disc imperforate, red-brown to black-brown. **Ascospores** ellipsoidal, 8 per ascus. **Conidiomata** pycnidial, laminal, immersed. **Conidia** cylindrical to fusiform. **Chemistry**: cortex: N+ violet; medulla: β -orcinol depsidones. **Ecology**: corticolous.

The small genus *Pleurosticta* is distinguished by a robust thallus (to 30 cm diam.) with broad lobes (to 17 mm wide), a lack of pseudocyphellae and by the cylindrical to fusiform conidia. In phylogenetic terms, it is related to *Montanelia* (Grewe *et al.* 2020), which has thalli with pseudocyphellae.

There is only one species in Britain and Ireland.

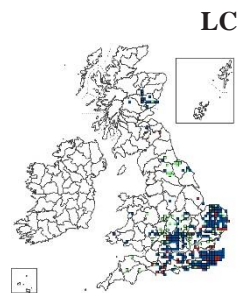
Literature:

Grewe *et al.* (2020), Louwhoff (2009g), Lumbsch *et al.* (1988), Westberg & Thell (2011f).

Pleurosticta acetabulum (Neck.) Elix & Lumbsch (1988)

Thallus 3–8 (–30) cm diam., lobes 5–10 (–17) mm broad, ± closely appressed centrally, coriaceous, with wavy, sometimes crisped and strongly upturned margins and incised rounded ends, often wrinkled or distinctly warted towards the centre (warts sometimes cracking open), contiguous and overlapping; upper surface grey-green to brown-grey, occasionally ± grey-pruinose, dark oily green when wet; lower surface pale brown; rhizines unbranched. Apothecia 5–15 mm diam., often present, disc red-brown; thalline margin ± unevenly crenulate, often strongly inflexed. Ascospores 14–17 × 7–8.5 μm. Pycnidia common, laminal, immersed; conidia cylindrical, 6–7 × ca 1 μm. Cortex: C–, K–, N+ violet; medulla: K+ red (crystals), KC–, Pd+ orange, UV– [norstictic acid (major), sometimes with related compounds (minor/trace)]. **BLS 0982**.

On nutrient-rich bark of trunks of broad-leaved trees, e.g. *Ulmus*, *Fraxinus*, *Acer pseudoplatanus* and *Sambucus* in well-lit, wayside situations, very rarely on ragstone memorials; local and decreasing, S.E. England, extending locally to E.C. Scotland & Wales.

**PROTOPARMELIA** M. Choisy (1929)

Thallus crustose, rimose, warted or areolate, corticate, rarely scurfy-isidiate, often glossy, pale grey-brown to dark or chestnut brown. **Cortex** of branched short-celled anticlinal hyphae, often terminated by brown pigmented ‘hoods’ and usually overlain by a distinct colourless epicortex; photobiont layer and medulla usually well defined. **Medulla** I–. **Photobiont** trebouxoid, cells sometimes dividing internally to form autospores. **Ascomata** apothecia, arising from within areoles or warts, immersed to sessile, usually glossy. Disc brown, often darker than the margin, not pruinose. **Thalline margin** ± concolorous with the thallus, with a medulla filled with algal cells and well-defined cortex (except in *P. oleagina*) similar to that of the thallus. **True exciple** colourless. **Hymenium** I+ blue. **Hypothecium** colourless. **Hamathecium** of simple or occasionally forked, septate paraphyses; apices sometimes slightly wider, each usually covered by a swollen gelatinous ‘hood’ which often contains a brown ‘cap’. **Asci** 8- or multi-spored [all British and Irish species are 8-spored], clavate, *Lecanora*-type, with or without an ocular chamber, but always with a distinct, non-amyloid apical cushion. **Ascospores** aseptate (or a few 1-septate when old), colourless, ellipsoidal or fusiform- or cylindrical-ellipsoidal to cylindrical; lacking a distinct epispore, sometimes with polar filiform appendages. **Conidiomata** pycnidia, immersed, the wall colourless except for brown pigmentation around the ostiole. **Conidiogenous cells** arising on branched conidiophores or in chains, ± cylindrical, proliferating percurrently. **Conidia** bacilliform, short-acicular or curved and thread-like, aseptate, colourless. **Chemistry**: orcinol depsides, β-orcinol depsidones, zeorin and several unidentified substances (incl. fatty acids) may be present. **Ecology**: saxicolous, less often corticolous or lignicolous, some species initially lichenicolous.

The genus is unusual within the Parmeliaceae in having a crustose thallus, and was accommodated in a separate subfamily *Protoparmelioideae* by Divakar *et al.* (2017). It may be separated from *Lecanora* by the brown pigmentation of the thallus, generally smaller (and especially narrower) ascospores, the usually straight conidia and lack of atranorin. Singh *et al.* (2013, 2015) demonstrated that *Protoparmelia* in the concept adopted by Coppins & Chambers (2009) is polyphyletic, and that *P. atriseda* and *P. nephaea* should be excluded from the genus and transferred to *Miriquidica*. The necessary new combinations were made in Cannon *et al.* (2022), and the species are retained in the key below to aid in continuity. Other phenotypic differential features are difficult to discern, although the conidia (when present) are curved in *Miriquidica* s.l. and straight in *Protoparmelia*. *Miriquidica*

species tend to have apothecia that are immersed or sessile, without a distinct thalline margin. *Bryonora* may also be difficult to distinguish from *Protoparmelia* in morphological terms, but the only British representative is a montane bryophilous species with 4 (–6)-septate spores and a swollen true exciple composed of conglutinated hyphae.

Singh *et al.* (2015) also demonstrated that several of the traditionally circumscribed species of *Protoparmelia* appear to be species complexes, building on previous observations of differences in chemistry. Indications are that *P. badia* contains between three and six cryptic taxa, *P. montagnei* could be divided into three groups, and *P. ochrocoeca* into two. More research is needed before any of these taxa can be formally recognized.

The tropical – mostly corticolous – *Protoparmelia* species have been accommodated in a distinct genus *Neoprotoparmelia* (Singh *et al.* 2018); the two genera are sister groups in phylogenetic terms.

Literature:

Aptroot *et al.* (1997), Barbero *et al.* (2006), Brodo & Aptroot (2005), Coppins & Chambers (2009), Divakar *et al.* (2017), Papong *et al.* (2011), Singh *et al.* (2013, 2015, 2018).

- | | | |
|------|--|-----------------------------|
| 1 | On rock | 2 |
| | On bark or wood | 6 |
| 2(1) | Thalloconidia present, produced from a sooty-black prothalline margin; areoles sometimes sorediate; below dry rock overhangs | <i>Miriquidica nephaea</i> |
| | Thalloconidia absent; soredia absent; on exposed rocks | 3 |
| 3(2) | Ascospores ellipsoidal or cylindrical with rounded apices | 4 |
| | Ascospores ellipsoidal-fusiform, apices pointed | <i>badia</i> |
| 4(3) | Thallus mostly >4 cm across; cortex K–, medulla sometimes K+ yellow or red | 5 |
| | Thallus forming small patches mostly <4 cm across; cortex of thallus and apothecia (in section) K+ yellow to red | <i>Miriquidica atriseda</i> |
| 5(4) | Medulla (at least upper part) C+ red, rarely C–; thallus with brown predominating, never blackish; on coastal rocks | <i>montagnei</i> |
| | Medulla C–; thallus usually with grey or black predominating, ± with olivaceous tinge; mainly on inland rocks | <i>memnonia</i> |
| 6(1) | Thallus of subglobose areoles, not isidiate or sorediate | <i>ochrocoeca</i> |
| | Thallus scurfy, granular-isidiate to minutely squamulose | 7 |
| 7(6) | Thallus olive to chestnut brown, squamulose granules not present; thallus in section producing oily exudates in K | <i>oleagina</i> |
| | Thallus pale grey-green to greenish brown, at least partially with minute squamules; no oily exudates in K..... | <i>hypotremella</i> |

Protoparmelia badia (Hoffm.) Hafellner (1984)

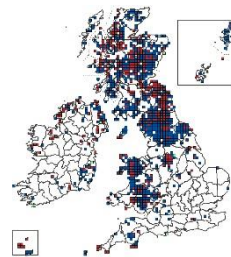
LC

Thallus very variable, thin and rimose to coarsely warted, to 2.5 mm thick, pale fawn-grey to dark brown, sometimes faintly olivaceous, usually ± glossy, effuse or rarely delimited by a dark prothallus line. Apothecia 0.4–2.2 mm diam., usually numerous, immersed to sessile, usually glossy; thalline margin concolorous with the thallus, mostly persistent; disc flat to convex, usually darker than the margin; hymenium 50–60 µm tall. Ascospores 8–13 × 3–5 µm, ellipsoidal-fusiform with distinctly pointed apices. Pycnidia often present, rarely abundant; conidia 8–11 × 0.7–1 µm. Sections C–, K–, KC+ pink (especially cortex), Pd–, usually UV+ white (lobaric acid, sometimes also zeorin and 3(–5) unidentified substances). **BLS 0633**.

On hard, usually exposed siliceous rocks in coastal and montane sites, tolerating some nutrient enrichment; frequent to locally abundant. Throughout upland Britain and in a few lowland areas, scattered in Ireland.

Very variable but usually easily recognized by the characteristic brown colour (rarely completely pale grey, var. *cinerascens* Flotow) and concolorous apothecia; distinguished from the rarer *P. montagnei* and *P. memnonia* complexes by the sharply fusiform ascospores.

The apothecia can be parasitized by *Tremella protoparmeliae* Diederich & Coppins (2006), but it appears not to have been recorded since the 19th century. Other lichenicolous fungi on this host are *Arthonia protoparmeliae* Etayo (2010) and *Muellerella ventosicola* (Mudd) D. Hawksw. (2003).



Protoparmelia hypotremella van Herk, Spier & Wirth (1997)

NE

Thallus composed of squamulose granules, grey to pale olivaceous or buff, paler along the margins of the granules, dull to slightly glossy, corticate, without a prothallus. Granules in part isidium-like, convex, rounded to elongate or globose, ca 100 µm high and 200 µm diam., or microsquamulose and crenate to lobate, convex to flat or slightly concave, gnarled, to 300 µm high and 600 µm diam. The squamulose granules randomly occur amongst the isidium-like granules, not predominantly along the margins of the thallus. Margins of the granules often eroding and less corticate, often whitish, always paler than the surface. Epinecral layer 5–10 µm thick, colourless; cortex 15–25 µm thick, pale brownish, with isodiametric lumina 6–9 µm diam.; medulla 60–150 µm thick, rather loose, composed of hyphae 3–5 µm diam., the walls partly encrusted with crystals; upper layer of the medulla filled with chlorococcoid algae 6–12 µm diam. Ascomata and conidiomata unknown in Britain and Ireland; they are described in Brodo & Aptroot (2005). Chemistry: medulla and cortex C+ yellow or C–, K–, KC+ pink or KC–, PD–, UV+ white. Lobaric acid (major), sometimes also unknowns (minor). **BLS 2777**.

On bark of older *Quercus* in parkland and on field trees, Sussex (Knepp Park, Eridge Park), Bedfordshire. The Bedfordshire population is on a rather polluted mature Oak in an intensive agricultural landscape, so this likely colonising species is probably not confined to the high quality sites in it was first detected.

The granular thallus is similar to that of *P. oleagina*, but the granules are larger and more obviously squamulose, and paler greenish brown as opposed to the consistent brighter olive to chestnut brown of *P. oleagina*. The "oily" reaction to K seen in *P. oleagina* does not occur in *P. hypotremella*.

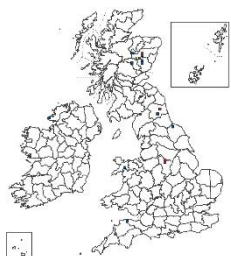
Protoparmelia memnonia Hafellner & Türk (2001)

NT

Like *P. badia*, but thallus usually darker, apothecia generally fewer and smaller, and ascospores 9–12 × 2.5–3 µm, cylindrical to cylindrical-ellipsoidal. Sections C–, K–, KC+ reddish or KC–, UV+ white (lobaric acid, various unidentified substances). **BLS 0664**.

On hard, siliceous rocks; rare and very scattered. Mainly in upland Britain.

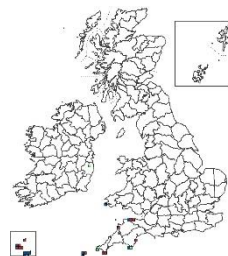
Two entities are recognized in Britain, based mainly on the presence of unidentified substances: (1) with two of the substances found in *P. badia*; (2) with two of the substances found in *P. montagnei* plus a terpenoid, this entity tending to have more swollen, often subsquamulose thalline warts. Entity (1) is known from N.E. Scotland (S. Aberdeen, near Braemar; Angus, Clova), also in the Harz Mts. in Germany. Entity (2) is known only from S.W. & N.E. England (N. Devon, Cleveland). A third entity lacking lobaric acid (medulla UV–) is found in Scandinavia and C. Europe. A thorough survey of a geographically wide range of material is needed to resolve the taxonomy of this complex.



Protoparmelia montagnei (Fr.) Sancho & A. Crespo (1987)

Nb

Like *P. badia*, but thallus usually paler with numerous pycnidia and often delimited (esp. when young). Best distinguished by its cylindrical-ellipsoidal ascospores 9–13 × 2–3.5 (–4.5) µm in size, and by its chemistry. There are three chemotypes (reactions are for upper medulla and cortex in sections): (1) gyrophoric and lobaric acids, C+ red, UV+ white; (2) lobaric acid, C–, KC+ reddish, UV+ white; (3) gyrophoric acid, C+ red, UV–; all chemotypes have traces of unidentified substances (but different



from those in *P. badia*). It should be noted that reactions of the lower part of the thallus can be unreliable as this tissue often belongs to another species overgrown by *P. montagnei*. **BLS 0671**.

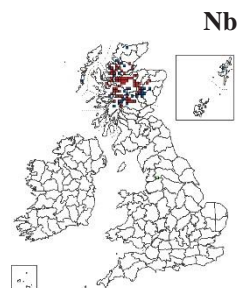
On coastal rocks in the xeric supralittoral zone, often overgrowing (? initially lichenicolous) other crustose lichens, e.g. *Circinaria (Aspicilia) cinerea* agg. and *Diploschistes caesioplumbeus*; locally abundant. Channel Isles. (chemotypes 1 & 2), S.W. England, Wales (Pembroke) (chemotype 3).

Protoparmelia ochrococca (Nyl.) P.M. Jørg., Rambold & Hertel (1988)

Thallus of rounded ± globose shiny chestnut-brown areoles 60–260 µm diam. Apothecia 0.3–1.1 mm diam., sessile and constricted below, flat with a raised thalline margin or sometimes becoming convex with the margin reflexed; margin concolorous with the thallus, smooth or crenulate; disc usually more reddish; hymenium 35–50 µm tall. Ascospores (7–) 8–12 × 2–3.5 µm, fusiform. Pycnidia rare; conidia 7–9 × ca 0.7 µm, shortly acicular, straight. Sections C–, K–, KC–, Pd– (lichen products not detected by TLC). **BLS 0755**.

On bark and wood of conifers (*Larix*, *Pinus*) and *Betula*, often in deep fissures, rarely on old fence-posts; local. Scotland (Highlands), Shetland Islands.

When sterile may resemble *Lopadium disciforme*, which has flatter, dull-matt squamules, often with a slightly paler margin.



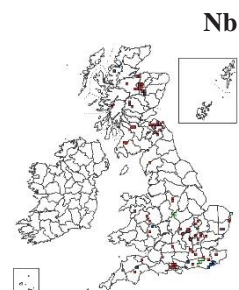
Protoparmelia oleagina (Harm.) Coppins (1992)

Like *P. ochrococca*, but with a dull olivaceous brown, scurfy granular, ± isidiate thallus and apothecial margin; disc also olivaceous. Sections C–, K–, KC–, Pd–, UV– (traces of two of the unidentified substances found in *P. montagnei* and one of the entities within the *P. memnonia* complex).

On *Pinus* wood in native Scottish pinewoods; on fences, chestnut palings and gate rails, and on hard well-lit natural *Quercus* lignum in old-growth woodlands and parklands in southern England. Sparingly fertile, and fertile thalli are mostly on natural substrata rather than anthropogenic materials. C., S. & S.E. England, N. Wales, C. & E. Scotland.

P. hypotremella van Herk, Spier & V. Wirth (1997) has a pale grey-olivaceous-buff thallus composed of isidioid squamulose granules, an identical chemistry and occurs in similar habitats. It is rapidly spreading in the Netherlands and Germany and has recently been recorded in S.E. England. The thallus is paler than *P. oleagina* and the isidia are larger.

Sphinctrina anglica occasionally occurs on the thalli of *P. oleagina* in S. England; also reported is *Lichenocodium lecanorae*.



PSEUDEPHEBE M. Choisy (1930)

Thallus fruticose, small, dark brown to black, shiny, richly branched, prostrate, ± closely attached to the substrate by disc-like haptera, lacking pseudocyphellae, soredia and isidia. **Cortex** composed of longitudinally orientated hyphae. **Photobiont** chlorococcoid. **Ascomata** apothecia. **Thalline margin** concolorous with the thallus. **Asci** clavate, thick-walled, 8-spored, K/I+ blue, *Lecanora*-type. **Ascospores** aseptate, ellipsoidal, without a distinct perispore, colourless at maturity. **Conidiomata** pycnidia, abundant, embedded in the thallus, causing slight swellings on the branches, opening to the surface through wide ostioles. **Conidia** aseptate, bacilliform, colourless. **Chemistry**: lichen products not detected by TLC. **Ecology**: on siliceous rocks.

Characterized by the low, prostrate habit and attachment by haptera. Distinguished from other alectorioid genera by the absence of lichen products, the distinctive cortical structure and lack of isidia, soredia and pseudocyphellae. It is placed in an uncertain position within the alectorioid clade of Parmeliaceae (Divakar *et al.* 2017, Grewe *et al.* 2020).

The study by Boluda *et al.* (2016) demonstrated that the traditional morphological distinctions between *Pseudephebe minuscula* and *P. pubescens* did not entirely correlate with phylogenetic data, with some strains with morphology typical of *P. pubescens* clustering within the *P. minuscula* clade. However, all of these originated from North and South America, and identification of European collections appears to be less problematic. However, none of the samples studied originated from Britain and Ireland.

Literature:

Boluda *et al.* (2016), Brodo & Hawksworth (1977), Divakar *et al.* (2017), Garrido-Benavent *et al.* (2021), Gilbert & Purvis (2009d), Grewe *et al.* (2020), Hawksworth (1972), Myllys *et al.* (2011a).

- 1 Not strongly appressed; branches terete, evenly thickened, the apices not attached to the substrate; internodes elongate, usually >1 mm, giving a loose appearance *pubescens*
Strongly appressed; branches becoming ± flattened, unevenly thickened, the tips becoming adnate; internodes short, usually <0.5 mm, giving a densely branched appearance *minuscula*

Pseudephebe minuscula (Nyl. ex Arnold) Brodo & D. Hawksw. (1977) **Nb**
Thallus dark, shiny, very closely appressed to the substrate, becoming ± crustose. Branches flattened, to 1 mm broad, but ± terete in parts, with numerous short lateral branchlets, internodal distance short, 0.2–0.5 (–1) mm. Not known fertile in the British Isles. **BLS 1971.**

On the top of windswept granite boulders at two sites in the Cairngorms, both over 900 m alt.; rare.

Similar to *P. pubescens* but with flattened branches, especially near the point of attachment where it may appear almost foliose.

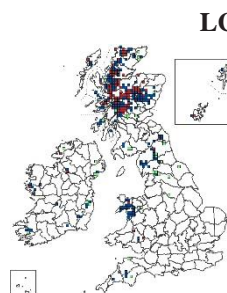


Pseudephebe pubescens (L.) M. Choisy (1930)

Thallus dark, shiny, to 1 cm tall, prostrate, forming entangled mats, closely appressed; branches to 0.2 mm diam., terete to slightly compressed; branching frequent, divergent isotomic-dichotomic, often interwoven; internodal distance 1–3 mm. Apothecia rare; disc to 5.5 mm diam., brown or grey-black. Ascospores 7–12 × 6–8 μm. Pycnidia on tubercles, abundant especially near the axils, to 0.4 mm diam., black; conidia 5–7 × ca 1 μm. **BLS 1191.**

On exposed siliceous rocks in windswept montane sites, locally abundant. England (Lake District, Cheviots, N. Pennines), N. Wales (Snowdonia), Scotland (Highlands), scarce elsewhere including Ireland.

The two species sometimes intergrade, but *P. pubescens* has finer, longer, rounder branches and a greater distance between the nodes (axils), and lacks a group I intron (see Boluda *et al.* 2016). Differs from the quite unrelated *Ephebe* in photobiont and habitat preferences.



PSEUDEVERNIA Zopf (1903)

Thallus foliose-shrubby, dorsiventral, with a single or a few points of attachment; lobes narrow, ± strap-shaped, branched ± dichotomously. **Isidia** or **soredia** present in some species. **Lower surface** without rhizines, at least partly black, channelled. **Photobiont** trebouxoid. **Medulla** compact. **Ascomata** apothecia, stalked. **Thalline margin** persistent, concolorous with the thallus. **Discs** ± concave, olive to dark red-brown, shiny. **Asci** 8-spored, clavate, *Lecanora*-type. **Ascospores** aseptate,

colourless, ellipsoidal. **Chemistry:** cortex contains atranorin, medulla depsides, depsidones and/or β -depsidones. **Ecology:** on acidic substrata.

There is only one species from Britain and Ireland.

Literature:

Ahti & Thell (2011a), Ferencova *et al.* (2010), Hale (1968), Hawksworth & Chapman (1971), Seaward & Purvis (2009b).

Pseudevernia furfuracea (L.) Zopf (1903)

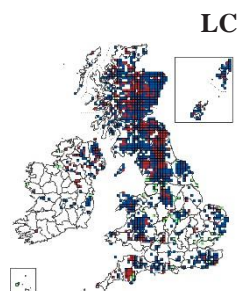
Thallus to 10 cm diam., composed of a few to numerous hanging strap-shaped lobes 1–4 mm broad, dichotomously branched in one plane, branching widely divergent with short side branches; upper surface grey-white, matt, often rough with isidia or small folioles; lower surface usually channelled, uniformly grey-black or \pm mottled black and brownish-white or pinkish, with incurved margins concolorous with the upper thallus. Apothecia infrequent, to 1.5 (–3) cm diam., lateral, on curved part of branches. Asci 30–40 \times 14–16 μ m. Ascospores 7.5–10 \times 4–5.5 μ m. Cortex K+ yellow (atranorin); medulla C– K–, KC–, Pd–, UV– (physodic acid). **BLS 2363.**

On exposed, well-lit bark and wood, on conifers and mainly acid-barked deciduous trees (particularly in slightly acid polluted sites) and fence posts, also more rarely on siliceous rocks; widespread throughout Britain (more particularly to the N. & W.), Ireland (especially towards the N.). Appears to be declining in the south east with the decline in SO₂ pollution.

Pseudevernia furfuracea var. *ceratea* (Ach.) D. Hawksw. (1969) **BLS 1193** is morphologically identical to var. *furfuracea* but differs in the C+ red reaction (olivetic acid) of the medulla; it also has a similar ecology. Var. *ceratea* is the commoner chemotype in the British Isles, being particularly abundant in the north; its distribution in Ireland, as with var. *furfuracea*, is less well-defined. It does not form a monophyletic group within *P. furfuracea* according to Ferencova *et al.* (2010). **BLS 1192** is the code to use for records where the two varieties are not distinguished.

P. furfuracea resembles *Evernia prunastri* in habit but is characterized by the presence of isidia and the naked, channelled, often at least partly blackened lower surface. *E. prunastri* is only weakly dorsiventral, with a greenish upper surface, has a lax medulla and contains usnic acid with either divaricatic or evermic acid. In W. Scotland it often occurs as a morph with very narrow lobes bearing few isidia. Apothecia are very rare, except in N.E. Scotland (Cairngorm region).

Host to the lichenicolous fungus *Diederichia pseudeverniae* (Etayo & Diederich) D. Hawksw. (2003). Also reported are *Lichenocodium erodens*, *Lichenostigma maureri*, *Spirographa* sp. (as *Cornutispora lichenicola*) and an unidentified species of *Endococcus* (spores 8.5–11 \times 3.5–4 μ m).



PUNCTELIA Krog (1982)

Thallus foliose, loosely to closely appressed, dorsiventrally flattened, corticate on both sides. **Lobes** subirregular to irregular, with roughly rounded, often wavy and \pm ascending margins, lacking cilia.

Upper surface grey to grey-green (atranorin), with or without soredia, pustules or isidia (species from Britain and Ireland are sorediate only, one developing isidiomorphs), with scattered, punctiform or \pm circular pseudocyphellae. **Upper cortex** of \pm isodiametric cells with a non-pored epicortex. **Cell walls** containing isolichenan. **Medulla** white. **Lower surface** white to pale tan or black, with rhizines, often with a narrow, non-rhizinate region along the margins; rhizines sparse to abundant, unbranched or \pm bunched, pale buff to black. **Ascomata** apothecial, laminal, \pm sessile or stalked; disc imperforate, pale to dark brown. **Asci** 8-spored, *Lecanora*-type. **Ascospores** broadly ellipsoidal. **Conidiomata** pycnidia, laminal, immersed, ostiole black. **Conidia** filiform, typically hooked at one end. **Chemistry:** cortex: atranorin; medulla: orcinol depsides, aliphatic acids. **Ecology:** corticolous, saxicolous, rarely terricolous.

Punctelia is separated from *Cetrelia* by the laminal pseudocyphellae that often become sorediate, the laminal rather than marginal pycnidia (though they may be concentrated towards the margin), the smaller lobes (3–10 mm broad) and the densely rhizinate lower surface. *Parmelia* resembles *Punctelia* but is readily separated from it by the pseudocyphellae on the upper surface, which are linear rather than punctiform.

Punctelia has a sister group relationship with the morphologically similar genus *Flavopunctelia*, which does not occur in Britain and Ireland. The study of Alors et al. (2016) demonstrated the existence of several phylogenetic clades within *Punctelia* which were correlated with secondary chemistry.

Divakar et al. (2017) presented a harmonised generic classification of the Parmeliaceae based on molecular clock estimates of the age of divergence of the taxa concerned. In most cases this has not proved controversial, but strict interpretation of the data showed that *Punctelia* and the lichen parasite *Nesolechia* A. Massal. (1856) should be incorporated into the same genus. As *Nesolechia* predates *Punctelia* by over 100 years, that would lead to name changes for a series of familiar British species unless a conservation proposal were to succeed. However, the *Nesolechia* and *Punctelia* clades are reciprocally monophyletic, and for the purposes of this publication they are kept as separate genera.

Literature:

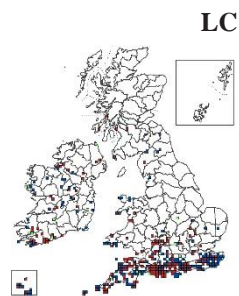
Alors et al. (2016), Divakar et al. (2017), Hale (1965), Krog (1982), Lendemer & Hodgkinson (2010), Louwhoff (2009h), Thell (2011c), Thell et al. (2008).

- | | | |
|------|--|-------------------|
| 1 | Medulla C–; soredia becoming partially corticate and developing into elaborate, erect isidiomorph structures | <i>reddenda</i> |
| | Medulla C+ pink; soredia not developing into elaborate, erect structures | 2 |
| 2(1) | Pseudocyphellae ± round, white, of very different size even on a single thallus; soredia only in the central part of the thallus, absent in a broad marginal zone | <i>borreri</i> |
| | Pseudocyphellae ± round to linear, not white but clearly paler than the thallus surface, not of very different size; soralia laminal but also marginal or at least submarginal | 3 |
| 3(2) | Soralia predominantly laminal, arising from pseudocyphellae; lacking dark brownish, pruinose lobe margins and ends | <i>subrudecta</i> |
| | Soralia mainly on ascending margins of the lobes; with ± dark brownish, ± pruinose lobe margins and ends | <i>jeckeri</i> |

***Punctelia borreri* (Sm.) Krog (1982)**

Thallus to 6 cm diam., often rosette-forming; lobes 5–10 mm broad, closely appressed and contorted centrally, more loosely appressed, contiguous to becoming overlapping and ± ascending at the apices; margins ± rounded, entire or with small indentations; upper surface pale grey, grey or rarely tinged yellow, becoming brownish at the apices (old preserved specimens can be discoloured red-brown), often uneven and pitted; pseudocyphellae white, of very different sizes even on single thalli, often developing into rounded, dot-like soralia; soredia coarse, occasionally becoming blackened or semi-corticate, mostly in the central part of the thallus, with a broad marginal zone devoid of soralia; lower surface darker towards the centre; rhizines dense, simple or clumped, often with slightly paler tips, not extending to the margin. Apothecia rare, very shortly stalked, to 6 mm diam. (in British specimens); disc imperforate, red-brown; exciple uneven, ± sorediate. Ascospores 15–18 × 12–15 μm, subglobose to ± ellipsoidal. Pycnidia laminal, 25–55 μm diam.; conidia 5–7 × ca 1 μm. Cortex K+ yellow; medulla C+ pink, K–, KC+ pink, Pd–, UV– (atranorin, chloroatranorin, gyrophoric acid (major), sometimes also fatty acids). **BLS 0985.**

On well-lit, ± nutrient-rich bark of broad-leaved trees in open situations, especially old orchards, less frequently on rocks in coastal regions; a species of low rainfall, sunny areas with milder winters, increasing and



becoming more widespread in England and Wales. S. & S.W. Britain, extending to S.W. Scotland (Solway Firth) where it is rare, scattered in Ireland.

Diagnostic features include the grey lobes, which when young are covered with minute round or slightly elongated white dot-like pseudocyphellae. The whole lobe is usually delicately frosted (pruinose). Soralia are found on the surface of lobes and sometimes also on margins. The underside of the marginal lobes can vary from pale to dark brown, but the whole of the thallus becomes darker towards the centre (some will have to be peeled off the bark to be certain of this).

Punctelia subrudecta is very similar, but differs in the smooth lobes, the underside uniformly pale brown, or darker at the edges becoming lighter towards the centre, the larger pycnidia and shorter conidia, and containing lecanoric acid. *P. jeckeri* has mainly marginal soralia.

There are several records of an unidentified *Abrothallus* (including its *Vouauxiomyces* anamorph) on this species; also reported are *Briancoppinsia cytospora* and *Spirographa* sp. (as *Cornutispora lichenicola*).

***Punctelia jeckeri* (Roum.) Kalb (2007)**

Thallus 3–5 (–10) cm diam.; lobes usually 1–3 mm broad, closely appressed and ± contorted centrally; margins ± rounded, irregular, appearing upcurved; upper surface (when fresh) pale greenish-grey and slightly shiny in centre, turning to pale brownish-grey and usually pruinose near the margin, young thalli entirely brownish to brownish-grey; outer margin always pruinose, dull, pale to medium brown; pseudocyphellae usually sparse or even absent, paler than the thallus surface but not white, not of very varied size; soralia primarily marginal along secondary lobes; soredia farinose to granular; lower surface creamy white to pale brown; rhizines dense, unbranched or ± clumped, often with slightly paler tips, not extending to the margin. Apothecia unknown. Pycnidia rare, laminal, immersed, brown; conidia unciform to short-filiform, 3–5 × ca 1 µm. Cortex K+ yellow; medulla C+ red, K–, KC+ red, Pd–, UV– (atranorin, lecanoric acid). **BLS 1989.**

In habitats similar to those of *P. subrudecta* and often growing alongside this species in Europe. Frequent and increasing in S. England, Midlands, less frequently encountered in Wales, N. England and Scotland, scattered in Ireland.

This grey, foliose lichen has tiny white circular fleck-like pseudocyphellae on the young lobes. The extreme edge of the young lobes is brown with a faint white frosting. Soralia are always present, and are mainly sited along the margins of the lobes, sometimes with a few on the surface.

There is a single report of the lichenicolous *Pronectria oligospora* Lowen & Rogerson (1995) on this host.

***Punctelia reddenda* (Stirt.) Krog (1982)**

Like *P. borrieri*, but with a C– medullary reaction. Upper surface grey-green or olive to yellowish-green, occasionally becoming ridged, soredia coarse and often becoming secondarily partly corticated and then forming elaborate isidiomorphs or small lacinia-like, sub-erect structures. Apothecia and pycnidia not seen on specimens from Britain and Ireland. Cortex K+ yellow; medulla C–, K–, KC–, Pd–, UV– (atranorin, several fatty acids). **BLS 1011.**

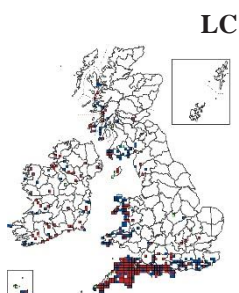
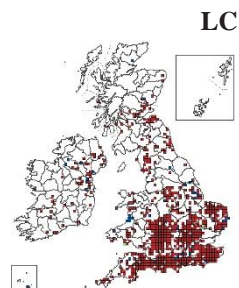
On mossy trunks of broad-leaved trees, more rarely on mossy rocks, in sheltered, humid and often shaded situations; mainly found in *Parmelietum revolutae* communities but occasionally also in *Lobarion* habitat, typically on older well-lit trees on trunks in both field trees and in open woodlands but also colonises sub-canopy twigs in sheltered humid woods, rather local. S. & W. Britain, including W. Scotland but scattered in Ireland.

P. borrieri, *P. jeckeri* and *P. subrudecta* have a C+ red medulla and lack the elaborate isidiomorphs and sub-erect structures of *P. reddenda*.

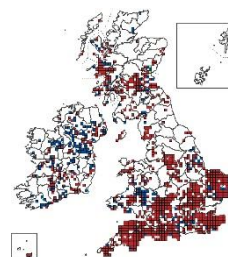
Lichenocodium erodens is the only lichenicolous fungus reported.

***Punctelia subrudecta* (Nyl.) Krog (1982)**

Thallus 3–7 cm diam.; lobes to ca 10 mm broad, closely appressed and ± contorted centrally; margins ± rounded, irregular, sometimes upcurved; upper surface (when fresh) pale greenish-grey, not pruinose; pseudocyphellae usually sparse or even absent in mature thalli, paler than the thallus surface but not white, not of very varied size; soralia laminal or marginal; soredia farinose to granular; lower surface creamy white to pale brown, not darker



towards the centre; rhizines dense, unbranched or \pm clumped, often with slightly paler tips, not extending to the margin. Apothecia very rare, hardly stalked, to 5 mm diam.; disc red-brown, deeply concave, thalline margin unevenly crenate, smooth or partially sorediate. Ascospores $14\text{--}17 \times 12\text{--}15 \mu\text{m}$, subglobose to ellipsoidal. Pycnidia occasionally present, visible on the thallus surface as black dots $90\text{--}125 \mu\text{m}$ diam., the conidia unciform, $4\text{--}5 \times ca 1 \mu\text{m}$. Cortex K+ yellow; medulla C+ red, K-, KC+ red, Pd-, UV- (atranorin, lecanoric acid). **BLS 2070**. [**BLS 1021** is used for *P. subrudecta* s. lat., where no distinction is made between *P. subrudecta* and *P. borrieri* and/or *P. jeckeri*].



On bark of broad-leaved trees, more rarely on wood, also amongst mosses on siliceous rocks, walls, roofing tiles or standing stones in well-lit situations; common and relatively abundant. Widespread throughout Britain and Ireland, less common in N. Scotland and industrialized areas in C. & N. England.

The lobes are grey, when young with minute round or slightly elongated white dot-like pseudocyphellae. The extreme lobe margin is smooth and shiny (not pruinose). Soralia are on the surface of lobes and sometimes also on margins. The underside of marginal lobes can vary from pale brown to dark brown, but the underside of the whole thallus is either light brown or becomes paler towards the centre (to see this it has to be peeled off the bark or underlying moribund bryophytes and lichens).

P. borrieri also has a C+ medulla reaction (containing gyrophoric acid) but more conspicuous pseudocyphellae and soralia concentrated in the central part of the thallus; *P. reddenda* is superficially similar but has a black lower surface, more conspicuously-developed isidiomorphs and a C- medulla. *Cetrelia olivetorum* has thalli to 20 cm diam., lobes to 2 cm broad, with raised, wavy margins, minute dot-like pseudocyphellae and marginal soralia not arising from pseudocyphellae, and a different chemistry. *P. jeckeri* is distinguished by a different thallus colour (dull grey-green), and by the \pm brownish shade and pruinosity of the lobe margins (see under that species).

Reported lichenicolous fungi on *P. subrudecta* s. str. are *Marchandiomyces corallinus*, *Nectriopsis rubefaciens*, *Pronectria oligospora* and an unidentified species of *Abrothallus*.

RAESAENENIA D. Hawksw., Boluda & H. Lindgr. (2015)

Thallus absent, lichenicolous. **Ascomata** forming on blackened, often geniculately deformed filamentous thalli of *Bryoria* and *Usnea* species, indeterminate, crustose, and lacking a distinct margin, very variable in size, most frequently domed or hemispherical, black and generally somewhat shiny, smooth or rugose. **Epithecium** dark brown, irregular. **Hymenium** with an olivaceous tinge. **Hypothecium** dark brown, intermixed with the cortical hyphae of the host whose walls also become pigmented, variable in height. **Hamathecium** of unbranched or sparsely branched paraphyses, the upper cells becoming brown to dark brown and somewhat rough-walled. **Asci** clavate, thick-walled, markedly thickened at the apex, with a distinct internal beak, 8-spored. **Ascospores** elongate-ellipsoidal to subfusiform, colourless, smooth-walled, the walls distinctly thickened and sometimes constricted at the apices which appear as if they have thickened caps. **Conidiomata** pycnidia, immersed in the host thallus or within the hymenium. **Conidiogenous cells** cylindrical, proliferating percurrently. **Conidia** bacillar, straight to slightly curved.

One of two lichenicolous genera of the Parmeliaceae to occur in our region (the other is *Nesolechia*, q.v., which has smaller round apothecia with a determinate structure). Two species are known, one associated with *Usnea* spp. in the Antarctic region and the other a widespread parasite of *Bryoria*.

Divakar *et al.* (2017) found that *Raesaenenia* and *Protousnea* (Motyka) Krog (1976) diverged more recently in evolutionary terms than other genera of the Parmeliaceae, and placed them in synonymy

despite their different morphology and nutritional status. As their methodology has not been universally accepted (see especially Lücking 2019), we retain them as separate genera for the time being.

Literature:

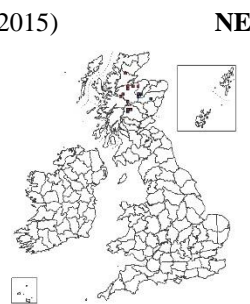
Divakar *et al.* (2015, 2017), Etayo *et al.* (2023), Hawksworth (1978), Hawksworth & Iturriaga (2006), Lücking (2019), Triebel & Rambold (1988), Triebel *et al.* (1995).

Raesaenia huuskonenii (Raesaenen) D. Hawksw., Boluda & H. Lindgr. (2015)

Ascomata forming on blackened, most often geniculately deformed branches of the host lichen, indeterminate, crustose, and lacking a distinct margin (similar in structure to arthonioid taxa), very variable in size, on one side of the branch or ensheathing it, black and generally somewhat shiny; epitecium dark brown, irregular, mainly 5–10 µm thick; hymenium with an olivaceous tinge, 30–50 µm tall; hypothecium dark brown, intermixed with the cortical hyphae of the host whose walls also become pigmented, variable in height. Paraphyses unbranched or sparsely branched, septate, with cells sometimes swollen between the septa, ± colourless and 3–5 µm diam. below, the upper cells becoming brown to dark brown, somewhat rough-walled and 4–6 µm diam. Asci clavate, thick-walled, markedly thickened at the apex with a distinct internal beak, 30–40 × 9–15 µm, 8-spored. Ascospores arranged in parallel or biserially arranged, elongate-ellipsoidal to subfusiform, colourless, smooth-walled, the walls distinctly thickened and sometimes constricted at the apices which appear as if they have 1–3 µm thick caps, (12–) 14–16 (–18) × 2–3.5 µm. Pycnidia immersed in the host thallus, with conidia bacillar, straight to slightly curved, 6–7 × 1.5–2 µm in size.

Parasitic on thalli of *Bryoria fuscescens* and *B. capillaris*, causing distinctive distortion of the host thallus; E. Scottish Highlands.

A very distinctive species, one of the few lichenicolous fungi identifiable without a microscope.



TUCKERMANNOPSIS Gyeln. (1933)

Thallus foliose or subfruticose, lobes weakly channelled, without marginal cilia, ± ascending. Upper surface pale to dark brown, weakly wrinkled, without pseudocyphellae. Lower surface white to pale brown, with sparse rhizines. **Soredia** present or absent. **Isidia** absent. **Photobiont** trebouxiioid. **Upper cortex** paraplectenchymatous. **Medulla** white. **Ascomata** apothecia, lateral and marginal, initially developing on the lower surface. **Asci** cylindrical, 8-spored, tholus rather small, ocular chamber broadly cylindrical, axial body distinctive and broad. **Ascospores** small, globose. **Conidiomata** pycnidia, marginal to submarginal, prominent. **Conidia** bifusiform. **Chemistry:** atranorin (cortex) and medullary orcinol depsidones and fatty acids. **Ecology:** corticolous, occasionally on siliceous rock.

Separated from *Cetraria* on the basis of its foliose habit, presence of (albeit sparse) rhizines, lack of pseudocyphellae and the finer details of ascus structure and anatomy.

Placed into synonymy with a broadly circumscribed *Nephromopsis* by Divakar *et al.* (2017) along with several other well-known genera, a justifiable action based on analysis of the age of evolutionary divergence. However, the genus is morphologically distinguishable and monophyletic, and is retained for the time being to aid continuity of recording.

The genus is also referred to as “*Tuckermanopsis*”, on the assumption that Gyelnik named it in honour of the well-known American lichenologist Edward Tuckerman (1817-1886), but he used the spelling *Tuckermannopsis* and there is no overt acknowledgement of the person in Gyelnik’s paper.

There is only one species in Britain and Ireland.

Literature:

Ahti & Thell (2011b), Divakar *et al.* (2017), Gilbert (2009b), Kärnefelt & Thell (2001).

Tuckermannopsis chlorophylla (Willd.) Hale (1987)

Nephromopsis chlorophylla (Willd.) Divakar, A. Crespo & Lumbsch (2017)

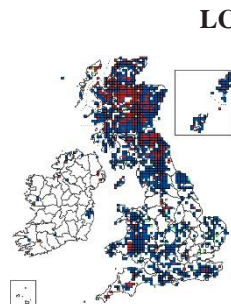
Thallus 1–6 cm diam., foliose, loosely tufted, rarely rosette-forming; lobes few to numerous, 1–3 × 0.2–1 cm, weakly channelled, wavy, crinkled, notched or often deeply incised, entirely ascending or raised at the margins; upper surface pale to medium brown, when wet becoming olive-green and semi-translucent; pseudocyphellae absent; soredia frequent, grey-white, entirely marginal; lower surface white to pale brown, becoming paler towards the centre, wrinkled, rhizines sparse and whitish, or absent. Apothecia very rare, sessile; disc to 3 mm diam.; thalline margin sorediate. Asci 30–40 × 7–10 μm; paraphyses straight, sparsely branched, with swollen tips. Ascospores globose, *ca* 5 μm diam. Pycnidia sparse, marginal and protruding. Conidia dumb-bell shaped, 5–6 × *ca* 1.5 μm. Medulla C–, K–, KC–, Pd–, UV– (protolichesterinic acid). **BLS**

0327.

On twigs, branches and trunks of wayside and woodland trees, shrubs, fence posts, also rarely on coarse-grained siliceous rock and gravestones. Throughout Britain, especially in the north and west, however rapidly declining or extinct in areas with high levels of ammonia pollution; rare in Ireland.

The marginal soralia, C– thallus and coloration are distinctive. Brown specimens of *Platismatia glauca* found in exposed situations remain unchanged in colour when wet, instead of turning semi-translucent. The underside of *T. chlorophylla* becomes paler towards the centre while that of *Platismatia glauca* becomes darker. *Cetraria sepincola* differs in the abundant apothecia, the darker thallus and absence of soredia.

Host to the gall-forming *Tremella cetrariicola* Diederich & Coppins (1996), with *Lichenodiplis lecanorae* also reported.

**USNEA** Dill. ex Adans. (1763)

Thallus shrubby, erect to longly pendent or decumbent, in most species attached by a compact holdfast, branching irregular, branches rounded to angled, even and smooth or pitted, with a network of ridges, shiny or matt, occasionally with annulations or jointed, then divided into segments which may be swollen and ± constricted at their point of attachment, with or without fibrils, tubercles, papillae, pseudocyphellae, isidia, isidiomorphs and soredia. **Outer cortex** present. **Photobiont** trebouxiod. **Medulla** lax or compact. **Central axis** a cartilaginous strand of solid tough compacted longitudinally arranged hyphae, white, rarely pinkish or yellow. **Ascomata** apothecia, lateral or terminal; disc rounded, flat or concave. **Thalline margin** persistent, often with short, ray-like projections. **Asci** 8-spored, elongate-clavate, *Lecanora*-type. **Ascospores** aseptate, ellipsoidal, colourless. **Conidiomata** pycnidia, mainly terminal or subapical. **Conidia** aseptate, colourless, bacilliform, bifusiform, thickened at one or both ends, straight or curved. **Chemistry:** usnic acid in the cortex of all species, the medulla with range of depsides, depsidones, terpenoids or fatty acids. **Ecology:** on trees and rocks in well-lit situations.

The 'beard lichens' somewhat resemble species of *Evernia* and *Ramalina*, which also grow as grey-green or yellow-green tufts on trees, but these in most cases have a flattened, less branched thallus and lack an elastic, cartilaginous central axis. Some *Usnea* species are extremely variable and in many instances TLC, ecological and distributional data are essential for identification. Young thalli are rarely identifiable using morphological characteristics alone.

There have been several studies evaluating the use of molecular barcoding sequences to identify *Usnea* collections (e.g. Kelly *et al.* 2011, Truong *et al.* 2013, Lücking *et al.* 2020, Moncada *et al.* 2020). The consensus appears to be that ITS barcoding in *Usnea* provides broadly reliable results for some species, but does not fully resolve aggregate taxa such as the *U. cornuta* complex. Simple BLAST searches of the public databases can be misleading due to misidentification of published sequences.

The species of *Usnea* present considerable difficulties in their delimitation. Indications are that some species groups are undergoing rapid evolution, and species as traditionally circumscribed may either contain multiple distinct clades, or are mixed within individual clades. In a number of cases it is not clear to which clade the types of species should be assigned, and much recent work is based on non-British material. Bearing in mind that there are conservation implications for hasty name changes in this group, the account here is based primarily on morphotypes rather than clades. The implications are discussed within the species accounts.

The following notes are included as an aid to resolving some of the problems that may be encountered. Chemical tests on the medulla, backed up where possible by TLC analyses, are important. The presence of a lax medulla (e.g. in *U. cornuta*) can be demonstrated by microscope examination of transverse sections of older branches or the cortex of main branches yielding to pressure from a fingernail. Evidence of a lax medulla is often also indicated by attenuation of the main branches where these join older supporting branches, a feature which is also often accompanied by the pale annulations of ring-like fractures of the same branches.

Many newer descriptions include measurements of the thickness of cortex, medulla and axis, or CMA measurements, reported as percentages of the entire branch thickness; these are to be taken on a longitudinal section of the thickest part of a primary branch (Clerc 1987a), sliced to the middle of the axis. They have proved useful for describing variation in anatomy among species and even for distinguishing certain taxa (e.g. *U. dasopoga* and *U. barbata*, Clerc & Naciri 2021). An example of a thin cortex and thick medulla would be CMA 4/36/20 for *U. cornuta*, indicating cortex makes up 4%, medulla 36%, and axis 20% of the thickness of the entire branch; cortex and medulla measurements are repeated on the opposite side of the axis, making up the 100%. Generally speaking, a thick medulla or axis would represent a value of over 30%. Longitudinal views of branch thickness are also important to distinguish regular (cylindrical) branches from those that taper (fusiform) or those that are irregular due to depressions, ridges or foveoles (pits).

Few species are truly 'isidiate' (e.g. *U. hirta*) but many produce fragile isidium-like outgrowths which often become eroded and develop into soralia. The soredia produced, some of which can become partly secondarily corticated, rounded or finger-like, are called isidiomorphs. Truly entirely sorediate species (e.g. *U. glabrata*, *U. fulvorea*, *U. esperantiana*) never produce isidiomorphs and thus are distinctive. Characteristics of the soralia are very important (outline in top view, profile in side view, size relative to branches and distribution, presence/absence of isidiomorphs), and are important to examine (e.g. to distinguish the severely underrecorded *U. wasmuthii* from *U. subfloridana*, and the segregate species of the *U. cornuta* group. Blackening of the holdfast area occurs in *U. flavocardia*, *U. fragilesce*, *U. subfloridana*, *U. silesiaca* and *U. wasmuthii*; in other shrubby species the holdfast remains pale. The illustrated key to European *Usnea* species contributed by Randle *et al.* (2009) is very helpful for interpreting the special morphological structures found in the genus, as is the key to shrubby/subpendulous sorediate species by Clerc & Otte (2018).

Specimens from our area assigned to *U. foveata* Vain. (1928) are referable to *U. hirta* and *U. wasmuthii*. Reports of *U. cavernosa* Tuck. (1850) are based on specimens probably collected from outside Britain and Ireland, or rare specimens of foveolate *U. barbata*.

Several species are regularly host to various lichenicolous fungi. Details can be found in a table after the key below.

Literature:

Clerc (1984, 1987a, b, 1992, 2011, 2016), Clerc & Naciri (2021), Clerc & Otte (2018), Degtjarenko *et al.* (2020), Gerlach *et al.* (2019), Harrold (2019), James (2003), James *et al.* (2009), Kelly *et al.* (2011), Lücking *et al.* (2020), Mark *et al.* (2016), Millanes *et al.* (2014), Moncada *et al.* (2020), Randlane *et al.* (2009), Saag *et al.* (2011), Törra *et al.* (2007), Truong *et al.* (2013).

- | | | |
|--------|--|----------|
| 1 | Thallus red-brown or grey-green, mottled red-brown at least on the main branches <i>rubicunda</i>
Thallus yellowish, green-grey, dark grey, only turning reddish or brown when moribund or
in old dried specimens.....2 | 2 |
| 2(1) | Older parts of thallus of conspicuous inflated sausage-like segments; surface smooth,
mainly without ornamentation <i>articulata</i>
Older parts of thallus not or only slightly constricted at the site of attachment of the main and
lateral branches, never in sausage-like segments; surface variously ornamented with tubercles,
papillae, soralia, isidiomorphs and isidia3 | 3 |
| 3(2) | Axis or adjacent part of medulla pigmented primrose or rose-pink, rarely white4
Axis and medulla always white, never pigmented5
[caution: fresh material of many <i>Usnea</i> species may have a pinkish axis, but the pigmentation disappears on drying] | 4
5 |
| 4(3) | Axis and inner medulla pale to primrose-yellow, CK-; thallus soft, pliant, ± erect, shrubby,
pale green; medulla lax, making the cortex fragile; psoromic acid present <i>flavocardia</i>
Axis ± rose-pink, CK+ yellow-orange; thallus rigid, inflexible, ± pendulous, dark grey-green;
medulla compact, supporting the cortex; barbatic and diffractaic acids present <i>ceratina</i> | 6
7 |
| 5(3) | Thallus without soralia6
Thallus with soralia, isidiomorphs or true isidia7 | 6
7 |
| 6(5) | Thallus with abundant papillae and fibrils; remaining erect when moist, usually fertile..... <i>florida</i>
Thallus without papillae but with ± numerous spine-like isidia: very flaccid when wet; very
rarely fertile..... <i>hirta</i> | 8
9 |
| 7(5) | Medulla and/or soralia Pd+ rust-red, K-8
Medulla and/or soralia Pd-, K-, or Pd+ yellow to orange-red and K+ yellow-red9 | 8
9 |
| 8(7) | Cortex thin and shiny, medulla lax; lateral branches narrowed at the point of attachment; soralia
conspicuous, excavate to irregularly efflorescent-excrescent, often exceeding width of branches,
without isidia or isidiomorphs..... <i>glabrata</i>
Cortex thick, medulla compact; lateral branches not constricted at the point of attachment; soralia
very small, punctiform, superficial, smaller than half width of branches, with fragile isidiomorphs
when young..... <i>subscabrosa</i> | 10
11 |
| 9(7) | Thallus ± pendulous (several times longer than wide); main branches ± parallel10
Thallus ± erect, shrubby or only subpendulous (then longer than wide); main branches ± diverging ...12 | 10
12 |
| 10(9) | Soralia large and circular, conspicuous <i>glabrescens</i>
Soralia absent, or when present punctiform, inconspicuous11 | 11
11 |
| 11(10) | Main branches usually distinctly irregular with the largest diameter not close to the basal
part; cortex thin to moderately thick (3–9 %); medulla moderately thick to thick (16–36 %),
lax to dense <i> barbata</i>
Main branches tapering or slightly irregular but then with largest diameter situated close to the
basal part; cortex moderately thick to thick (7–16 %); medulla thin to moderately thick (10–26 %),
dense to compact <i>dasopoga</i> | 11
12 |

- 12(9) Main branches round in section; thallus often with \pm discrete soralia; isidiomorphs if present, in clusters often associated with soralia; medulla compact or lax 13
Main branches with indentations, not round in section; usually with numerous irregularly scattered or crowded spine-like isidia, sometimes leaving scars which develop into soralia; medulla lax..... *hirta*
- 13(12) Main branches constricted at their point of attachment or barrel-shaped, and/or segments \pm swollen, articulated 14
Main branches never constricted, segments cylindrical, not or hardly swollen 19
- 14(13) Soralia minute, punctiform, smaller than half of branch diameter (on larger branches), numerous, often coalescing to form larger eroded patches, isidiate when young *cornuta s. lat.*
Soralia conspicuous, larger than half of branch diameter, often \pm discrete, isidiate or not when young 15
- 15(14) Soralia never with isidiomorphs even when young; branch apices often markedly flexuose, twisted, resembling skeletal fingers, crowded with large soralia; medulla K+ yellow \rightarrow red (salazinic and (sometimes) bourgeanic acids) *esperantiana*
Soralia with isidiomorphs, at least when young, sparse; branch apices straight or curved; medulla K+ yellow to yellow-orange (norstictic and/or stictic acids) 16
- 16(15) Basal part pale, usually with numerous paler annular cracks, especially near the holdfast, cortex matt; medulla usually dense; soralia irregular in shape, usually rich with isidiomorphs; branching isotomic-dichotomous *flammea*
Basal part dark brown, reddish or jet-black, without conspicuous pale annular cracks; cortex shiny, medulla lax 17
- 17(16) Soralia well-spaced, plane in profile, usually neat and well-spaced; isidiomorphs present when young..... *fragilescens*
Soralia becoming crowded, usually convex-efflorescent, with or without isidiomorphs or isidiofibrils; branches strongly to slightly irregular..... 18
- 18(17) Medulla K-, P-, UV+ pale blue (lobaric acid); fibrils few to absent on terminal branches *arianae*
Medulla K+ yellow, P+ yellow-orange (stictic acid); fibrils numerous and dense on terminal branches *subpectinata*
- 19(13) Basal part concolorous with the branches or paler, not conspicuously blackened..... 20
Basal part jet black, at least for 1-2 mm..... 21
- 20(19) Branches with numerous conspicuous pale annulations; soralia minute, punctiform; papillae sparse or absent *flammea*
Branches with few or no annulations; soralia conspicuous, excavate; papillae numerous *perplexans*
- 21(19) Isidiomorphs never present; soralia flat to excavate 22
Isidiomorphs usually present (at least on juvenile soralia), sometimes sparse, very fragile; soralia flat to tuberculate 24
- 22(21) Branches irregular, often deformed or irregularly swollen and with depressions in the cortex; soralia deeply excavate; medulla moderately thick, lax to dense *perplexans*
Branches cylindrical, not or rarely deformed; soralia various; medulla thin, \pm dense 23

- 23(22) Thallus erect, rarely sub-pendulous, lateral branches numerous, of \pm equal length and appearing like a fish-bone; soralia irregular, often crowded and coalescing, deeply excavate, reaching central axis; with stictic acid (in quantity), norstictic and \pm diffractaic acids *fulvoraegens*
Thallus \pm densely branched towards the base with a few extended unbranched and mainly pendulous, flexuose main branches; soralia very regular, rounded, scarcely excavate, usually not reaching central axis, never coalescing (or only on very thin branches at the extremities); either with norstictic acid (in quantity) and \pm salazinic or stictic acids, or psoromic acid *glabrescens*
- 24(21) Thallus blackened at base only, or if above without annular cracks; soralia various, but rarely transversely elliptical; soralia Pd+ instant yellow-orange 25
Thallus \pm extensively blackened towards base and often also on main branches, here and above with numerous distinct annulations and cracks; soralia flat or slightly excavate, transversely elliptical or irregularly rounded; soralia Pd+ yellow (after one minute) or Pd-;
salazinic acid only *silesiaca*
- 25(24) Medulla K+ canary yellow; soralia Pd+ yellow-orange (instantly); soralia typically slightly tuberculate and raised, developing from the cortex; isidiomorphs abundant even when mature *subfloridana*
Medulla K+ yellow \rightarrow red or K-; soralia flat to slightly excavate 26
- 26(25) Short fibrils formed on young branches which are shed soon after formation, leaving pseudocyphella-like scars; medulla K+ yellow \rightarrow red (salazinic and norstictic acids), UV- *praetervisiva*
Fibrils not formed on young branches, when mature \pm oval in section, longitudinally stretched; isidiomorphs present only on young soralia *subfloridana*

Lichenicolous fungi from Britain and Ireland associated with *Usnea* species

Species	Host species
<i>Abrothallus usneae</i> Rabenh.	<i>U. cornuta</i> , <i>U. fragilesccens</i> , <i>U. subfloridana</i> , <i>U. wasmuthii</i>
<i>Biatoropsis hafellneri</i> Millanes <i>et al.</i>	<i>U. articulata</i> , <i>U. cornuta</i> , <i>U. esperantiana</i> , <i>U. flammea</i> , <i>U. fragilesccens</i>
<i>Biatoropsis usnearum</i> Räsänen s.l. (? indicates confirmation needed; other <i>Biatoropsis</i> spp. maybe involved)	? <i>U. ceratina</i> , <i>U. dasopoga</i> , <i>U. florida</i> , ? <i>U. glabrata</i> , ? <i>U. hirta</i> , ? <i>U. rubicunda</i> , <i>U. subfloridana</i> , <i>U. wasmuthii</i>
<i>Catillaria usneicola</i> Etayo	<i>U. cornuta</i> , <i>U. dasopoga</i> , <i>U. wasmuthii</i> , <i>U. sp.</i>
<i>Cyphobasidium usneicola</i> (Diederich & Alstrup) Milanés <i>et al.</i>	<i>U. sp.</i> (Isle of Skye)
<i>Endococcus apiciicola</i> (J. Steiner) R. Sant.	<i>U. ceratina</i> , <i>U. cornuta</i> , <i>U. flammea</i> , <i>U. florida</i> , <i>U. subfloridana</i>
<i>Everniicola flexispora</i> D. Hawksw.	<i>U. subfloridana</i>
Cf. <i>Hyaloscypha</i> sp. (apothecia pale yellow)	<i>U. fragilesccens</i> , <i>U. sp.</i> (Westernness)
<i>Kalchbrenneriella cyanescens</i> (Kalchbr.) Diederich	<i>U. cornuta</i> , <i>U. flammea</i> , <i>U. hirta</i> , <i>U. subfloridana</i> , <i>U. wasmuthii</i>
<i>Lichenocodium cargillianum</i> (Linds.) D. Hawksw.	<i>U. subfloridana</i>
<i>Lichenocodium erodens</i> M.S. Christ. & D. Hawksw.	<i>U. cornuta</i> , <i>U. florida</i> , <i>U. wasmuthii</i>
<i>Lichenocodium usneae</i> (Anzi) D. Hawksw.	<i>U. articulata</i> , <i>U. flammea</i> , <i>U. subfloridana</i> , <i>U. sp.</i>
<i>Lichenostigma maureri</i> Hafellner (<i>Phaeosporobolus usneae</i> D. Hawksw. & Hafellner; anamorph)	<i>U. cornuta</i> , <i>U. dasopoga</i> , <i>U. hirta</i> , <i>U. fragilesccens</i> , <i>U. subfloridana</i> , <i>U. wasmuthii</i>
<i>Marchandiomyces corallinus</i> (Roberge) Diederich & D. Hawksw.	<i>U. subfloridana</i> , <i>U. wasmuthii</i>
<i>Pseudoseptoria usneae</i> (Vouaux) D. Hawksw.	<i>U. sp.</i> (<i>U. cornuta</i> or <i>U. esperantiana</i>).
<i>Spirographa fusisporella</i> agg. (incl. <i>Cornutispora ciliata</i> state)	<i>U. subfloridana</i>
<i>Zevadia peroccidentalis</i> J.C. David & D. Hawksw.	<i>U. flammea</i>

Usnea arianae P. Clerc, E. Caviro & A. Gerlach (2020)

NE

Thallus to 5 cm in length, shrubby, with anisotomic-dichotomous branching, main branches often strongly irregular in longitudinal section with lateral branches constricted at the point of attachment, and terminal branches with foveolae and transverse furrows. Base blackened for *ca* 1 mm. Medulla thick and lax, axis thin.

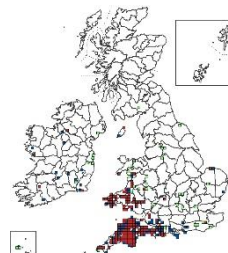
Separated from *U. cornuta* by having large soralia (wider than half of the branch width at maturity) which rarely coalesce, but tend to remain individual and become efflorescent, often with abundant isidiomorphs. Four chemotypes occur: (A) medulla K⁻, P⁻, (usnic, lobaric and fatty acids), (B) medulla K⁻, P⁻, (usnic and fatty acids), (C) medulla K⁺ yellow→red, P⁺ yellow-orange (usnic, norstictic and fatty acids), (D) medulla K⁺ yellow→red, P⁺ yellow-orange, (usnic, norstictic, lobaric acids). The lobaric acid chemotypes are present in most European material (and the single British specimen – lobaric and usnic acids only), with a minority of European specimens containing norstictic acid. **BLS 2854**.

A segregate in the *U. cornuta* group, recently described and so far with a single specimen known from the Isle of Wight but distributed more widely in Europe, Macronesia and the tropics. Young specimens cannot be distinguished from *U. cornuta* without TLC analysis, and the UV test for lobaric acid cannot easily or reliably be applied due to low concentrations of the compound. The only other *Usnea* with lobaric acid is *U. flammaea*, which lacks a shiny cortex and usually has annular rings near the holdfast. *U. subpectinata* tends to have fibrils and isidiofibrils on the branches with a denser but still thick medulla, typical for the *U. cornuta* group.

Usnea articulata (L.) Hoffm. (1796)

NT IR

Thallus to 1 m or more long in favoured sites, pendent or scrambling, main branches to 3 mm diam., the older portions strongly inflated, ± cylindrical, forming sausage-like segments, young or terminal branches less inflated, adjacent segments interconnected by a cartilaginous axil or with annulations, sparingly branched at the base, more richly and irregularly branched towards the apices, with few, ± flexuose lateral branches, often in a loose, flexuose tassel; cortex thin (5–7% of diam.), surface pale green-grey, uniformly smooth or rarely in part minutely roughened-papillate, or with scattered slightly raised white comma-like pseudocyphellae; medulla thick, lax, cottony-arachnoid, especially in inflated parts; cortex thin. Apothecia unknown in Britain. Medulla C⁻, K⁻, KC⁻, Pd⁺ red (fumarprotocetraric and usnic acids). **BLS 1456**.



In well-lit, xeric situations, especially on inclined branches in crowns of trees, or more rarely scrambling over low vegetation, also on the ground in a few coastal sites; locally abundant. S. & S.W. England, Wales, N. to Isle of Man, Ireland, formerly extending to N. England. Rapidly recolonizing in Wales.

Usually easily identified by the prostrate to untidily hanging, inflated, sausage-like older parts of the thallus. There is little surface ornamentation apart from a few white comma-like pseudocyphellae, and soralia and isidia are absent. One of the most sensitive species to SO₂ air pollution, less so to ammonia. Young specimens, which lack the characteristic articulations, could be confused with *U. flammaea* which is more erect, has a bottle-brush appearance and a K⁺ yellow-red medulla (stictic acid complex).

Usnea barbata (L.) F.H. Wigg. (1780)

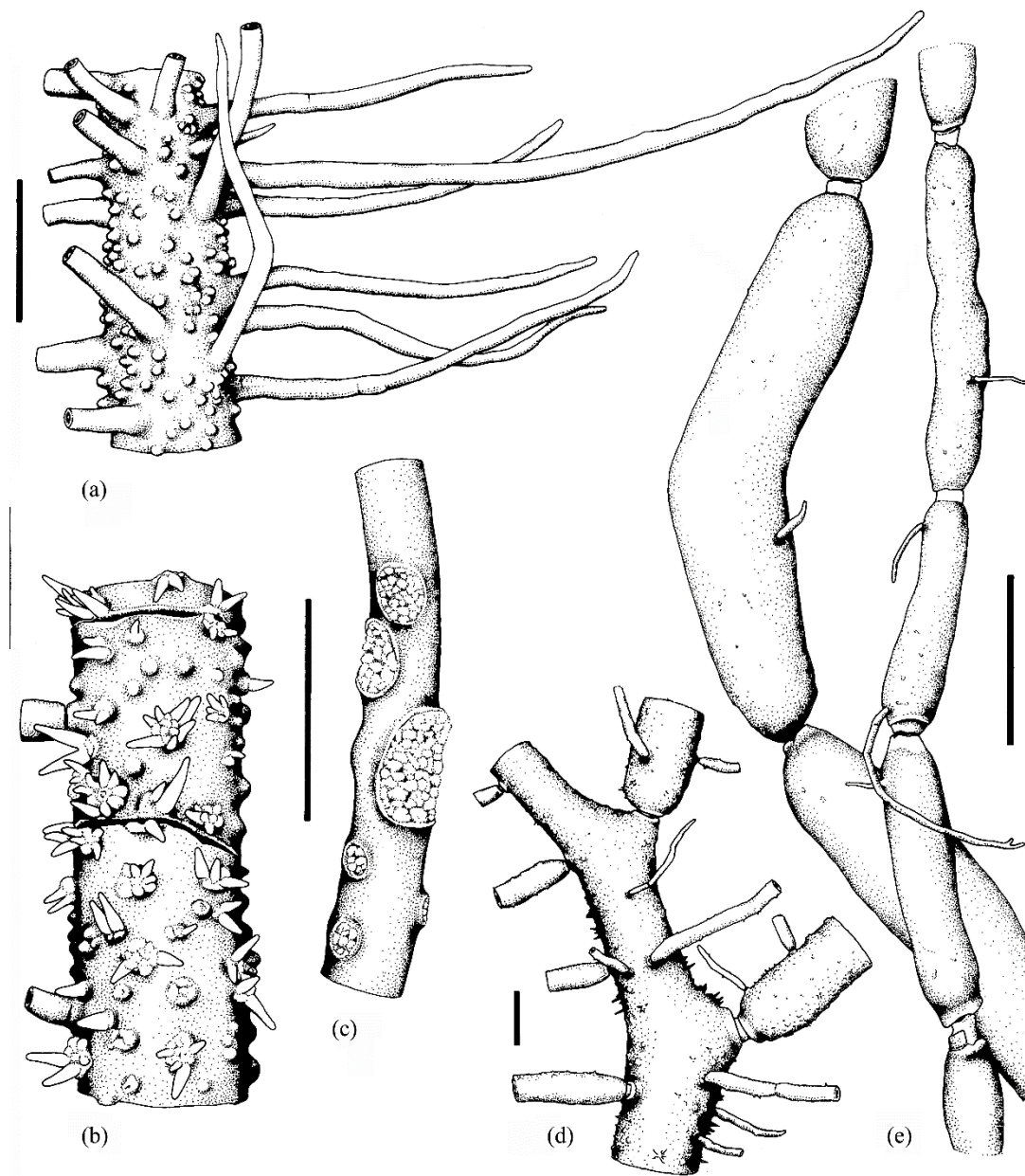
NE

Similar to *U. dasopoga*, but with distinctly irregular branches with slightly to strongly inflated segments, a thinner cortex and a rather thick and dense to lax medulla. Medulla C⁻, K⁺ yellow then reddish orange, Pd⁺ orange (salazinic acid) or C⁻, CK⁻, Pd⁻ (no secondary substances by TLC). **BLS 1780**.

On bark of *Larix*, Scottish Highlands (Angus and Easternness).

The name *U. barbata* has been applied to various British *Usnea* species over the years, but Clerc (2016) discovered a few historical specimens in **BM** that correspond to the genuine taxon. This and *U. dasopoga* were shown to be distinct by Clerc & Naciri (2021). More research is needed into the status of this species in Great Britain and Ireland.

Material with numerous short broken segments along the main branches and lacking fibrils has sometimes been named *U. chaetophora* (**BLS 1459**), but this morphology can develop in both *U. barbata* and *U. dasopoga* and it should be considered a morphotype probably arising from environmental conditions.



Thallus features in *Usnea*. (a) Papillae and fibrils (*U. florida*); (b) eroding tubercles giving rise to clusters of isidiomorphs (*U. rubicunda*); (c) soralia with soredia (*U. glabrescens*); (d) inflated branches constricted at base (*U. cornuta*); (e) main branches constricted into segments (*U. articulata*). Scale bars a-d = 1 mm, e = 5 mm.

Usnea ceratina Ach. (1810)

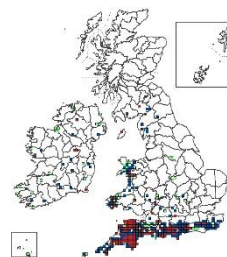
Thallus normally \pm stiffly pendent, often long and straggling, to 30 cm long, juvenile specimens more erect and tufted, rigid, pale at the base, main branches coarse, to 1.5 mm diam., of uniform thickness, only tapering at the apices, typically rather straight when well-developed or somewhat twisted, often \pm angular; branching usually sparse, occasionally with numerous irregularly arranged lateral branches, with scattered or sometimes abundant single or clusters of thin fibrils to 1 cm in length arising at right-angles to the branches, surface dark grey-green, conspicuously coarsely warted with numerous white raised \pm hemispherical tubercles, these often bursting to form coarsely granular ulcerose soralia and occasionally isidiomorphs, main branches also with smaller low translucent paler papillae; medulla very compact, pale to deep pink, rarely white; axis thick. Apothecia rare, lateral on main branches, disc with few marginal rays. Thallus C+ yellow-orange, K-, CK+ yellow-orange, Pd-, medulla C+ yellow (diffractaic, barbatic and usnic acids and sometimes several accessory substances). **BLS 1458**.

On acid-barked old trees, particularly *Quercus* and *Fagus*, in relict woodlands and parklands where it is characteristic of well-lit sites on trunks of ancient trees particularly along waysides and in glades, also often on inclined or horizontal trunks and boughs in thin tree canopies; locally frequent. S. & S.W. Britain, Wales, Scotland (Dumfries, Lochwood), rare in Ireland.

Characterized by the rigid \pm inflexible coarse scabrid texture, \pm coloured axis and conspicuous white tubercles, often bursting with coarse soredia. Young thalli can be identified by their flesh-coloured to pink medulla (almost white when the pigment is in low concentration) and the presence of barbatic and diffractaic acid (CK+ yellow-orange). The combination of the stiffly pendent thallus and C+ yellow reaction of the medulla is distinctive.

Richly branched morphs may resemble *U. dasopoga* but that species is usually more regularly branched with a fishbone-like appearance, lacks conspicuous white hemispherical tubercles which become eroded and sorediate, has a K+ red medulla and is usually abundantly spinulose on the main branches, especially towards the holdfast. Small, erect, pollution-damaged specimens superficially resemble *U. cornuta* which, however, has a lax medulla, persistently colourless axis and a different chemistry.

LC

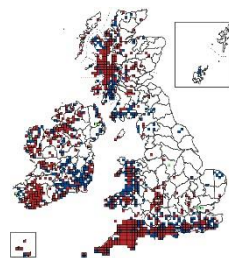
**Usnea cornuta** Körb. (1865)

Thallus 2–6 (–10) cm, \pm erect, tufted, rarely subpendent, main branches to 1.5 mm diam., inflated, with few to numerous short lateral branches clearly constricted and often annulated at the point of attachment to the main stems, mostly curved, often widely divergent to 90° in terminal branches, branching anisotomic-dichotomous, surface dull grey-green becoming \pm dark brown in dried preserved collections, the base usually concolorous or paler, rarely blackened, cortex often smooth and \pm shiny-glassy in lower parts of the main branches, more rarely corrugate-areolate, sparsely to densely papillate above; scattered or clustered isidium-like structures (isidiomorphs) present together with \pm roughened whitish grey erose \pm erumpent soralia; soralia minute, 0.06–0.2 mm diam., numerous, often becoming confluent and spreading; soredia coarsely granular, often mixed with a few to many secondarily corticate isidiomorphs; papillae absent on the upper branches; medulla very lax and thick. Two chemotypes occur: (A) medulla K+ yellow \rightarrow red, Pd+ yellow to orange-red (salazinic and sometimes protocetraric and/or constictic acids); (B) medulla K+ yellow \rightarrow blood-red, Pd+ yellow-orange (stictic [major], norstictic, menegazziaic, constictic and sometimes salazinic acids); chemotype A appears more frequent in our area, and a minority of specimens appear to lack salazinic acid entirely. **BLS 1469** [s. lat.], **BLS 2855** [s. str.].

On mossy woodland or wayside trees, more rarely siliceous rocks; widely distributed and locally frequent in lowland areas and returning to many previously air-polluted habitats. W., S.W. & S.E. Britain and Ireland, scattered elsewhere.

A complex of several related species similar in morphology, several of which occur in our area (Gerlach *et al.* 2020). *U. cornuta* s. str. is characterized by the shrubby habit, lateral branches that are typically distinctly inflated and constricted at the attachment and diverging at 90°, with a claw-like appearance of the main and terminal branches, presence of small papillae, minute soralia remaining level with the cortex which coalesce to form extensive and irregular soralia, few to many fragile secondarily corticate isidia (isidiomorphs), and spinules and occasionally naked smooth surface areas. *U. arianae* and *U. subpectinata* are similar overall, but differ in soralium development, both remaining simple, and becoming efflorescent, and both differing in chemistry.

LC



Young material may be impossible to determine, and should be recorded at *U. cornuta* s. lat. *U. flammea*, which often occurs in similar habitats, has pale annulations on its main stems, lacks inflated attenuated branches and generally has a smoother surface. *U. fragilescens* differs in the size and density of soralia and chemistry.

Usnea dasopoga (Ach.) Nyl. (1876)

Usnea filipendula Stirt. (1881)

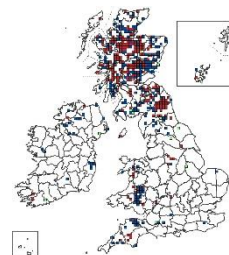
Thallus to 30 cm long, pendent, often rather narrow, composed of 4–6 main branches arising from the point of attachment, branches rather thin, 0.2–0.6 mm diam., mostly even in thickness, usually with many short (to 1 cm long) fibrils arising at right-angles from the main branches, regularly but unevenly distributed along their entire length in a fishbone-like arrangement, branching variously sympodial or dichotomous, upper surface grey-green, often darker in the older parts and blackened towards the base, main branches typically densely papillate and with tubercles, these may produce isidia or isidiomorphs and can also occur on side branches where they are usually less frequent, but are absent towards the apices which narrow to a point and are often laterally fractured into \pm cylindrical segments. Medulla C–, K+ yellow→red, KC–, Pd+ orange (salazinic and usnic acids). **BLS 1460**.

On bark of *Pinus*, *Larix*, *Betula* and rarely *Salix*, especially in exposed mountain woods; locally abundant. S.W. and N. England, Wales, Scotland; rare in Ireland.

A markedly pendulous species, very variable regarding the number of main branches (2–30); also varied in the abundance and shape of the tubercles and papillae, the formation of soredia and isidiomorphs, the frequency of associated fibrils, the degree of subsidiary branching, the presence of cylindrical segments and colour which may range from pale yellow-grey to dark green-black.

U. barbata is similar but with irregular branching and \pm inflated segments. Material with numerous short segments and lacking fibrils has sometimes been named *U. chaetophora* (**BLS 1459**), but this morphology can develop in both *U. barbata* and *U. dasopoga* and it should be considered a morphotype probably arising from environmental conditions.

LC



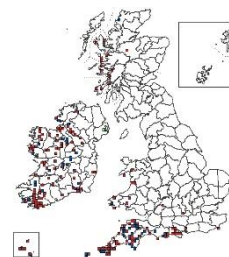
Usnea esperantiana P. Clerc (1992)

Thallus 4–6 cm, erect, rarely subpendent, shrubby, main branches 1–2 mm diam., conspicuous, lateral branches disproportionately thinner, 0.3–0.5 mm diam., numerous, entangled, often irregularly branched, markedly flexuose and contorted at the apices, surface grey-green, not blackened at the base, main branches thickly scabrid, papillate, fibrils numerous over the whole thallus, secondary branches smooth, becoming \pm eroded towards the tips with numerous \pm rounded white flat to somewhat excavate irregularly shaped soralia, often recurved and resembling skeletal fingers, especially when heavily sorediate; medulla somewhat lax to compact. Apothecia very rare. Medulla C–, K+ yellow→red, KC–, Pd+ orange-red (salazinic, consalazinic and bourgeanic acids). **BLS 1816**.

On twigs and small branches of broad-leaved trees, hedgerows, orchards and garden shrubs, rarely on worked timber; locally frequent. S. & W. England, Ireland; it appears to be spreading north and east.

This distinctive shortly tufted richly branched species is always only sorediate and lacks isidiomorphs. It has numerous curled or contorted branch endings with numerous discrete to fusing soralia simulating skeletal fingers. It is easily distinguished in mixed populations of *Usnea* spp. by the presence of many delicate, paler, twisted, abraded branch endings. *U. esperantiana* may be confused with *U. cornuta* but is neither inflated with a lax medulla nor has main branches which are attenuated at their point of attachment and is truly sorediate. *U. glabrata* is K–, Pd+ rust-red and without papillae on the main branches.

Nb IR

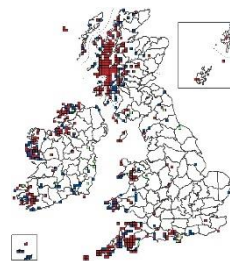


Usnea flammea Stirt. (1881)

Thallus to 3 (–8) cm long, erect to subpendulous, sometimes scrambling, forming sparsely branched lax to compact dense tufts, main branches several, often arising 3–5 mm above the annulated stalk above the holdfast, rather stout, to 1 mm diam., sparingly to richly branched, the branches often originating at \pm the same level

LC

forming a brush or tassel-like tuft of finer secondary branches towards the apices, surface matt, pale green- to yellow-grey, not blackened at the base, usually with \pm numerous, pale annular cracks especially towards the holdfast, forming non-constricted segments, scarcely narrowed at their point of attachment; papillae often scarce or absent in patches on main branches, when present warted, sometimes eroded to form soralia; soralia flat or slightly tuberculate, efflorescent, rounded, with clusters of very fragile easily abraded isidiomorphs; medulla moderately compact to lax, yielding to the fingernail. Apothecia very rare. Medulla C-, K+ yellow or sometimes blood-red, KC-, Pd+ yellow-orange (usnic, stictic, menegazziaic, constictic and sometimes norstictic and/or lobaric acids). **BLS 1461.**



This is the most frequent (but easily overlooked) species on rock faces and occasionally decorticated wood, also common on wayside trees and scrub and *Calluna* stems, especially in wind-swept coastal areas; widespread and locally frequent. S. & W. Britain, Ireland.

Characterized by the pale annulations and pale holdfast area, irregular branching and pollarded appearance arising from the coarse main branches and finer secondary branches terminating at about the same level. Sometimes the main branches may arise together some distance (up to 10 mm) from the holdfast. Lobaric acid occurs only in two European *Usnea* species, in about 80% of *U. flamma* specimens and in the newly reported *U. arianae* (for differences, see that species).

Usnea flavocardia Räsänen (1936)

Thallus to 4 cm long, \pm erect, pale green or yellowish, becoming red-brown in dried collections, paler below but with a blackened base, branches rounded, rather stout, tapered and often \pm constricted at the base, distinctly segmented by conspicuous annular cracks bordered by white rings of medullary tissue on the main branches, indicating conspicuous gaps between the segments at the point of attachment and on main stems, papillae numerous, low, inconspicuous on main branches, fibrils sparse or absent; pseudocyphellae numerous on \pm eroded papillae, later becoming sorediate; isidiomorphs absent or rare; soralia numerous, especially towards the apical parts of the thallus, slightly excavate, soredia rather coarse, medulla lax, outer part white, inner part pale lemon to primrose yellow adjoining axis, axis yellow-white to yellow. Apothecia unknown. Soralia C-, K+ brownish yellow, KC-, Pd+ yellow; medulla C+ yellow-orange, K+ yellow-orange, KC+ orange, Pd+ faint yellow (usnic, psoromic, sometimes 2-O-demethylpsoromic acids and/or 2 unidentified substances). **BLS 1731.**



In boggy, undisturbed scrub and *Salix* carr, rarely on mossy boulders; rare, but probably overlooked. S.W. England, thinly scattered records in the rest of England, Wales (Pembroke), W. Scotland, N.W. Ireland.

Usnea cornuta differs in having a white, not pale yellow, inner medulla and axis, contains salazinic or stictic acids and has different soralia involving isidiomorph development. In *U. flavocardia* the main and secondary branches may be distinctly inflated and constricted at their point of attachment, with a very lax medulla; the presence of psoromic acid, which is concentrated in the soralia, is diagnostic. Also many specimens have minute purple spotting of the cortex ($\times 20$ lens). *U. flavocardia* may superficially resemble *U. glabrata* which has a sward-forming, smaller thallus, with branches which have a smooth, shining cortex without papillae and large, convex, efflorescent soralia, often wider than the branches; it contains fumarprotocetraric acid (Pd+ rust-red) and lacks the yellow pigment of the axis and inner medulla.

Usnea florida (L.) Weber ex F.H. Wigg. (1780)

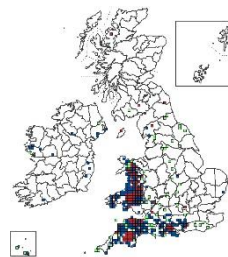
NT

Thallus 2–5 (–10) cm tall, \pm erect, forming often dense shrubby tufts, main branches to 1 mm diam., often curved, often with a few inconspicuous annulations, branching irregular, thinner branches often contorted, surface grey-green, blackened at the base, main stems covered with low, inconspicuous dense papillae and numerous fibrils to 1 cm long, mostly arising at right angles from branches and becoming curved. Apothecia frequent, arising at apices of main and major lateral branches; disc 0.5–1 cm diam., at first \pm concave, becoming flat, smooth or wrinkled, with abundant, often branched fibril-like marginal projections to 5 mm long. Ascospores 8.5–11 \times 5.5–7 μ m, ellipsoidal. Medulla C-, K+ yellow, KC-, Pd+ orange (thamnolic and rarely alectorialic acids, the latter especially in the apothecia). **BLS 1462.**

On twigs and branches in the canopy of broad-leaved trees, rarely on trunks, also on shrubs, palings and fence-posts, mostly in exposed, well-lit sites; locally frequent but declining possibly due to rising levels of ammonia. S. & W. Britain, S. Scotland, rare (Dumfries, Lochwood, Loch Rannoch).

A distinctive and attractive species, typically richly fertile with abundant papillae and fibrils and always lacking isidia and soralia. *U. florida* and *U. subfloridana* form a species complex incorporating several clades that do not correlate well with their morphological distinctions (Saag *et al.* 2011, Mark *et al.* 2015, Degtjarenko *et al.* 2020). Difficulties occur especially when richly fertile thalli of *U. subfloridana* are encountered, which may only produce a small number of soralia. Juvenile forms of *U. florida* and *U. subfloridana* are usually indistinguishable.

The two taxa as understood here have different overall distribution patterns and tend to occur in differing habitats - particularly tree canopies for *U. florida* and a more diverse range of sites for *U. subfloridana*. They are kept apart pending the possible recognition of further taxa within the combined *U. florida/U. subfloridana* clade. See also *U. wasmuthii*.



Usnea fragilescens Hav. (1921)

Thallus 3–5 (–8) cm tall, mostly subpendulous to erect, flaccid, often richly branched, main branches 1.5–2 mm diam., originating over the whole of the length with relatively few thinner side branches which often arise at \pm right angles from these main branches, primary branches much elongate, distinct, thick, often divided into long somewhat inflated segments, often constricted and annulate where they join the main stem giving a characteristic overall combed appearance; fibrils few or absent, axils at an angle of 60–90°; surface very pale grey to green, often \pm pellucid when wet, brown to jet-black for 1–2 mm at the base that is rarely attenuated, shiny (resembling broken glass), smooth; papillae usually numerous, evenly and densely distributed, low, broader than high, often inconspicuous; soralia even, \pm flat to slightly concave, large, conspicuous, distinctively rounded, discrete, widely spaced; isidiomorphs usually present and often dense; medulla lax. Medulla C–, K+ yellow-red, KC–, Pd+ red (usnic, stictic, menegazziaic and sometimes cryptostictic, norstictic and/or constictic acids). **BLS 1817.**

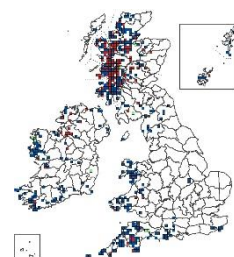
Most British populations fall within var. **mollis** (Vain.) Clerc (1987), but the two varieties are not distinguished by Clerc (2011).

On broad-leaved trees in moist sheltered woodland by rivers and *Salix* carr, rarely on rocks; rather rare and local, most frequent in W. Scotland. W. Britain and Ireland.

This is a semi-pendulous species with a blackened base. Often a very pale green when fresh, it has a distinctly pellucid appearance, especially when moist. The surface of the main branches, which together have a distinct combed appearance, is minutely marbled and appears glassily uneven ($\times 20$). The main branches are gradually tapered towards their point of attachment where they are often cracked. The medulla is very lax and the cortex easily yields to pressure. Isidiomorphs are numerous on young branchlets and when these are abraded they are more or less replaced by neatly rounded soralia in older parts.

U. fragilescens is a distinctive species, usually with a pallid, subpendulous thallus with combed main branches. It is larger than *U. cornuta*, has larger and more discrete soralia and a different branching pattern and a blackened holdfast area.

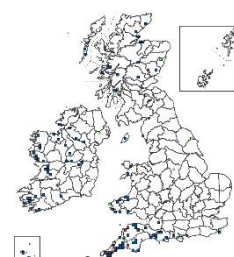
LC



Usnea fulvoviregens (Räsänen) Räsänen (1935)

Thallus 2–10 cm tall, erect, rarely subpendulous; branching mostly isotomic-dichotomous; main branches to 1.5 mm diam., cylindrical, not inflated, often richly branched with numerous laterals (fibrils) mostly of equal length giving a fish-bone appearance to the branches, often densely papillose; surface grey-green or yellow-grey, blackened at the basal part; soralia conspicuous, without isidiomorphs, deeply excavate, typically reaching the central axis, mostly bursting from low pustules (tubercle-like structures but much wider than high) and a tearing off of the adjacent cortex, broader than the branch diameter and irregular in shape. Medulla C–, K+ yellow-red, KC–, Pd+ yellow-orange (usnic, norstictic, stictic acids and sometimes diffractaic acid). **BLS 1465.**

NE



On trees or shrubs in rich pastureland; rare. S.W. England and Wales, scattered in Scotland, throughout Ireland; however records from England and Wales may need reinterpretation.

U. fulvoreaegens is a misunderstood species that has been merged with *U. glabrescens* by many authors. North American and European populations appear to represent two separate clades based on phylogenetic investigations (Mark *et al.* 2016), and the European group is a sister clade to *U. glabrescens*. Both the “European” *U. fulvoreaegens* and *U. glabrescens* are represented by sequenced specimens from the UK.

U. fulvoreaegens appears like a smaller version of *U. glabrescens* but the younger branches have ulcer-like irregular soralia that contain coarse agglomerations of soredia. The holdfast area is blackened and like *U. glabrescens* there is a noticeable extension of several branch endings beyond the bushy part of the main thallus. These extensions differ from *U. glabrescens* in having scattered short branchlets (rather similar to *U. dasopoga*) forming an interrupted herring-bone-like arrangement. In its chemistry, norstictic acid is dominant, plus stictic acid and occasionally (in Europe) diffractaic acid.

Usnea glabrata (Ach.) Vain. (1915)

Thallus to 3 cm tall, ± erect, tufted, main branches 1–1.5 mm diam., inflated, markedly articulate and constricted at the point of attachment, richly branched with frequent fibrils ± attached at right angles, surface pale grey-yellow, becoming deep brown in the herbarium, not blackened at the base, cortex smooth, shiny throughout, without distinct papillae or tubercles; soralia conspicuous, usually exceeding the width of the branch, mostly erumpent, convex-globular, soredia coarsely granular, whitish, mainly situated towards apices, without isidiomorphs; medulla very lax, axis thin. Medulla C–, K–, KC–, Pd+ red (fumarprotocetraric and sometimes protocetraric acids). **BLS 1466.**

On coastal shrubs, old walls and tarmac in open situations, often in swards of many individuals; very rare but easily overlooked, from N.W. Scotland to S.E England.

A distinctive but easily overlooked species, characterized by the small size, smooth shiny surface, lax medulla and coarse granular efflorescent soredia in soralia often wider than the branches. Fumarprotocetraric acid is otherwise only present in the much larger *U. articulata*. The branching habit, lax medulla and articulated lateral branches recall *U. cornuta*, but *U. glabrata* differs in the smaller size, absence of papillae, soralia never forming isidiomorphs, smoother cortex and chemistry. The eroded terminal branches are similar to those in *U. esperantiana*, but that species has papillose main branches, different soralia, a more compact medulla and a different chemistry.

Nb IR



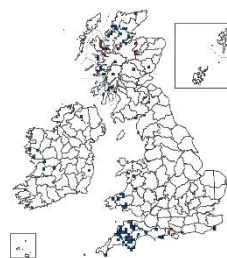
Usnea glabrescens (Nyl. ex Vain.) Vain. (1925)

Thallus 3–10 (–15) cm tall, ± erect at the base, usually becoming ± pendulous towards the apices, main branches to 1.5 mm diam., often very richly branched and crowded towards the base, with long side branches, fibrils few or absent, surface grey-green or yellow-grey, blackened at the base; main branches with evenly spaced densely papillate thinner branches, smooth; soralia conspicuous, frequent, rounded and even to slightly tuberculate or regularly shaped and distinctively rounded, never broader than half branch diameter, discrete or occasionally forming paler eroded patches, exclusively sorediate. Three chemotypes occur: medulla (A) thallus C–, K+ yellow→blood-red, KC–, Pd+ orange (usnic, norstictic and stictic acids); (B) C–, K+ yellow→blood-red, Pd+ yellow to orange (norstictic and salazinic acids); (C) thallus C–, K–, KC–, Pd+ yellow (usnic and psoromic acids). **BLS 1467.**

On deciduous trees in open damp humid situations, especially *Salix* carr; rare and local. Throughout W. Britain, a few records from Ireland.

This is a very elegant pendulous to subpendulous species, often densely tufted towards the base but with elongate ± hanging little-branched flexuose extensions that extend noticeably beyond the main part of the thallus. Only soralia are present; isidiomorphs are almost never produced. The soralia are frequent, usually neatly rounded, conspicuous (often pale yellow-green) and barely excavate, rarely (but sometimes deeply so) exceeding the width of the supporting branch and then difficult to distinguish from *U. fulvoreaegens*, to which it is closely related. The base is markedly blackened and the medulla is very compact. Differs from subpendulous morphs of *U. subfloridana* in the small, rounded, ± excavate soralia, always without isidiomorphs, as distinct from the

LC NS



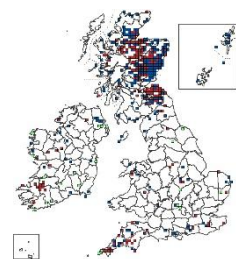
abrasions left by shed isidiomorphs in *U. subfloridana*, and in chemistry. The chemotype with psoromic acid may merit separate recognition. Most British reports of *U. glabrescens* refer to *U. esperantiana* (q.v.).

Usnea hirta (L.) Weber ex F.H. Wigg. (1780)

Thallus 1–4 cm tall, ± tufted, erect, rarely subpendulous, notably flaccid when wet, main branches to 10 mm long, angular in cross-section, ± slightly swollen, surface often with incomplete net-like ridges with ill-defined depressions, richly branched, papillae absent, fibrils few or absent, grey-green, yellow-green or blackish grey, not blackened at the base; isidia abundant, scattered or densely clustered, short and spinule-like, sometimes arising from the ridges; medulla rather lax. C–, K–, KC–, Pd– (usnic and sometimes fatty acids [murolic acid complex]); reported K+, reported Pd+ specimens are probably due to contamination. **BLS 1468.**

Most frequent on conifers, more rarely on wayside and woodland acid-barked deciduous trees, especially *Betula* and *Quercus*, decorticated wood and *Calluna* stems; locally frequent. Predominantly E. & N. Britain, rare in Wales & S. England, scattered in Ireland. It is interesting to note that in Holland this species is recolonising in urban areas (roadside trees, etc) where it is tolerant of some degree of eutrophication.

Distinguished by the ± angular main stems, the flaccid and limp habit when wet, absence of papillae or tubercles, abundant long spinule-like isidia and the absence of a blackened base. A very variable species, consisting of few ± pendulous contorted strands to small erect densely tufted and compact thalli. *U. subfloridana* and *U. wasmuthii* are not flaccid when wet, have a different chemistry, isidiomorphs usually in clusters and associated with soralia, have papillae, are without depressions in main branches and have a blackened basal part.



Usnea perplexans Stirt. (1881)

Usnea lapponica Vain. (1925)

Thallus to 12 cm long, erect to subpendulous, the branching sympodial, divergent, sometimes conspicuously blackened at the base; main branches irregular, sometimes with longitudinal depressions and/or transverse furrows; secondary branches not constricted at the junction with the main stem, ± cylindrical, terete or ± angular in section; papillae usually numerous especially on main branches; fibrils short and irregularly distributed. Soralia conspicuous, larger than half the branch diameter, deeply excavate; isidiomorphs absent. Medulla moderately thick, loose to dense. Three chemotypes occur: medulla (A) C–, K+ yellow→red, KC–, Pd+ orange-yellow (usnic, salazinic acids), (B) C–, K–, KC–, Pd+ yellow (usnic, psoromic acids) and (C) C–, K–, KC–, Pd– (usnic acid, no medullary compounds detected by TLC); so far only the salazinic acid chemotype is known in our area. **BLS 2742.**

Currently known only from a single recent collection on *Betula* bark from Morar, conforming to chemotype A; it could be overlooked elsewhere in northern and western Scotland.

Similar to *U. glabrescens* but with strongly excavate soralia and irregular branching that can be reminiscent of a large version of *U. esperantiana*.

Usnea praetervisa (Asahina) P. Clerc (2004)

Similar to *U. subfloridana* but with short fibrils formed initially on young branches which are shed soon after formation, leaving scars which have the appearance of pseudocyphellae. These lack a cortical rim and often coalesce to form large, flat soralium-like structures which may later develop soredia and isidiomorphs. The medulla is thin and dense. The thallus is shrubby to subpendent, richly branched and with a black base; papillae are present, largely on the main branches. Medulla C–, K+ yellow→red, KC–, Pd+ yellow-orange (salazinic and norstictic acids). **BLS 2743.**

Reported recently from *Quercus* branches in Argyll and Galloway (western Scotland).

Usnea rubicunda Stirt. (1881)

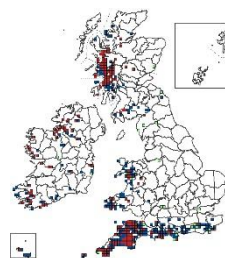
Thallus 3–10 (–20) cm long, not blackened at the base, at first ± erect, sometimes becoming elongate and pendulous, main branches to 1.5 mm diam.; often rather straight, irregularly branched with few to abundant fibrils to 1 cm long, arising at right angles from the branches, surface reddish brown, more rarely ± green-grey with ± numerous red-brown flecks, often irregularly articulate but segments not conspicuously inflated, tubercles abundant and conspicuous on main branches, often eroded at the apices forming coarsely granular soredia that

LC

are occasionally intermixed with a few secondarily corticate isidiomorphs, papillae rather frequent on main branches but absent on fibrils. Medulla compact. Two chemotypes occur: medulla (A) C⁻, K⁺ yellow-red, KC⁻, Pd⁺ orange (usnic, stictic, constictic and sometimes norstictic and psoromic acids); (B) C⁻, K⁺ yellow→red, KC⁻, Pd⁺ orange (usnic, salazinic and sometimes norstictic acids). **BLS 1470.**

On deciduous trees and shrubs, characteristic of sheltered, often moist situations e.g. in *Salix* carr; locally frequent. Mainly in S. & W. England, Wales and W. Scotland; throughout Ireland.

Characterized by the mottled to ± continuous red-brown colour; pale morphs in shade may resemble *U. ceratina* which is Pd⁻. The salazinic acid chemotype is rare. Abraded specimens with little or very pale mottling can be misidentified as *U. cornuta*, *U. flammea* or stressed forms of *U. ceratina*. Care should also be taken in separating moribund specimens of other species, especially those with salazinic acid, which discolour reddish or brownish on decomposition. Well-developed thalli are abundantly sorediate with few to numerous, partially corticate granules (isidiomorphs).



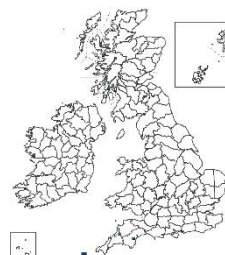
Usnea silesiaca Motyka (1930)

Thallus often ± robust, erect, shrubby to pendulous, 6–12 cm long, richly and irregularly branched, branches rounded, tapered, never constricted at the point of attachment; papillae and fibrils few; surface pale green, main branches often ± coarsely papillate towards the holdfast, matt, basal part of thallus black and here and above with numerous annular cracks; medulla compact, narrow, cortex thick; soralia even, ± flat to slightly tuberculate, raised and then concave, large, conspicuous, punctate to transversely elliptical to irregularly rounded, remaining discrete, moderately dense to dense but rarely becoming confluent; isidiomorphs irregularly present, generally absent on mature soralia. Medulla K⁺ yellow→red, Pd⁺ yellow-red (salazinic acid). **BLS 1818.**

On deciduous trees, shrubs and rock outcrops in windy situations; very rare. S.W. England, W. Scotland (Kintyre), recorded last century also from Cornwall and Kent.

Differs from *U. subfloridana* and *U. wasmuthii* in the soralium type, the more frequent, distinct annulations on the main branches and on the often extended blackened base and the usually paler thallus colour; *U. wasmuthii* additionally contains barbatic acid.

VU(D2)



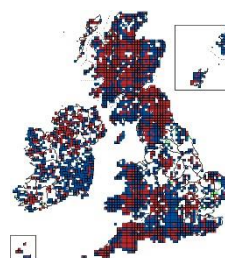
Usnea subfloridana Stirt. (1882)

Thallus 2–8 (–20) cm tall, at first erect, ± tufted, sometimes ± becoming pendulous, main branches to 1.5 mm diam., cylindrical, not inflated, branching irregular, isotomic-dichotomous with numerous laterals of unequal length, surface pale to dark grey-green, often conspicuously blackened at the base, with minute transverse cracking without interconnecting longitudinal cracks (×50) (see *U. wasmuthii*), main branches often densely papillose, especially towards the base, occasionally with white rounded or oval abraded areas, terminal parts and fibrils smooth with scattered papillae and pseudocypbellae giving rise to ± tuberculate, irregularly rounded soralia with coarsely granular soredia, sometimes intermixed with secondarily ± corticate isidiomorphs which tend to persist on mature soralia; medulla dense. Apothecia occasional. Two chemotypes occur: medulla (A) C⁻, K⁺ yellow, KC⁻, Pd⁺ yellow-orange (instantly), UV⁻ (thamnolic and sometimes alectoralic acids, especially associated with apothecia); (B) C⁻, K⁻, KC⁻, Pd⁻, UV⁺ whitish blue (squamic and usnic acids). Occasionally specimens with no or very low concentrations may be encountered. **BLS 1471.**

On trees, more rarely on mossy rocks, also in *Salix* carrs; common. Widespread throughout Britain and Ireland.

The most abundant and widespread *Usnea* species in our region and also the most tolerant of SO₂ air pollution. The thallus is very variable in the degree of branching, some individuals being reduced to a single main stem with a few lateral branches and others being extremely richly branched and tufted. A few terminal branches may be ± pendulous, the rest of thallus remaining erect and shrubby; very rarely entire thalli may be shortly pendulous. The combination of a dense medulla, lack of articulation, blackened base, nature of the soralia and chemistry define this polymorphic species; the squamic acid race is very rare and confined to the Scottish Highlands. See also *U. wasmuthii*.

LC



U. subfloridana and *U. florida* together form a complex clade and are not obviously separable in molecular terms. Fertile morphs of *U. subfloridana* can easily be mistaken for *U. florida*, especially where soralia are poorly developed; for more information see under *U. florida* above.

Usnea subjectinata Stirt. (1881)

NE

Thallus similar to *U. cornuta*, shrubby to subpendulous when well-developed (then 4–12 cm long), with anisotomous-dichotomous branching, base brownish-black to pale reddish on the first millimetre, lateral branches constricted, slightly to strongly irregular longitudinally, slowly tapering along their length. Fibres scattered and conspicuous on main branches, fibrils numerous and dense, thin and slender, usually 1 (–3) mm in length. Soralia punctiform at first, becoming rounded to irregular, flat to slightly raised in profile, eventually convex-efflorescent, mostly remaining single, sometimes aggregating but rarely fusing into consoralia. Isidiomorphs usually numerous, often clustered. Medulla thick, dense to compact. Medulla K+ yellow, P+ yellow to yellow-orange; soralia K–, P– or P+ pale yellow-orangish (usnic, stictic, [major], sometimes also constrictic, cryptostictic, menegazziaic, norstictic and/or salazinic acid). **BLS 2856.**

Distribution poorly known due to confusion with *U. cornuta*. European records so far are from western parts of GBI and Brittany. Some material may be difficult to distinguish, but well developed specimens have distinct and large soralia, usually a dark zone at the base of the holdfast, often a denser but still thick medulla, and numerous spinulose fibrils. Fresh material is needed for confirmation via sequencing.

Usnea subscabrosa Motyka (1937)

VU(D2)

Thallus to 4 (–6) cm tall, pale green, erect to subpendulous (4–10 cm) or scrambling (up to 25 cm), forming loose, rather irregular tufts; main branches rather stout, inflexible, to 1 mm diam., richly branched especially towards the ends, lateral branches finer, not constricted at the base; cortex thin, 8-15% of diam., vitreous, surface pale green- to yellow-grey, not blackened at the base, smooth and shining, at times with inconspicuous annulations; soralia minute, even and flat with respect to cortex, numerous, mainly on terminal branches, with isidiomorphs that rapidly become abraded; medulla compact. Medulla C–, K–, KC–, Pd+ red (usnic and protocetraric acids). **BLS 1908.**

Amongst low vegetation (*Calluna*) and on rocks; locally frequent. Cornwall (Lizard), Isles of Scilly.

A rather coarse scrambling species, with conspicuous main branches with a tendency to form loose, disorganized tufts. It has a dense compact medulla, a relatively smooth hard cortex ± mottled with minute, punctiform soralia, bearing short fragile isidiomorphs which are often poorly developed; extensive areas of the cortex may remain smooth and ± shining except for the soralia. *U. glabrata* is erect and shrubby, contains fumarprotocetraric acid (also Pd+ red), has a lax medulla, a smooth, shining cortex and large soralia. The habit of *U. subscabrosa* recalls that of *U. flammea* which has a semi-lax medulla and contains stictic acid.



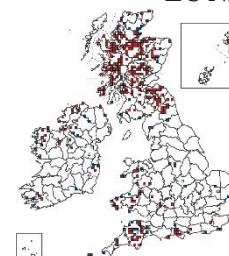
Usnea wasmuthii Räsänen (1932)

LC NS

Like *U. subfloridana*, but soralia slightly excavate, ulcer-like, longitudinally stretched (at least when mature), isidiate only when young, basal blackened part of thallus with faint transverse and longitudinal cracking (×50) forming a fine rimose areolation. Apothecia occasional. Soralia and medulla K–, Pd– (barbatic acid) or medulla K+ yellow→red, Pd yellow→orange (salazinic and barbatic acids). In a survey of material from GBI, about 30% represented the K–, Pd– chemotype. **BLS 1640.**

On deciduous trees; local. Throughout N. & W. Britain and Ireland.

This is one of our most often confused but commonest species, often growing with and indistinguishable at a distance from *U. subfloridana*. The best clue is the soralia which are more elliptical in outline, flat in profile and lacking isidiomorphs (these are soon shed and often restricted to the youngest branchlets) compared with persistent isidiomorphs and convex soralia, but also usually differing in spot tests in *U. subfloridana*. The base is blackened in both taxa but in *U. wasmuthii* the cracking is similar to a brick wall (×50 lens); unfortunately this is not always clearly exhibited. The reactions with Pd and K on the medulla are often helpful for British and Irish populations: in *U. wasmuthii* the soralia turn Pd+ yellowish after one minute, K+ yellow-orange to red (salazinic and barbatic acids); *U. subfloridana* is instantly Pd+ yellow-orange, K+ yellow (thamnolic acid). Any difficulties in identification are best resolved by TLC.



VULPICIDA J.-E. Mattsson & M.J. Lai (1993)

Thallus foliose, forming rosettes or subfruticose, lobes narrow, usually dorsiventral with at least raised tips. Upper surface yellow to almost grey-green, often wrinkled, with or without soredia, pseudocyphellae and isidia absent. Lower surface pale yellow, central parts black; rhizines sparse, laminal, pale or black; medulla bright yellow. **Photobiont** trebouxiioid. **Apothecia** sessile, submarginal to laminal, margin prominent, often crenulate, the disc brown. **Asci** broadly clavate, tholus strongly K/I+, wide ocular chamber and large axial body, *Lecanora*-type. **Ascospores** subglobose, aseptate, 8 per ascus. **Conidiomata** pycnidia, often abundant, marginal and laminal, conspicuous, black, on raised projections, with a black wall. **Conidia** bottle- or crescent-shaped. **Chemistry**: usnic acid (cortex), pulvinic acid derivatives (medulla), fatty acids. **Ecology**: epiphytic, lignicolous, rarely saxicolous.

Placed into synonymy with *Cetraria* by Divakar *et al.* (2017), but the genus is morphologically distinguishable and monophyletic. The genus may be distinguished from *Cetraria* by the bright yellow colour of the thallus, especially the medulla, the strong amyloid reaction of the tholus, \pm globose ascospores, the bottle-shaped to crescent-shaped conidia and the absence of cilia and pseudocyphellae.

Literature:

Divakar *et al.* (2017), Gilbert (2009), Mattsson (1993), Saag *et al.* (2014), Thell *et al.* (2011).

- 1 Bright yellow soralia present on thallus margins; pycnidia rare; apothecia absent *pinastri*
Soralia absent; black, stalked pycnidia frequent on thallus margins; apothecia frequent *juniperinus*

Vulpicida juniperinus (L.) J.-E. Mattsson & M.J. Lai (1993)

Cetraria juniperina (L.) Ach. (1803)

Thallus foliose, loosely adnate, forming irregular rosettes to 3 cm diam. Lobes 1–5 mm broad, flattened, raised, the upper surface glossy, bright yellow in well-lit situations, dull greenish grey-yellow in shaded habitats; lower surface pale yellow to buff, veined, with squarrose pale brown rhizines. Apothecia frequent, submarginal, the disc 2–6 mm diam., red-brown with a thin thalline margin. Ascospores broadly ellipsoidal to subglobose, 5–6 μ m diam. Pycnidia frequent, marginal, black and distinctly stalked. Conidia 6–8 \times 1–2 μ m, sublageniform. Medulla C–, K–, KC–, Pd–, UV+ blackish red or UV– (pinastric, usnic and vulpinic acids, zeorin [minor]). **BLS 0335**.

Formerly present in ancient Caledonian pine forests, also N. England (on *Juniperus*), Upper Teesdale, but now considered to be extinct in Britain.

Like *V. pinastri* but the lobe-margins lack soredia and have abundant black, stalked pycnidia, and apothecia are frequent. Chemistry as *V. pinastri*.

Ex



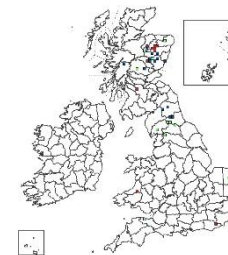
Vulpicida pinastri (Scop.) J.-E. Mattsson & M.J. Lai (1993)

Cetraria pinastri (Scop.) Gray (1821)

Thallus 1–2 cm diam., foliose, forming irregular rosettes; lobes 1–3 mm wide with rounded apices, margins ascending, somewhat crenate; upper surface pale yellow, green-yellow when wet; soredia brighter yellow, abundant along lobe margins and spreading to the upper surface; medulla yellow; rhizines brownish white, squarrose. Apothecia not seen in British material. Medulla C–, K–, KC–, Pd–, UV+ blackish red or UV– (pinastric, usnic and vulpinic acids, zeorin [minor]). **BLS 0337**.

Locally abundant on *Juniperus* in S. Aberdeenshire, with scattered records on other trees and shrubs (*Betula*, *Pinus*, *Calluna*, *Vaccinium*), fence posts and pebbles in E. Scotland, extending locally to W. Scotland & N.E. England and very occasionally to southern England. Outside of the eastern Highlands, occurrences are usually ephemeral and may represent vagrants from continental Europe.

NT



XANTHOPARMELIA (Vain.) Hale (1974)

Thallus foliose to subcrustose or rarely subfruticose, loosely to very closely appressed, dorsiventrally flattened, often large, corticate on both surfaces. **Lobes** irregular to linear, weakly concave or flat to strongly convoluted, lacking cilia; apices \pm incised. **Upper surface** pale yellow to yellow-green or grey-green (usnic acid) or a shade of brown (cortex N+ bluish-green, lacking usnic acid), becoming irregularly cracked, \pm maculate; with or without soredia or isidia (species in Britain and Ireland are mainly isidiate or sorediate), lacking pseudocyphellae. **Upper cortex** of vertically oriented hyphae or angular isodiametric cells, with a pored epicortex. **Cell walls** containing *Xanthoparmelia*-type lichenan. **Medulla** loosely packed, white or pigmented (species in Britain and Ireland with white medulla only). **Lower surface** pale ivory to yellow, tan, brown or black, sparsely to densely rhizinate; rhizines usually unbranched. **Ascomata** apothecia, laminal, sessile or shortly stalked; disc imperforate, concave, becoming flattened and undulating, distorted with age, red-brown to brown or black. **Ascospores** ellipsoidal, small, with an arachiform vacuolar body, 8 per ascus. **Conidiomata** pycnidia, immersed, usually laminal. **Conidia** typically bifusiform, British and Irish species more commonly cylindrical. **Chemistry**: cortex: usnic acid or an unknown brown pigment; medulla: orcinol depsides, orcinol depsidones, β -orcinol depsides, β -orcinol depsidones, anthraquinones, aliphatic acids, amino acid derivatives. **Ecology**: predominantly in arid and semi-arid areas, mainly on rocks and soil in open habitats and less commonly on wood; the brown species are predominantly coastal in the British Isles.

Molecular data has demonstrated that *Neofuscelia* is more appropriately accommodated in *Xanthoparmelia* (Blanco *et al.* 2004b, Divakar *et al.* 2017), the arrangement accepted by Louwhoff *et al.* (2009c).

The ascospores of *Xanthoria* species possess an arachiform vacuolar body (Del Prado *et al.* 2007), which gives them an appearance similar to the polarilocular ascospores found in the Teloschistaceae.

Literature:

Amo de Paz *et al.* (2012), Blanco *et al.* (2004b), Del Prado *et al.* (2007), Elix & Thell (2011b), Hale (1990), Leavitt *et al.* (2018), Louwhoff *et al.* (2009c), Thell *et al.* (2006).

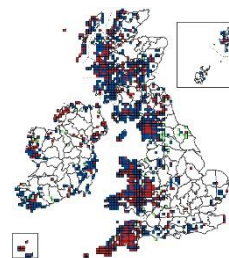
1	Upper surface uniform shades of brown, not or \pm white maculate 2 Upper surface predominantly yellow-green 6
2(1)	Thallus isidiate 3 Thallus not isidiate 4
3(2)	Isidia short and compact, in stumpy, cauliflower-like clusters; upper surface grey-brown or pale brown; glomelliferic, glomellic, perlatolic acids <i>loxodes</i> Isidia coarse, \pm elongate and becoming elaborately branched, \pm scattered; upper surface dark brown; divaricatic acid <i>verruculifera</i>
4(2)	Lower surface uniformly pale tan to brown; divaricatic acid <i>luteonotata</i> Lower surface black, only brown under the lobe ends and margins 5
5(4)	Upper surface yellowish to pale brown, \pm white-maculate; glomelliferic, glomellic and perlatolic acids <i>delisei</i> Upper surface grey-brown to dark brown, not maculate; stenosporic/divaricatic acid <i>pulla</i> and <i>perrugata</i>
6(1)	Thallus very closely appressed, with narrow (<1 mm), \pm radiating lobes; sorediate <i>mougeotii</i> Thallus moderately to loosely appressed, with often \pm overlapping broad lobes (>2 mm); lacking soredia 7

- 7(6) Thallus lacking isidia; medulla Pd+ rust-red (fumarprotocetraric acid)*protomatrae*
Thallus isidiate; medulla Pd+ orange8
- 8(7) Isidia cylindrical, rounded and intact at the apices; medulla K+ yellow to yellow-orange
(stictic acid)*conspersa*
Isidia globose, flattened or erupting at the apices; medulla K+ yellow→red (salazinic acid)*tinctina*

Xanthoparmelia conspersa (Ehrh. ex Ach.) Hale (1974)

LC

Thallus 1–6 (–10) cm diam., forming rosettes or coalescing into larger patches or of ± scattered or radiating lobes, closely appressed; lobes (1–) 2–4 mm broad, slightly broadened towards the ends, discrete, contiguous or overlapping, margins often indented, not raised; upper surface yellow-grey, ± shining, smooth, isidiate; isidia mostly numerous, occasionally very sparse, laminal, globose and constricted at base or usually cylindrical, simple or branched, coralloid, scattered or ± continuous, especially on older parts of thallus; lower surface jet-black, with short, unbranched rhizines. Apothecia occasional; disc to 1 mm diam., concave, becoming flat and undulating with age, red-brown; thalline margin thin, crenulate, ± inflexed, ± isidiate. Ascospores 6–10 × 4–5 μm. Conidia 4–5 × ca 1 μm, cylindrical. Cortex K–; medulla C–, K+ yellow-orange, KC+ orange-red, Pd+ orange, UV– (usnic, stictic [major], constictic, norstictic and cryptostictic acids [all minor]). **BLS 0988.**



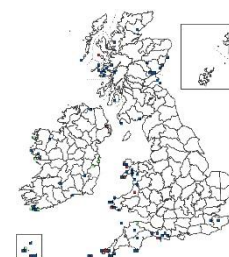
A saxicolous species of well-lit siliceous rocks, often slightly nutrient-enriched, also walls, memorials and roof tiles, often in water-seepage tracks, rarely on hard lignum and acid-barked trees in coastal and inland sites. Common in S.W., W. & N. British Isles, rarer in the E., fairly tolerant of SO₂ air pollution and on the increase.

The form and abundance of the isidia can be very variable, ranging from short, rounded and constricted at the base, to thin, crowded, coralloid, cylindrical and forming a dense, coarsely areolate crust, ± obscuring the thallus, or lacking altogether in which case the specimen is often richly fertile. *X. tinctina* has globose isidia which are often flattened at the top or occasionally erupting at the tips and has salazinic acid (major) in the medulla. *X. protomatrae* always lacks isidia and has fumarprotocetraric acid (Pd+ rust-red) in the medulla.

Xanthoparmelia delisei (Duby) O. Blanco *et al.* (2004)

Nb

Thallus to 3–12 cm diam., sometimes coalescing to form larger patches (to 15 cm diam.), moderately to closely appressed; lobes 1–4 mm broad, elongate, rarely discrete, often contiguous, radiating towards the margins, often pruinose at tips, ± strongly maculate or (rarely) not, often with overlapping and intermixed laciniae; upper surface mostly yellowish- to grey-brown, less commonly red-brown, unevenly rumpled and transversely wrinkled, lacking isidia; lower surface black, often paler near tips; rhizines unbranched, frequent. Apothecia 2–7 (–12) mm diam., common, concentrated on older parts of thallus, concolorous with the thallus; disc red-brown, becoming flattened with age; thalline margin ± entire, occasionally lacerate. Ascospores 7–11 × 4–6 μm, ellipsoidal. Conidia 5–7 × ca 1 μm, bacilliform. Cortex K–, N+ blue-green; medulla C+ pink-red or C–, K–, KC+ pink-red, Pd–, UV+ white (glomelliferic, glomellic, perlatolic and sometimes gyrophoric acids). **BLS 0990.**



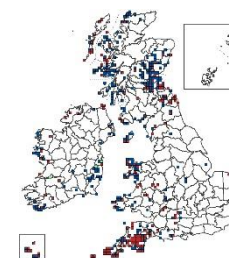
On siliceous coastal rocks, xeric-supralittoral, rarely inland on hard siliceous rocks, churchyard memorials (Kent), slate roofs and sarsens (Dorset), often with *X. pulla*; uncommon. S.W. England, N. Wales, W. & E. Scotland.

See discussion under *X. pulla*.

Xanthoparmelia loxodes (Nyl.) O. Blanco *et al.* (2004)

LC

Thallus wide-spreading, to 20 cm diam., ± loosely appressed; lobes to 5 mm broad, flat, elongate, often overlapping especially towards the centre, spreading marginally; upper surface pale yellowish grey-brown to reddish brown, uneven, frequently ± transversely wrinkled; sparsely to densely isidiate; isidia coarse, clustered, erupting into ± sessile, cauliflower-like outgrowths; lower surface black; rhizines unbranched, frequent. Apothecia frequent; thalline margin often isidiate. Ascospores (7–) 8–10 ×



4–5 μm . Conidia not known. Cortex K–, N+ blue-green; medulla C+ red or C–, K–, KC+ orange-red, Pd–, UV+ white (glomelliferic, glomellic, perlatolic and sometimes gyrophoric acids). **BLS 1003**.

On coastal siliceous rocks, xeric-supralittoral and on coastal cliffs; also inland in upland massifs on moorland rocks and walls; locally common. S.W. England, Wales, much of Scotland (N. to Sutherland), locally frequent in Ireland.

See discussion under *X. pulla*.

Xanthoparmelia luteonotata (J. Steiner) O. Blanco *et al.* (2004) **Nb**

Similar to *X. loxodes* but with thicker, olive-brown to black-brown lobes, without isidia and with a pale tan to brown (never truly blackened) underside. Rarely fertile in the UK. Cortex K–, N+ blue-green; medulla C+ red or C–, K–, KC–, Pd–, UV+ white (divaricatic acid [major], stenosporic and sometimes gyrophoric acids). **BLS 2343**.

Recently recorded from slate roofs in multiple sites in Suffolk and also Wiltshire, widely distributed in S. Europe. The British records are the most northern of this, possibly overlooked, species.

See discussion under *X. pulla*.

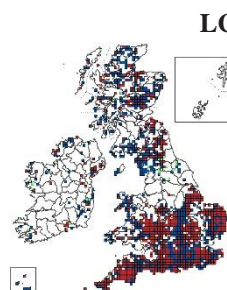


Xanthoparmelia mougeotii (Schaer. ex D. Dietr.) Hale (1974) **LC**

Thallus 0.5–1 (–1.5) cm diam., \pm forming rosettes and coalescing to form larger patches, or partially scattered, very closely appressed, inner part subcrustose, cracked; lobes narrow, to 1 (–3) mm broad, radiating, \pm discrete and scattered, or contiguous, fan-like, not overlapping, elongate, incised, \pm flat; upper surface yellow-grey, becoming \pm darker grey-yellow at the centre, sorediate; soralia *ca* 1 mm diam., laminal, rounded, \pm convex, flat or excavate, scattered; lower surface black, rhizines short, stout, unbranched. Apothecia rare, to 2 mm diam.; disc brown; thalline margin entire, often sorediate. Ascospores 6–9 \times 4–5 μm , ellipsoidal. Conidia 4–5 \times *ca* 1 μm , cylindrical. Cortex K–; medulla C–, K+ yellow-orange, KC+ orange, Pd+ orange, UV– (usnic and stictic acids). **BLS 1005**.

On well-lit siliceous rocks, also on roofing tiles, slate, memorials and quartzite chips in churchyards, occasionally on lignum. Widespread and common in upland Britain and Ireland, locally common and increasing in S. & E. England on artificial substrata.

Parmeliopsis ambigua is separated by the predominantly corticolous habitat and different medullary chemistry (UV+ white and containing divaricatic acid). *Arctoparmelia incurva* resembles *X. mougeotii* but differs in the laminal, convex to globose soralia, markedly convex lobes and medulla K–, KC+ pink, Pd+ rust-red or Pd–, UV+ glaucous blue.



Xanthoparmelia perrugata (Nyl.) O. Blanco *et al.* (2004) **Nb**

This may best be considered a chemotype of *X. pulla* containing divaricatic acid as the major medullary substance. **BLS 2473**.

Occurs on hard coastal siliceous rocks, principally in the xeric-supralittoral zone; local. N. Devon (Valley of Rocks), Outer Hebrides (S. Uist & Lewis) (map left). It may well be under-recorded due to difficulties in separation from *X. pulla*; see under that species for further discussion.



Xanthoparmelia protomatrae (Gyeln.) Hale (1974) **Nb**

Superficially resembling *X. conspersa* but consistently lacking isidia, with more crowded, convex lobes (especially in older thalli), pale brown lower surface and numerous black pycnidia with bifusiform conidia. *X. conspersa* also has a different chemistry (stictic acid). Cortex K–; medulla C–, K+ dirty brown, KC–, Pd+ rust-red, UV– (usnic and fumarprotocetraric acids). **BLS 1784**.

On slate roofs. Only recently recorded for Britain (East Suffolk) where it is rare (map right).



Xanthoparmelia pulla (Ach.) O. Blanco *et al.* (2004)

Like *X. delisei* but with a grey-brown to dark brown thallus and lobes that are not usually strongly white-maculate. The colour of the upper cortex as well as the presence of maculae vary greatly for both species and are not by themselves reliable characters for separating them. Reagent tests on both species: cortex K–, N+ blue-green; medulla C+ pink-red or C–, K–, KC+ pink-red, Pd–, UV+ white are the same. However, the medullary chemistry differs: stenosporic, sometimes also divaricatic and/or gyrophoric acids in *X. pulla*; glomelliferic, glomellic, perlatolic and sometimes gyrophoric acids in *X. delisei*. **BLS 1009.**

On (hard) coastal siliceous rocks in the xeric-supralittoral zone, occasionally overgrowing mosses, also on slate roofs; locally common on south-facing, greywacke crags usually in the *Parmelietum glomelliferae* with other saxicolous calcifuge *Parmelia* species, also in the *Ramalinetum scopularis* on coastal cliffs; widespread. W. & N. coasts of Britain, N. to Shetland, W. Ireland; also more rarely inland – Dartmoor, N & C. Wales, Charnwood Forest (Leicestershire) & Lake District; very rare in Scottish Highlands, Suffolk & Norfolk.

The separation of *X. delisei*, *X. loxodes*, *X. pulla*, *X. perrugata*, *X. luteonotata* and *X. verruculifera* presents considerable difficulties. This is particularly so with juvenile or poorly developed specimens; TLC is essential for verification of those determinations primarily based on thallus colour of the upper and lower surfaces, presence of isidia and distribution and habitat data. The two isidiate species, *X. loxodes* and *X. verruculifera*, are usually readily separable. The former has a yellow-brown, rarely darker, upper surface with scattered, coarse, cauliflower-like clusters of isidia and is almost confined to the coast. *X. verruculifera* has a dark brown thallus with individual, ± scattered to crowded, terete, simple or branched isidia; it is the most widespread of the complex in the British Isles and, as well as on the coast, occurs in many inland sites. *X. verruculifera* has divaricatic acid, *X. loxodes* glomelliferic, glomellic and perlatolic acids.

X. loxodes appears to intergrade morphologically with *X. delisei* particularly when (occasionally) the isidia in the former are absent. These non-isidiate forms of *X. loxodes* (glomelliferic, glomellic and perlatolic acids) can only be reliably separated from *X. pulla* (stenosporic acid) and *X. perrugata* (divaricatic acid) by careful examination of their chemistry.

X. luteonotata (divaricatic and stenosporic acids) has a similar chemistry as *X. pulla* but the lower surface is never truly blackened. The undersurface of this species needs careful examination, particularly of specimens growing on slates. The thalli of *X. luteonotata* tend to be less appressed to the substratum and to have short, imbricate, or sometimes ± upright, lobes towards the centre of the thallus. The study of Amo de Paz *et al.* (2012) demonstrated that both of these species as currently delimited are polyphyletic and the phenotype-based classification does not match the molecular phylogeny.

Xanthoparmelia tinctina (Maheu & A. Gillet) Hale (1974)

Like *X. conspersa* but with distinctly globose and ± inflated isidia, often with flattened or erupting apices. Cortex K–; medulla C–, K+ yellow→red or red-brown, KC+ red, Pd+ orange, UV– (usnic, salazinic and sometimes norstictic acids). **BLS 1025.**

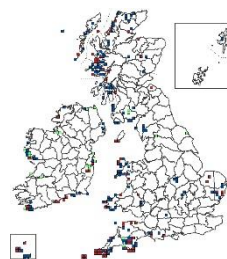
On well-lit, siliceous rocks, serpentine boulders, slate roofs and horizontal granite flagstones along a sea wall, also on tarmac; very rare. W. Pembrokeshire, Cornwall (Lizard), Somerset, Channel Islands.

Isidia alone are not always a reliable character for separating *X. tinctina* and *X. conspersa* because those of the latter species are very variable and are also occasionally ± globose. The two taxa are more reliably separated by a simple spot test – the medulla of *X. tinctina* being K+ red (salazinic acid) whilst that of *X. conspersa* is K+ yellow-orange (stictic acid).

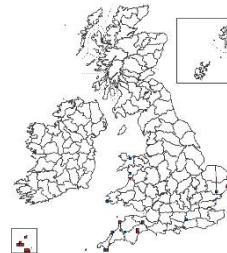
Xanthoparmelia verruculifera (Nyl.) O. Blanco *et al.* (2004)

Like *X. loxodes* but with thinner, darker, dull brown to black-brown lobes with scattered, coarse isidia. The isidia are taller than those of *X. loxodes* and may form elaborately branched-coralloid structures, ± erupting at the tips, becoming ± contiguous to form extensive, ill-defined, ± continuous patches on older parts of the thallus. Cortex K–, N+ blue-green; medulla C+ pink-red or C–, K–, KC+ pink or KC–, Pd–, UV+ white (divaricatic and sometimes gyrophoric acids). **BLS 1026.**

LC



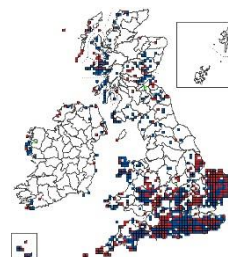
VU(D2)



LC

On siliceous rocks in coastal and inland areas, preferring well-lit xeric situations, typically at low altitude, on memorials, standing stones, roadside walls, roofing tiles, also on very acid, rocky shores in the west. Widespread N. to Sutherland, E., S. & W. British Isles, rare in Ireland but possibly under-recorded.

Montanelia disjuncta can be separated by the proportionally smaller thallus and *Melanelixia fuliginosa* has a shiny upper surface with thinner isidia. Both also differ from *X. verruculifera* in their chemistry. *X. perrugata* has a similar chemistry but lacks isidia. See discussion under *X. pulla*.



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Index

ALECTORIA, 6

Alectoria nigricans, 7

Alectoria ochroleuca, 7

Alectoria sarmentosa, 7

Alectoria sarmentosa subsp. *vexillifera*,
7

ALLANTOPARMELIA, 8

Allantoparmelia alpicola, 8

ARCTOPARMELIA, 9

Arctoparmelia incurva, 9

BRODOA, 9

Brodoa intestiniformis, 10

BRYORIA, 10

Bryoria bicolor, 11

Bryoria capillaris, 11

Bryoria chalybeiformis, 13

Bryoria furcellata, 12

Bryoria fuscescens, 13

Bryoria implexa, 13

Bryoria lanestris, 13

Bryoria nadvornikiana, 13

Bryoria nitidula, 14

Bryoria smithii, 14

Bryoria subcana, 13

Bryoria tenuis, 14

Cavernularia hultenii, 26

CETRARIA, 14

Cetraria aculeata, 16

Cetraria commixta, 18

Cetraria delisei, 19

Cetraria ericetorum, 16

Cetraria islandica, 17

Cetraria islandica subsp. *crispiformis*,
17

- Cetraria juniperina*, 81
Cetraria muricata, 17
Cetraria pinastri, 81
Cetraria sepincola, 17
CETRARIELLA, 18
Cetrariella commixta, 18
Cetrariella delisei, 19
CETRELIA, 19
Cetrelia cetrarioides, 20
Cetrelia chicitae, 20
Cetrelia monachorum, 21
Cetrelia olivetorum, 20, 21
CORNICULARIA, 21
Cornicularia normoerica, 21
EVERNIA, 22
Evernia prunastri, 22
FLAVOCETRARIA, 23
Flavocetraria nivalis, 24
FLAVOPARMELIA, 24
Flavoparmelia caperata, 25
Flavoparmelia sooredians, 25
Gowardia nigricans, 7
HYPOGYMNIA, 25
Hypogymnia farinacea, 26
Hypogymnia hultenii, 26
Hypogymnia physodes, 27
Hypogymnia tubulosa, 27
Hypogymnia vittata, 28
HYPOTRACHYNA, 28
Hypotrachyna afrorevoluta, 29
Hypotrachyna britannica, 29
Hypotrachyna endochlora, 30
Hypotrachyna horrescens, 30
Hypotrachyna laevigata, 31
Hypotrachyna minarum, 31
Hypotrachyna revoluta, 32
Hypotrachyna sinuosa, 32
Hypotrachyna taylorensis, 32
IMSHAUGIA, 33
Imshaugia aleurites, 33
MELANELIA, 34
Melanelia disjuncta, 42
Melanelia hepatizon, 34
Melanelia stygia, 35
MELANELIXIA, 35
Melanelixia fuliginosa, 36
Melanelixia fuliginosa subsp. *glabratula*,
36
Melanelixia glabratula, 36
Melanelixia hawksworthii, 37
Melanelixia subargentifera, 37
Melanelixia subaurifera, 37
MELANOHALEA, 38
Melanohalea elegantula, 39
Melanohalea exasperata, 39
Melanohalea exasperatula, 39
Melanohalea laciniatula, 40
Melanohalea septentrionalis, 40
MENEGAZZIA, 40
Menegazzia subsimilis, 41
Menegazzia terebrata, 41
MONTANELIA, 42
Montanelia disjuncta, 42
Nephromopsis chlorophylla, 66
Nephromopsis nivalis, 24
NESOLECHIA, 43
Nesolechia oxyspora, 43
PARMELIA, 44
Parmelia discordans, 44
Parmelia encryptata, 47
Parmelia ernstiae, 46
Parmelia omphalodes, 45
Parmelia saxatilis, 45
Parmelia serrana, 46
Parmelia submontana, 46
Parmelia sulcata, 46
PARMELINA, 47
Parmelina carporrhizans, 48
Parmelina pastillifera, 48
Parmelina quercina, 49
Parmelina tiliacea, 49
Parmelinopsis horrescens, 30
Parmelinopsis minarum, 31
PARMELIOPSIS, 49
Parmeliopsis ambigua, 50
Parmeliopsis hyperopta, 50

- PARMOTREMA**, 51
Parmotrema arnoldii, 52
Parmotrema crinitum, 52
Parmotrema perlatum, 52
Parmotrema pseudoreticulatum, 53
Parmotrema reticulatum, 53
Parmotrema robustum, 54
PLATISMATIA, 54
Platismatia glauca, 54
Platismatia norvegica, 55
PLEUROSTICTA, 55
Pleurosticta acetabulum, 56
PROTOPARMELIA, 56
Protoparmelia badia, 57
Protoparmelia hypotremella, 58
Protoparmelia memnonia, 58
Protoparmelia montagnei, 58
Protoparmelia ochrococca, 59
Protoparmelia oleagina, 59
PSEUDEPHEBE, 59
Pseudephebe minuscula, 60
Pseudephebe pubescens, 60
PSEUDEVERNIA, 60
Pseudevernia furfuracea, 61
PUNCTELIA, 61
Punctelia borreri, 62
Punctelia jeckeri, 63
Punctelia oxyspora, 43
Punctelia reddenda, 63
Punctelia subrudecta, 63
RAESAENENIA, 64
Raesaenenia huuskonenii, 65
TUCKERMANNOPSIS, 65
Tuckermannopsis chlorophylla, 66
USNEA, 66
Usnea arianae, 71
Usnea articulata, 71
Usnea barbata, 71
Usnea ceratina, 73
Usnea cornuta, 73
Usnea dasopoga, 74
Usnea esperantiana, 74
Usnea filipendula, 74
Usnea flammea, 74
Usnea flavocardia, 75
Usnea florida, 75
Usnea fragilescens, 76
Usnea fulvoreaegens, 76
Usnea glabrata, 77
Usnea glabrescens, 77
Usnea hirta, 78
Usnea lapponica, 78
Usnea perplexans, 78
Usnea praetervisa, 78
Usnea rubicunda, 78
Usnea silesiaca, 79
Usnea subfloridana, 79
Usnea subpectinata, 80
Usnea subscabrosa, 80
Usnea wasmuthii, 80
VULPICIDA, 81
Vulpicida juniperinus, 81
Vulpicida pinastri, 81
XANTHOPARMELIA, 82
Xanthoparmelia conspersa, 83
Xanthoparmelia delisei, 83
Xanthoparmelia loxodes, 83
Xanthoparmelia luteonotata, 84
Xanthoparmelia mougeotii, 84
Xanthoparmelia perrugata, 84
Xanthoparmelia protomatrae, 84
Xanthoparmelia pulla, 85
Xanthoparmelia tinctina, 85
Xanthoparmelia verruculifera, 85