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Lecanorales: Ramalinaceae [revision 1]

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to compile new printed editions of the entire lichen biota of Britain and Ireland is extensive, and many parts are out-of-date even as they are published.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: Ramalinaceae [revision 1]

including the genera *Bacidia*, *Bacidina*, *Bellicidia*, *Biatora*, *Bibbya*, *Bilimbia*, *Cliostomum*, *Kiliasia*, *Lecania*, *Megalaria*, *Mycobilimbia*, *Phyllopsora*, *Ramalina*, *Scutula*, *Thalloidima*, *Toninia*, *Toniniopsis* and *Tylothallia*.

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RAMALINACEAE C. Agardh (1821)

Thallus varied in form; crustose, fruticose, squamulose or granular, a few species lichenicolous; usually pale, sometimes with isidia or soralia. **Photobiont** chlorococcoid, cephalodia absent. **Ascomata** apothecia, superficial or sometimes shortly stalked, pale and concolorous with the thallus to \pm black; thalline margin usually absent, true exciple present but often becoming excluded, disc flat to strongly convex. **Hamathecium** of unbranched or branched paraphyses, the apices often swollen. **Asci** mostly of *Bacidia* or *Biatora* type; cylindrical to clavate, apical dome K/I+ dark blue with a pale, \pm conical apical cushion and sometimes a dark, tubular ring-structure, with a K/I+ blue outer layer, usually 8-spored. **Ascospores** varied in shape, broadly ellipsoidal to filiform and aseptate to multiseptate, colourless, usually without a distinct perispore. **Conidiomata** pycnidia, immersed to sessile. Conidia varied in form, sometimes septate.

The Ramalinaceae is one of the larger families of lichens, containing nearly 1000 species (Lücking *et al.* 2016) and around 40 genera. The family definition and generic arrangement follows the recent phylogenetic study by Kistenich *et al.* (2018), and includes genera previously assigned to the Bacidiaceae and Megalariaceae. The placement is uncertain of some genera with British representatives that have previously been assigned to the Ramalinaceae; these include *Adelolecia*, *Catinaria*, *Frutidella*, *Japewia* and *Schadonia*. Pending further studies, they will be treated in this work as genera of uncertain affinity within the Lecanorales, as will the recently established *Lithocalla* (Orange 2021), which was assigned with some doubt to the Ramalinaceae.

Catillaria aphana, C. modesta and *C. scotinodes* (see Reese Naesborg *et al.* 2007, Kistenich *et al.* 2018) and perhaps other species with *Bacidia-* or *Biatora-*type asci treated in that genus by Fletcher & Coppins (2009) belong within the Ramalinaceae, but further research is needed to establish their position. They are listed at the end of this treatment, and included in the key to *Toninia* s.l.

A traditional key to genera of the Ramalinaceae would be difficult to construct, so a table of genera with their useful diagnostic features is included here, with characters focused on species from Great Britain and Ireland.

Bacidia	Thallus crustose, granular or squamulose, sometimes sorediate; thalline margin absent; true exciple composed of thick-walled gelatinous hyphae with narrow lumina; asci <i>Bacidia-</i> or rarely <i>Biatora-</i> type; ascospores mostly filiform to acicular, multiseptate; with violet/blackish pigments
Bacidina	As <i>Bacidia</i> , but with the true exciple composed at least in large part of thin-walled cells with isodiametric to ellipsoidal lumina rather than radiating hyphal tissue with narrow lumina; without violet/blackish pigments
Bellicidia	As <i>Bacidia</i> , but with the true exciple hyphal in construction with globose outer cells, dark red-brown pigment in the apothecia and pycnidial walls, cylindrical ascospores and often prominent pycnidia with \pm ellipsoidal conidia
Biatora	Thallus crustose to granular-verrucose, sometimes sorediate; true exciple <i>Bacidia</i> -like but hyphal walls usually indistinguishable from the gelatinous matrix in between; asci <i>Biatora</i> -type; ascospores ellipsoidal to filiform
Bibbya	Thallus various, soredia and isidia absent; apothecia marginate at first; true exciple and epithecium with red- to purple-brown K+ red pigments; asci <i>Bacidia</i> -type; ascospores various
Bilimbia	Thallus crustose to effuse, not sorediate; true exciple <i>Bacidia</i> -type but with dark brown or pinkish brown, K+ intensifying, N+ purple pigmentation; asci <i>Biatora</i> -type; paraphyses relatively thick-walled; ascospores with a finely warted perispore.
Cliostomum	Thallus crustose to granular-verrucose, sometimes sorediate; thalline margin sometimes present; true exciple with radiating hyphae; asci <i>Biatora</i> -type; ascospores ellipsoidal to bacilliform, usually 1- or 3-septate

Kiliasia	The only GBI species is lichenicolous; true exciple dark with cellular structure obscure; asci Bacidia-
	type; ascospores ellipsoidal to cylindrical, 1- to 3-septate
Lecania	Thallus various, sometimes sorediate or with goniocysts; thalline margin usually present at least
	initially; asci Bacidia- or Biatora-like; ascospores ± ellipsoidal, mostly 1- or 3-septate
Megalaria	Thallus crustose to granular, sometimes sorediate; apothecia large, dark, the exciple with radiating
	hyphae; epithecium and hypothecium K+ intensifying greenish to dark purple; asci varied; ascospores
	ellipsoidal, 1-septate
Mycobilimbia	Thallus crustose, sometimes sorediate; true exciple Bacidia-type; epithecium poorly developed; asci
	Biatora-type; ascospores ellipsoidal to ± cylindrical, 1- to 3-septate, perispore not warted
Phyllopsora	Thallus squamulose or granular; prothallus often distinct; apothecia often tuberculate; true exciple
	and asci Bacidia-type; ascospores ± ellipsoidal, mostly aseptate; perispore absent
Ramalina	Thallus shrubby, often tufted, often sorediate; apothecia shortly stalked; thalline margin present at
	least initially; asci Bacidia-type; ascospores ellipsoidal to reniform, 1-septate
Scutula	Thallus poorly developed or absent (lichenicolous); apothecia various, thalline margin ± distinct; true
	exciple Bacidia-type; ascospores various; pycnidia prominent
Thalloidima	Thallus squamulose, often strongly pruinose, initially often associated with cyanolichens; apothecia
	with Sedifolia-grey pigments; thalline margin absent; asci Bacidia-type; ascospores fusiform to
	ellipsoidal, 1-septate; perispore absent
Toninia	Thallus squamulose to granular, not pruinose, or absent (lichenicolous); apothecia with Bagliettoa-
	green pigments; thalline margin absent; asci Bacidia-type; ascospores various
Toniniopsis	Thallus crustose to squamulose, not or weakly pruinose; hypothecium and inner part of exciple reddish
	brown; Bagliettoa-green pigments present; asci Bacidia-type; ascospores various
Tylothallia	Thallus warty-verrucose; apothecia convex, dark blue-grey to black; thalline exciple absent; true
	exciple becoming excluded; asci Biatora-type; ascospores usually septate

Literature

Ekman (2001, 2023), Fletcher & Coppins (2009), Kistenich *et al.* (2018), Llop (2007), Lücking *et al.* (2016), Miądlikowska *et al.* (2014), Spjut *et al.* (2020).

BACIDIA De Not. (1846)

Thallus crustose, smooth, cracked, warted, or granular, sometimes sorediate, isidiose or microsquamulose, usually whitish, pale green, green-grey, pale grey or fawn. **Photobiont** chlorococcoid; cells globose or broadly ellipsoidal. **Cephalodia** absent. **Ascomata** apothecia, flat to strongly convex, \pm sessile, variously coloured, mostly to 1 (–1.3) mm diam. **Thalline margin** absent. **True exciple** always present, but sometimes reflexed, composed of \pm coherent radiating thick-walled gelatinized hyphae with narrow lumina at least in the outer part. **Hymenium** I+ blue. **Hypothecium** colourless or variously coloured. **Hamathecium** of paraphyses, few to numerous, rarely branched, the apices often swollen. **Asci** clavate to cylindrical-clavate, 8-spored; *Bacidia*-type, apical dome K/I+ dark blue with a pale, \pm conical apical cushion or in a few species *Biatora*-type with a darker staining zone around the apical cushion, wall pale, outer layer dark blue. **Ascospores** colourless, mostly 3– or more septate at maturity, mostly filiform to acicular or sigmoid but in a few species cylindrical to fusiform, without a distinct perispore. **Conidiomata** pycnidia, immersed to sessile, variously shaped and coloured. **Conidia** colourless, variously shaped, sometimes transversely septate. **Chemistry**: thalli all C–, K–, KC–, Pd–, I–, UV–; a wide range of pigments in apothecia and pycnidia. **Ecology**: various, but few species found on very acidic substrata.

Despite referral of a large number of species to other genera, *Bacidia* remained heterogenous in the circumscription of Coppins & Aptroot (2009). Following removal of several further genera (including *Bacidina*) the species that are now retained are broadly monophyletic. Coppins & Aptroot (2009) also recognized that three species then referred to *Bacidia* (*B. carneoglauca*, *B. trachona* and *B.*

viridifarinosa) should be excluded from the genus and assigned to the *Pilocarpaceae*. Aptroot *et al.* (2018) introduced the genus *Aquacidia* for these species. Additionally, Kistenich *et al.* (2018) discovered that *B. auerswaldii* and *B. circumspecta* were congeneric with the formerly exclusively lichenicolous genus *Scutula*; they are treated there in this volume. Three further species formerly treated in *Bacidia, B. bagliettoana, B. coprodes* and *B. inornata*, are transferred to the genus *Toniniopsis* in this volume.

Literature:

Aptroot *et al.* (2018), Brand *et al.* (2009), Coppins & Aptroot (2009), Czarnota (2016), Ekman (1996, 2004, 2014), Ekman *et al.* (2021), Kistenich *et al.* (2018), Kondratyuk *et al.* (2019), Llop (2007), Llop & Ekman (2007), Reese Næsborg *et al.* (2007).

Key to species of *Bacidia*, *Bacidina* and similar genera with biatorine apothecia and multiseptate ascospores

Many species are very variable, especially in the pigmentation of apothecia and the colour and extent of thallus development, particularly in specimens from shaded habitats. The key below includes the species excuded from *Bacidia* since the 2009 treatment, and also some that were already transferred to the genera *Bilimbia*, *Lecania* and *Mycobilimbia*. It thus includes most fertile crustose species with biatorine apothecia, sparingly branched paraphyses and at least 3-septate ascospores. Sterile material is not keyed out here; with presumed sterile *Bacidia* s.l. specimens, the general keys to sterile taxa should be consulted.

1	Ascospores ± filiform or acicular, length/breadth ratio 10:1 or more
Filifor	m or acicular ascospores
2 (1)	Epithecium remaining green in K
3 (2)	On rocks or soil, sometimes on bryophytes
4 (3)	Hypothecium (upper part) dark, K+ dark red- or purple-brown
5 (4)	Hypothecium brown in upper part; thallus granules 15–60 (–80) μm diam
6 (3)	Hypothecium dark brown, at least in upper part
7 (6)	Upper hypothecium yellow-brown, K-; ascospores acicular
8 (7)	Upper hypothecium and inner exciple dark red-brown, K± purplish; ascospores ± cylindrical
9 (6)	Ascospores ± filiform, straight, not markedly tapering at lower end

10 (9)	$ \begin{array}{ll} Ascospores \ 30-55 \ \mu m \ long, \ 3- \ to \ 7-septate \ \ldots & 11 \\ Ascospores \ 45-80 \ \mu m \ long, \ 7- \ to \ 16-septate \ \ldots & 12 \\ \end{array} $
11 (10)	True exciple blue-green; pycnidia with blue-green walls, 30–50 µm diam
12 (10)	Thallus white, grey or greenish, thin, \pm smooth to granular-warted, but without discrete granules
	Thallus blue-green or blue-grey, granular with discrete granules 40–100 µm diam. Bacidia caesiovirens
13 (2)	Epithecium or hymenium greenish in water, K+ violet, C+ violet
14 (13)	On coastal rocks in the xeric-supralittoral zone; inner exciple and upper hypothecium pale to dark red-orange or orange-brown in K
	Not on coastal rocks; if on rocks with granular thallus then inner exciple and hypothecium K+ dulling (without red or orange tints in K)
15 (14)	Thallus usually thick and warty granular or granular-sorediate
16 (14)	Hypothecium dark coloured, at least in upper part 17 Hypothecium colourless, pale straw, or very pale coloured 23
17 (16)	Ascospores 15–25 μm long, filiform to cylindrical
18 (17)	Thallus smooth, cracked or warted, never with distinct soredia or granules 19 Thallus granular or sorediate 20
19 (18)	Apothecia red-brown, most remaining flat and with a raised thalline exciple; upper hypothecium orange-brown, K–
20 (18)	Thallus granules (areoles) >100 μm diam., never soredium-like
21 (20)	Thallus sulphur- to light apple-green, sometimes forming extensive leprose patches; pycnidia not known
22 (21)	Conidia filiform, arched or curved, without hook; generally saxicolous
23 (16)	Ascospores $14-28 \times 2-3 \mu m$, narrowly fusiform to bacilliform, on rocks or soil (on bryophytes, plant debris), never on bark or wood
24 (23)	Apices of paraphyses to 3 μm diam., colourless; conidia 10–20 μm long <i>Lecania cuprea</i> Apices of paraphyses to 5 μm diam., often dark coloured; conidia 31–55 μm long

25 (24)	Apothecia flat to moderately convex, not clustered; hymenium and epithecium containing blue-green pigment; hypothecium pale orange-brown
26 (23)	On bark, or if on wood then with \pm black apothecia
27 (26)	Epithecium and exciple edge brown, K+ yellowish tinge, never purple
28 (27)	$ \begin{array}{l} \mbox{Ascospores} \leq \!$
29 (28)	Apothecia dark purple-brown to black, margin concolorous with disc
30 (29)	Ascospores 21–40 × 2–3 (–4) μ m, strongly curved, sigmoid, worm-like, or a few short-acicular; conidia 7–9 × 0.5–1 μ m, ± bacilliform
31 (28)	Thallus granular or granular-isidiateBacidia biatorina Thallus smooth to warted, often cracked, never with distinct granulesBacidia laurocerasi
32 (26)	Exciple edge and epithecium pale to dark fuscous brown, sometimes K+ yellow-tinged
33 (32)	Apothecia (0.2–) 0.3–0.7 mm diam., red-brown; thallus varnish-like or minutely granular-warted; on bryophytes or plant debris on calcareous substrata
34 (33)	Thallus distinctly sorediate or isidiate, usually with only a few scattered apothecia
35 (34)	Thallus, at least in part, with fine granules or soredia 20–50 µm diam
36 (35)	Apothecia reddish brown to brown-black; upper exciple edge (and sometimes epithecium) reddish brown, K+ purplish, never with aeruginose-blue pigment; soredia often in rather discrete soralia
	Apothecia pale pink to dark blue-black; upper exciple and/or epithecium colourless or partly aeruginose-blue or orange-brown, K–
37 (36)	Thallus often thick (up to 1 mm); upper exciple edge aeruginose-blue or orange-brown <i>Bacidina adastra</i>
	Thallus usually thin; upper exciple and other apothecial tissues colourlessBacidina delicata
38 (35)	Thallus finely coralloid-isidiate, isidia to 30 µm diam. and 300 µm tallBacidina celtica Thallus granular, granular-isidiate or microsquamulose, granules >50 µm diam

39 (38)	Apothecia pink-buff to flesh-coloured, never pruinose; hymenium 40–60 µm tall; ascospores ≤2 µm diam
	Apothecia pale to dark red-brown, margin sometimes white pruinose; hymenium 70–105 μm tall; ascospores 2.5–3 (–4) μm diam
40 (34)	Apothecia 0.1–0.3 (–0.45) mm diam
41 (40)	Apothecia whitish or pink-orange to pale grey-brown; internally without ascomatal pigments; exciple \pm entirely composed of hyphae with \pm globose lumina to 5(–7) μ m diam. in K <i>Bacidina chloroticula</i>
	Apothecia pale to dark brown; internally usually with some brownish or olivaeous pigments; exciple of narrow hyphae that abruptly swell to form large, ovoid or globose, vesicle-like cells to $20 \times 12 \ \mu m$ in KBacidina saxenii
42 (40)	Prothallus usually conspicuous, white; pycnidia usually present; semi-aquatic, on rocks (or more rarely bark or wood) in streams or along lake marginsBacidina inundata Prothallus usually absent; mostly on bark, not semi-aquatic
43 (42)	Apothecia pale, beige or pale orange-pink; 0.2–0.5 mm diam., hymenium $35-50 \mu$ m high; ascospores $29-45 \times 1.5-2 \mu$ m
44 (43)	Thallus thinly to richly granular-isidiate
45 (44)	Hypothecium and exciple K± yellow, or outer part of exciple brownish and K+ purple
46 (45)	Apothecia red-brown or brick-red; hymenium $45-60 \ \mu m$ high; paraphysis apices rarely swollen but a few to 3 μm diam.; ascospores (30–) $42-54 \times 1.5-2 \ \mu m$, 3- to 7-septate
	<i>Bacidia assulata</i> auct. br., non (Körb.) Vězda Apothecia pink-brown; hymenium 65–90 μ m high; paraphysis apices often distinctly swollen to 5 μ m diam.; ascospores 34–70 (–86) × 2.5–4 μ m, 7- to 16-septate

Cylindrical, ellipsoidal or fusiform ascospores

Lichenicolous, on Peltigera	. Bacidia killiasii
Thallus present	
Ascospores with warted epispore (best seen in K or in old ascospores), 5–8 μm diam. Bilim	bia sabuletorum
Ascospores without warted epispore, generally <4.5 µm diam. (for species with wider	ascospores,
compare with couplet 57)	
Hypothecium dark brown	
Hypothecium colourless or pale	
Pycnidia sessile and conspicuous, black; thallus Pd+ red; on rocks or tree roots, mostly	below
overhangs	uacidia trachona
Pycnidia absent or immersed and inconspicuous; thallus Pd	
))	Lichenicolous, on <i>Peltigera</i>

51 (50)	0 On rock On bark or wood	
52 (51)) On base-rich rock; apothecia sometimes lobed but not tuberculate	is coprodes is inornata
53 (51)) Ascospores 9–13 μm long	ıbturgidula 54
54 (53)) Epithecium green	separabilis a incompta
55 (49)) Hymenium or epithecium dull green, K+ violet	beckhausii 56
56 (55)) On bark (or mosses over bark) on tree trunks or branches On rocks or soil, or on roots below overhangs; if on mosses then not over bark	57 59
57 (56)	Thallus thickly and entirely granular; ascospores (3-) 5- to 6 (-7)-septate	t ula effusa 58
58 (57)) Apothecia black, raised above the thallus; ascospores consistently 3-septate, $<3 \mu m$ diam.	ula ioniarii
	Apothecia variably coloured (piebald/grey), but not black, often flush with the thallus; ascos variably (0-) 3 (-5)-septate, >3 µm diam.	pores nia naegelii
59 (56)	Pycnidia 0.2–0.4 mm diam., always abundant, prominent, white, pubescent; apothecia with pubescent margin; thallus UV+ pink-orange	ia antricola 60
60 (59)) Ascospores 2–3 μm diam. Ascospores 4–8 μm diam.	61 63
61 (60)	Apices of paraphyses to 3 μm diam., colourless; conidia 10–20 μm longLecc Apices of paraphyses to 5 μm diam., often dark coloured; conidia 31–55 μm long	inia cuprea 62
62 (61)) Apothecia flat to moderately convex, not clustered; hymenium and epithecium containing blue-green pigment; hypothecium pale orange-brown	cumpallens subfuscula
63 (60)) Exciple with rectangular lumina; growing directly on rock	<i>fuscoviridis</i> ebris 64
64 (63)) Thallus sorediate	<i>xanthoides</i> 65
65 (64)	Apothecia whitish, without pigmentation	rneoalbida a tetramera

Thallus white, pale green-grey or grey, thin, granular-warted; photobiont cells 5–12 (– 14) um diam. Apothecia 0.3–0.8 (–1) mm diam., usually black but grey or even pallid in shade forms, mostly flat and marginate, but sometimes a few becoming convex and immarginate; true exciple persistent, dark green, K+ intensifying green at the upper outer edge, internally pale red-brown (K± purple) and with abundant minute colourless crystalline inclusions (less than 1 µm diam.) dissolving in K; epithecium blue-violet or purple-brown (rarely green), K+ green, N+ purple-violet with blue crystals; hymenium 65-90 µm high, colourless; hypothecium colourless or pale yellow-brown; paraphyses 1–1.5 µm diam., unbranched or forked above, the apices often pigmented and swollen to ca 4 μ m diam. Ascospores 45–80 \times 2–3 (–4) μ m, 7- to 16-septate, acicular. Pycnidia inconspicuous, immersed in the thallus; conidia filiform, curved, $7-32 \times ca$ 0.5 µm.



Unidentified orcinol meta-depsides have been detected by TLC. BLS 0129.

On \pm acid bark of deciduous trees, mainly in old woodlands, but also on dead *Picea* twigs; common in Scotland (Highlands), occasional in western Ireland, rare elsewhere. Records in southern England need checking.

Often confused with B. laurocerasi but easily separated by the granular warted thallus and epithecium pigmentation. Morphs with a green epithecium can be confused with *B. friesiana*, which differs in the shorter (30–50 µm), 3- to 7-septate ascospores and colourless inner exciple that lacks crystalline inclusions.

Bacidia arceutina (Ach.) Arnold (1869)

Thallus white, pale green-grey or grey, \pm immersed or thin, smooth or rimose, sometimes minutely granular- warted; photobiont cells 5-12 µm diam. Apothecia 0.2-0.6 (-0.8) mm diam., pale brown to brown-black, at first flat and marginate but often becoming convex and immarginate; true exciple colourless but the outer edge usually brown, of narrow (ca 1 µm diam.) radiating hyphae bound in a gel matrix that swells in K, but usually with a single row of swollen rounded lumina (to $6 \mu m$ diam.) at the outer edge; epithecium yellow- to dark brown, K-, N-; hymenium 45-65 µm high, colourless; hypothecium colourless or the upper part (subhymenium) straw or yellowbrown, K \pm intensifying yellow; paraphyses 1–1.5 µm diam., unbranched or a few irregularly forked above, apices slightly broadening to 2.5(-4) µm diam., colourless.

Ascospores (32–) 35–55 (–67) × 1.5–2 (–2.5) µm, narrowly 3- to 7-septate, acicular. Pycnidia inconspicuous, immersed in the thallus; conidia filiform, curved, $9-17 \times ca 0.7 \mu m$. BLS 0131.

On trunks and branches of trees and shrubs with \pm basic or nutrient-rich bark, more rarely on sheltered, often slightly calcareous rocks or on mosses or plant debris on them; rare in air-polluted areas. Throughout Britain and Ireland.

Distinguished from other Bacidia species of similar appearance by the lack of greenish or purplish apothecial pigments. The rare "Lecidea" erythrophaea, with aseptate ellipsoidal ascospores, also has a similar appearance and often grows with it.

Bacidia assulata auct. brit., non (Körb.) Vězda (1967)

Thallus green-white or pale green-grey, thin or minutely warted; photobiont cells 5– 10 µm diam. Apothecia (0.2–) 0.3–0.6 mm diam., flat, marginate, pale red-brown or brick-red; true exciple colourless or very pale orange-brown, of radiating hyphae, the outer edge with a single row of rounded lumina to 7 µm diam.; hymenium 45-60 µm high, colourless; hypothecium pale orange-brown (K-) above, pale or colourless below; paraphyses 1-1.5 µm diam., a few becoming clavate to ca 3 µm diam. Ascospores (30–) $42-54 \times 1.5-2 \mu m$, 3- to 7-septate, acicular. BLS 0133.

Recently recorded only from small wound tracks on ancient Fagus trees in the New Forest, where it is rare, but there are old records from the bark of *Eucalyptus, Fraxinus* and Populus trunks in S.W. England, Isles of Scilly, N.W. England and S.W. Ireland.

The apothecia are similar to those of Bacidia rubella but are smaller, and the hymenium and ascospores are shorter, whilst the thallus is not granular. Distinguished from B. phacodes by the darker apothecia and hypothecium.

British material is not conspecific with B. assulata (Körb.) Vězda (= Bacidina assulata (Körb.) Ekman)







LC

according to Ekman (1996, 2023), and British and Irish specimens require critical study; a suiatble name within *Bacidia* s. str. appears not to exist. Further examination of the New Forest populations indicate that these have shorter ascospores than those in the description, and these may represent yet another undescribed taxon.

Bacidia biatorina (Körb.) Vain. (1922)

Thallus pale- to grey-green, granular or granular-isidiate, the granules often brown or grey on their upper surface; pigment N–; photobiont cells $5-12 \,\mu\text{m}$ diam. Apothecia very like those of *B. laurocerasi*, but larger, (0.5–) 0.7–1.3 mm diam. and ascospores mostly longer (43–) 60–75 (–88) × 2.5–3 (–4) μm and 9- to 16 (-22)- septate. Pycnidia rare, inconspicuous, pale orange, 50–130 μm diam.; conidia filiform, curved, 9–16 × *ca* 0.5 μ m. No lichen substances detected with TLC. **BLS 0136**.

On trunks of mature trees (mainly *Quercus*) in ancient parkland or woodland. Frequent in S. & W. England and Wales, less frequent in N. England and W. Scotland, local in Ireland and absent from the central plain.

Often sparingly fertile or sterile; can be confused with sterile B. rubella, although

the isidiate granules of the latter are usually coarser and never dark-coloured on their upper surface. In the oceanic woodlands of W. Scotland and Ireland, the related *B. caesiovirens* occurs, differing in its blue-grey to blue-green thallus granules, with N+ purple pigmentation and green (not purplish brown) epithecium. Distinguished from *Scutula effusa* only by size and shape of its ascospores; it may be better placed in that genus but molecular data are not available.

Bacidia caesiovirens S. Ekman & Holien (1995)

Thallus thin to rather thick, blue-green, granular-isidiate, composed of discrete or aggregated granules, a very thin white to grey-blue endophloeodal hypothallus and a \pm wide endophloeodal grey, grey-blue, or blue-black prothallus; granules globose, shortly cylindrical or clavate, 40–100 µm diam., often \pm blue, dark grey-blue, or blue-black at the top; blue pigment K+ green, C–, N+ purple; photobiont cells 4–9 µm diam.; mycobiont loosely enclosing photobiont; at surface of granules composed of irregularly branching hyphae of thick-walled cells that are very different in size in relation to each other making numerous short or long hyphal projections. Apothecia very rare, 0.6–1.0 mm diam., pure black, brown-black, or grey-brown, not pruinose, \pm flat with a rather thick, *ca* 100 µm wide margin which is level with or slightly raised

above the disc; true exciple black-brown in a thin distinct zone along the outer edge consisting of ellipsoidal cells with lumina to 4 μ m diam., internally pale brown with streaks of black-brown pigment reaching in from the outer edge, the interior consisting of gelatinized, sparsely septate, richly branched hyphae with thin lumina *ca* 1 μ m diam., without crystals; epithecium dark green, the coloration caused by a dominating, evenly distributed dark grey-green pigment, K+ pure green, C–, N+ purple with a precipitate of small blue crystals and a sparsely occurring, patchily distributed black-brown pigment, K+ purplish, C–, N+ orange-red; hymenium 80–100 μ m high; hypothecium very pale yellow; paraphyses unbranched or sparingly branched in the uppermost part, 1.2–1.6 μ m diam., apices not or only slightly thickened, 1.6–2.4 μ m diam., unpigmented or with a faint grey hood. Asci cylindrical or narrowly clavate, with 8 ascospores. Ascospores acicular, straight, curved or sigmoid, 46–72 × 2.5–3.7 μ m, 7- to 15-septate. Pycnidia not seen. Trace amounts of atranorin or no lichen substances detected with TLC. **BLS 1926**.

On bark or overgrowing bryophytes on *Betula*, *Quercus* and other deciduous trees in coastal woodlands. Frequent in W. & N.W. Scotland, occasional in W. Ireland.

Usually sterile. The blue-green, N+ purplish pigmentation of the thallus granules separate this species from the related *B. biatorina* and *Scutula effusa*; all three species may be better placed in *Scutula* but molecular data are needed.

Bacidia endoleucoides (Nyl.) Zahlbr. (1926)

Thallus white or pale grey, thin or thick and irregularly warted, cracked or areolate; photobiont cells 5–10 μ m diam. Apothecia 0.3–0.5 (–0.7) mm diam., flat to moderately convex, mostly with a prominent margin, bluish grey to bluish black; true exciple blue-green (K+ intensifying) in the uppermost part close to the hymenium, ± brown (K+ purplish) along the edge, colourless inside or with pale brownish yellow pigment (K–) extending from the hypothecium, without crystalline inclusions, lumina long and narrow, to 1.0 μ m diam. but up to 5 μ m



LC

diam. in terminal 1–2 cells; epithecium blue-green (K+ intensifying); hymenium 70–85 μ m high, colourless; hypothecium distinctly yellow-brown (K–) in the upper part, colourless below; paraphyses 0.9–1.6 μ m diam., unbranched or sparsely branched in the uppermost part, apices \pm narrowly clavate or not at all thickened, 1.2–3.6 (–5.4) μ m diam. Ascospores 40–60 (–70) × 2.3–3.1 (–3.6) μ m, (3-) 7- to 9 (-14)-septate, acicular. Pycnidia not seen. **BLS 2786**.

In wound tracks on veteran deciduous trees. S. England (Hampshire, New Forest).

Superficially similar to *B. absistens*, but separated by the consistently blue-green epithecium, yellow-brown upper hypothecium, and lack of crystalline inclusions in the exciple. *B. endoleucoides* has historically been confused with *B. friesiana*, which is set apart by the more or less granular thallus, thinner and more prominent apothecial margin, bluish and piebald apothecia, and a paler hypothecium. See Ekman *et al.* (2021) for more information on this species, which elsewhere appears confined to Macaronesia; it should be sought in oceanic areas of Britain and Ireland.

Bacidia fuscoviridis (Anzi) Lettau (1912)

Thallus grey-green, turning whitish in preserved material, irregularly cracked to areolate with areoles 0.1-0.4 mm diam., with a white, arachnoid prothallus to 0.5 mm broad, sorediate; soralia pale green, discrete and developing from the surface of areoles, 0.15-0.3 mm diam., or irregular and developing from margins of areoles, soredia $30-50 \mu$ m diam.; photobiont cells $6-12 (-14) \mu$ m diam. Apothecia 0.3-1 mm diam., at first flat and thickly marginate but soon convex and immarginate, pale redbrown to dark grey-brown; true exciple colourless or upper and outer parts pale orange or pink, sometimes mottled brown (K+ purplish brown), hyphae with ± rectangular lumina $7-12 \times 2-4 \mu$ m in size; hymenium $80-95 \mu$ m high, colourless or pale yellow-brown in upper part in places; hypothecium colourless or pale straw, K± yellow.



Paraphyses $1.5-2 \mu m$ diam., unbranched, the apices only slightly widening to $2.5(-3) \mu m$ diam. Ascospores $12-18 \times 4-4.5 \mu m$, (1-) 3-septate, fusiform-ellipsoidal to fusiform. Pycnidia not seen. No lichen substances detected by TLC. **BLS 0148**.

On shaded limestone or calcareous mica-schist of outcrops, old walls and gravestones, often inhabiting a zone covered by grasses during the summer; probably overlooked when sterile and has been recorded frequently when searched for in S. England. Sparse records to the north and west. Some sterile collections from siliceous rocks by rivers may belong to this species.

Apothecia resemble those of the montane, muscicolous *Mycobilimbia tetramera*, which has narrower excipular hyphae. Sterile thalli could be confused with *Lecidella scabra*, which is C+ orange. The generic placement of this species requires further investigation; research by Reese Næsborg *et al.* (2007) indicates a relationship with *Bilimbia* rather than *Bacidia*. Its recent placement in the new genus *Coppinsidea* by Kondratyuk *et al.* (2019) needs confirmation.

Bacidia herbarum (Stizenb.) Arnold (1865)

Thallus white, thin and varnish-like or thicker and minutely granular-warted; photobiont cells 7–14 μ m. Apothecia (0.2–) 0.3–0.7 mm diam., red-brown, mostly remaining flat and marginate, distinctly constricted at the base; true exciple colourless or straw, often orange- or red-brown at the outer edge, composed of radiating narrow hyphae but with 1–2 rows with swollen lumina (to 6 μ m diam.) at the outer edge; hymenium 45–60 μ m high, colourless or very pale orange-brown above; hypothecium pale orange-brown and K– in upper part (subhymenium), lower part pale orange-brown, straw to colourless; paraphyses 1–1.5 μ m diam., unbranched, apices to 3 (– 4.5) μ m diam., clavate. Ascospores 36–60 × 2–2.5 μ m, 3- to 7-septate, acicular. Pycnidia not seen. **BLS 0151**.



On bryophytes, small perennial plants or plant debris on calcareous turf or amongst limestone rocks, from sealevel to *ca* 800 m; rare. Scattered throughout Britain and very rare in Ireland, usually either maritime or montane.

Most similar to *Toniniopsis bagliettoana*, which has black apothecia with a green epithecium. In montane situations it should be compared with *Mycobilimbia tetramera*, which has soon-convex apothecia and fusiform ascospores, and with "*Caloplaca*" *cinnamomea*, which has a K+ purple epithecium and polarilocular ascospores. Many historical records refer to other species, including *B. rubella*, *B. scopulicola* and *Bacidina saxeni*.

Merismatium heterophractum (Nyl.) Vouaux (1913) has been found on its thallus.

Bacidia laurocerasi (Delise ex Duby) Zahlbr. (1926)

Thallus pale grey or green-grey, usually thin, smooth, often cracked or \pm warted; photobiont cells 5–12 (–14) µm diam. Apothecia (0.2–) 0.4–1 (–1.2) mm diam., usually numerous, flat and marginate to convex and immarginate, pink-brown (in shade) to black; true exciple purple-brown, K+ intensifying purple at the outer edge, internally pale red-brown but often darker and sometimes with a purple tinge in the upper part, without crystalline inclusions; epithecium pale grey-brown (K–) to dark (\pm purple) brown, K+ intensifying purple, N+ red; hymenium 65–90 µm tall, colourless; hypothecium colourless or pale straw, but lower part often pale orange- or red-brown towards the exciple, the coloration rarely extending to the centre; paraphyses 1–1.5 µm diam., unbranched or branched above, apices often pigmented and swollen to *ca* 5 µm



diam. Ascospores 34–70 (–86) × 2.5–4 μ m, 7- to 16-septate at maturity, acicular. Pycnidia immersed, *ca* 100 μ m diam.; walls colourless; conidia 13–17 × *ca* 1 μ m, curved. **BLS 0155**.

On \pm basic or nutrient-rich bark of trunks and branches of trees and shrubs, usually in open situations or secondary woodland; frequent. S. England, W. Wales, Ireland, very local in W. Scotland.

Similar to *Scutula effusa* and *B. biatorina*, which both have granular thalli. *B. absistens* differs in its granular-warted thallus, purple-violet, K+ green, or green epithecium and minute crystalline inclusions in the exciple.

Bacidia polychroa (Th. Fr.) Körb. (1860)

Thallus white or pale green-grey, thin or thick and irregularly warted; photobiont cells 7–14 μ m diam. Apothecia (0.3–) 0.5–1 (–1.5) mm diam., flat and marginate to sometimes convex, brown-orange to dark red- or purplish brown; true exciple and hypothecium yellow, yellowish brown or orange-brown, K+ purple-red in upper parts, \pm colourless below, true exciple lumina 1.5–3.5 μ m diam. but 5(–6) μ m at outer edge; hymenium 70–100 μ m high, colourless or yellow (K \pm mauve) in the upper part; paraphyses 1–1.5 μ m diam., unbranched, apices scarcely swollen or to 3 μ m diam. Ascospores (43–) 50–70 × (2.5–) 3–4 (–4.5) μ m, (3-) 7- to 14-septate, acicular. Pycnidia immersed, reddish; wall K+ purple-red; conidia 10–18 × *ca* 0.7 μ m, filiform, curved. **BLS 0163**.

On mature trees; not recorded since 1886. S. and C. England, Anglesey, Argyll.

Identified by the yellow, K+ purple-red pigment in the exciple and hypothecium.

Bacidia rubella (Hoffm.) A. Massal. (1852)

Thallus grey- to yellow-green, thinly to richly granular-isidiate; granules $60-120 \,\mu\text{m}$ diam.; photobiont cells $5-17 \,\mu\text{m}$ diam. Apothecia often absent, $(0.4-) \, 0.7-1 \, (-1.3) \,\mu\text{m}$ diam., usually distinctly constricted below, flat, sometimes convex, pale to dark red-brown, margin sometimes white-pruinose; true exciple colourless but upper part pale yellow-orange or yellow-straw, sometimes (pruinose morphs) with radiating streaks of minute crystals, hyphae with lumina $1-2 \,\mu\text{m}$ diam. or to $5 \,\mu\text{m}$ diam. towards the outer edge; hymenium 70–105 μm high, colourless or faintly orange-red or yellow in upper part; hypothecium colourless, or upper part pale yellow or orange-straw, K \pm yellow intensifying; paraphyses $1-1.5 \,\mu\text{m}$ diam., unbranched or forked above, the apices often slightly swollen to *ca* 2.5 μ m diam. Ascospores (35–) 40–70 (–75) × 2.5–

3 (-4) μ m, 3- to 7 (-13)-septate, acicular. Pycnidia 85–125 μ m diam., pale pink to red-brown; conidia 16–24 \times *ca* 0.5 μ m, curved or sigmoid. **BLS 0164**.

On trunks of mature trees with nutrient-rich bark (especially *Acer, Fraxinus* and *Ulmus*) in parklands, waysides and woodlands on rich soils, very rarely on sheltered gravestones or walls; absent from polluted areas. Throughout Britain and Ireland, but less frequent in W. Scotland.

Easily recognized when fertile, but sterile morphs can be confused with *B. biatorina*. Apothecia are sometimes infected by the minute black perithecia of *Muellerella hospitans* Stizenb. (1863).

Bacidia scopulicola (Nyl.) A.L. Sm. (1911)

Thallus pale olive-green to fawn-brown (sometimes dark green in extreme shade), mostly thick, warted and coarsely granular, with short coralloid isidium-like protuberances, extreme morphs with soredium-like, \pm loose granules 40–80 µm diam.; photobiont cells 5–10 µm diam. Apothecia 0.4–1.3 mm diam., often few or absent, at first flat but soon convex and often irregularly shaped or tuberculate, pale to dark brown, often with a pink tinge,



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rarely black; margin thick and usually darker than the disc but often becoming excluded; true exciple orange-brown (K⁻) in inner part, outer and sometimes lower parts colourless, of radiating, thick, densely gelatinized hyphae with narrow (to 2 μ m diam.) lumina, but lumina near outer edge often widening to 5 (-7) μ m diam.; hymenium 45–60 μ m high, colourless or lower part pale red-orange; hypothecium colourless except the upper part (subhymenium) which is usually pale red-orange; paraphyses 1–1.5 μ m diam., often forked above, apices sometimes slightly swollen to 2 (-4) μ m. Ascospores (21–) 29–45 (-51) × 1.7–2 μ m, 3- to 7-septate, acicular. Pycnidia red-brown, \pm immersed; conidia 18–30 × *ca* 0.7 μ m, strongly curved. No lichen substances detected by TLC. **BLS 0166**.

On siliceous coastal rocks in the xeric-supralittoral zone in crevices and below overhangs, rarely on soil or decaying tufts of *Armeria*; locally abundant. W. & N. Britain, Channel Islands, Ireland.

Very variable in the colour of the apothecia. The only other *Bacidia* with acicular ascospores in shade and shelter on seashores is *B. sipmanii*, which has a much thinner thallus. Specimens of *B. scopulicola* on soil and *Armeria* tufts have often been misidentified as *B. herbarum*.

Bacidia sipmanii M. Brand, Coppins, van den Boom & Sérus. (2008)

Thallus pale green to brown, sometimes pale grey, thin (less than 0.3 mm thick), smooth or sometimes slightly rugose, typically rimose in well-developed specimens; prothallus absent or whitish. Apothecia as in *B. scopulicola*. Ascospores $26-40 \times 1.5-2.5 \mu m$, shape and septation as in *B. scopulicola*. Conidia filiform, strongly curved, $22-27 \times 0.7-1.0 \mu m$. **BLS 2501**.

On siliceous coastal rocks in the xeric-supralittoral zone in crevices and below overhangs, rarely on soil; rare. S.W. England (Cornwall), S.W. Ireland (Kerry), S.W. Wales (Pembroke), western Scotland.

Occurs in the same places as *B. scopulicola* and has essentially the same apothecia, ascospores and conidia, but that species differs in the thick and isidioid to soredioid thallus.

Bacidia subturgidula (Nyl.) Zahlbr. (1926)

Thallus immersed, white; photobiont cells 6–12 (–14) μ m diam. Apothecia 0.16–0.4 (–0.5) mm diam., flat to convex, bluish grey, grey-brown or brown-black, weakly to strongly blue-white pruinose, immarginate; true exciple inconspicuous, brown, K–, but pale and ± colourless at the outer edge, of radiating hyphae coherent in K, 1.5–4 μ m diam. with lumina 1–1.5 μ m diam.; hymenium 30–40 μ m high, pale brown above due to minute granules that dissolve in K; hypothecium concolorous with the inner exciple; paraphyses 1–1.5 μ m diam, unbranched or sparsely branched, ± slightly swollen at the apices. Asci *Bacidia-* or *Biatora-*type. Ascospores 9–13 × 2.5–4 μ m, (1-) 3-septate, cylindrical to fusiform. Pycnidia 30–50 μ m diam., numerous, immersed, brown, the wall red-brown, K–; conidia 9–11 × 1–1.5 μ m, cylindrical. **BLS 0169**.

On lignum of old *Ilex* and *Quercus*; very rare. S. and S.W. England, Cumbria, S.W. Ireland (Killarney). Probably endemic; reports from Bermuda appear to be of a different species.

In outward appearance the apothecia and pycnidia resemble those of "*Lecidea*" turgidula, though the apothecia are very different anatomically and the pycnidia black and twice the diameter. The generic placement of both species requires investigation.

BACIDINA Vězda (1991)

As *Bacidia*, but with the true exciple composed at least in large part of thick-walled cells with isodiametric to ellipsoidal lumina rather than radiating hyphal tissue with narrow lumina.

Bacidina has been generally accepted as a distinct taxon for some years, either as a group within









Bacidia or a separate genus. Molecular research has confirmed that separation at genus level is appropriate (Ekman 2001, Kistenich *et al.* 2018).

Species may be keyed out using the combined key to *Bacidia* and similar genera.

Literature

Coppins & Aptroot (2009), Czarnota & Guzow-Krzemińska (2018), Ekman (2001, 2023), Ekman *et al.* (2019), Gerasimova & Ekman (2017), Kistenich et al. (2018), Llop (2007).

Bacidina adastra (Sparrius & Aptroot) M. Hauck & V. Wirth (2010)

Bacidia adastra Sparrius & Aptroot (2003)

Thallus often forming large patches, sometimes up to 0.5 m diam., thinly sorediate to thickly leprose, typically consisting of a cracked layer of soredia to 1 mm thick, usually vivid yellow-green and resembling free-living chlorococcoid algae, dried collections turning green-grey or brown-grey, young or poorly developed thalli consist of a darker green rimose thallus with vivid yellow-green punctiform soralia 0.1–0.2 mm diam.; soredia 30–50 μ m diam.; photobiont cells 7–14 μ m diam. Apothecia rare, sessile, constricted at the base, (0.2–) 0.4–0.7 mm diam.; disc flat to flexuose, pale pink to dark blue-black, often only partly coloured, the darkened parts with an aeruginose-blue pigment in section; apothecial margin conspicuous, 0.1–0.2 mm broad, flush with

the disc, pinkish with aeruginose-blue or dark brown flecks; apothecial base colourless; true exciple welldeveloped, 25–35 μ m thick, hyphae with isodiametric to slightly ellipsoidal lumina 5–7 × 5–10 μ m, colourless but in part (especially the upper part bordering the epithecium) aeruginose-blue or orange-brown, without crystals; epithecium colourless to aeruginose-blue or orange-brown, 5–10 μ m thick, K– or the coloured parts intensifying; hypothecium colourless or very pale straw, 40–60 μ m thick; hymenium colourless or orange-brown, K+ intensifying brown-purplish, 60–70 μ m high; paraphyses numerous, *ca* 1 μ m diam., the apices widened to *ca* 5 μ m. Ascospores 40–50 × 0.9–1.2 μ m, acicular, 3- to 10-septate, straight to slightly curved. Pycnidia rare, white, immersed, *ca* 0.1 mm diam.; conidia filiform, 35–50 × 1.0–1.2 μ m, indistinctly 4- to 6-septate. K–, C–, Pd–. No lichen substances detected by TLC. **BLS 2384**.

Usually corticolous, but lignicolous, terricolous and saxicolous collections are known. It typically grows on hypertrophicated bases of trees with neutral to basic bark (e.g. *Populus, Salix, Ulmus*) and on trees with neutral to slightly acid bark (e.g. *Frangula alnus, Quercus robur*), also found in wound tracks on veteran trees, especially *Fagus*, usually in half-shaded habitats, especially parks. Widespread but not particularly common in lowland areas of Britain. Often sterile and perhaps overlooked, but non-lichenized algal crusts can also be mistaken for this species.

B. caligans has shorter conidia $(25-35 \,\mu\text{m})$, a thinner thallus of farinose soredia and a tendency to form discrete soralia, an exciple that becomes excluded and a somewhat different ecology: saxicolous or terricolous on substrata with a high pH, rarely on trees with basic bark (e.g. *Sambucus, Ulmus* or on dust-impregnated bark). Furthermore, it contains a pinkish to red-brown, K+ purple pigment in the exciple and completely lacks a green pigment. *B. neosquamulosa* differs in its thinner thallus of subsquamulose granules and conspicuous, partly brown-coloured conidiomata. Sterile forms of *B. delicata* are separated by their thinner, usually small, delimited thalli and the medium to dark green colour. Sterile specimens of *B. arnoldiana* and *B. modesta* differ by the presence of many pycnidia and the larger goniocysts. Sterile material of *Fellhanera viridisorediata* is distinguished by the presence of roccellic acid, best seen by applying a droplet of acetone to a thallus fragment on a glass slide, when a ring of crystals appears on evaporation.

Bacidina arnoldiana (Körb.) V. Wirth & Vězda (1994)

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Bacidia arnoldiana Körb. (1860)

Thallus dull yellow-green to fawn, finely granular, of goniocysts 20–40 μ m diam.; photobiont cells 5–10 (–12) μ m diam. Apothecia 0.3–0.7 (–1.2) mm diam., usually few and scattered or altogether absent, flat, white-grey to grey-brown, the margin raised, usually paler and often white-pruinose; true exciple with the inner part concolorous with the hypothecium, the outer part colourless; hyphae towards the outer part with ellipsoidal lumina 3–7 × 1.5–5 μ m; hymenium (35–) 40–50 μ m high, colourless; hypothecium dark reddish brown, K+ dull olive-brown in upper part, \pm colourless below; paraphyses 1–2 μ m diam., unbranched or a few forked above; apices often swollen to *ca* 5 μ m. Ascospores (19–) 24–46 × 1–2 μ m, narrowly 1- to 3-septate, acicular. Pycnidia

LC

sometimes present, 0.1–0.2 mm diam., white, \pm immersed; conidia filiform, 25–40 × 1–1.5 µm, curved but not hooked, 0- to 3 (-5)-septate. **BLS 0132**.

On shaded damp calcareous rocks or stonework, once on rusty ironwork; tolerant of urban conditions. Throughout Britain, but rare in the north of Scotland and Ireland.

See under *B. adastra* for a comparison with related species in similar habitats. Differs from poorly developed material of *B. neosquamulosa* in the shorter and less conspicuously septate conidia. An identical hypothecium pigmentation (Arnoldianabrown) is shared by *B. brandii* (thallus with larger granules) and *B. egenula* (greenish, N+ red-violet pigment in epithecium). *B. modesta*, which is mostly corticolous, has conidia that are more strongly curved and 'hooked' at one end.

Bacidina assulata (Körb.) S. Ekman (1996)

Bacidina mendax Czarnota & Guz.-Krzem. (2018)

Thallus straw-coloured to bright green, composed of minute merged granules to form a thin scurfy uneven crust or small warts. Photobiont cells to 17 μ m diam. Apothecia 0.2–0.7 mm diam., constricted at the base, variable in colour from whitish and flesh-coloured to beige, pinkish-buff, brownish to grey-brown and dark fuscous brown, the margin becoming excluded, concolorous, paler or darker than the disc. True exciple (30–) 40–60 (–70) μ m thick, composed of radiating hyphae with 1–2 rows of cells of the outermost part with lumina widening to 5–7 μ m; upper and outer part pinkish orange, brown, fuscous brown and then K– or K± pinkish to purplish or olivebrown, K± intensifying; hypothecium to 60 μ m tall, colourless to ± straw-coloured. Hymenium (40–) 50–60 (– 65) μ m tall, colourless or sometimes with a ± pinkish to olive-brown, K– or K+ intensifying epithecium as well as vertical streaks; pigment confined to walls of paraphyses and asci. Paraphyses of two types: unbranched, 1·5– 2 μ m diam. with globose apical cells to 2.5 (–3) μ m diam.; also irregular, stout, 3–4 μ m diam., forked with pigmented globose to elongate apical cells to 6 μ m diam. Asci cylindrical to narrowly clavate. Ascospores acicular, (25–) 30–38 (–40) × 1.2–1.5 μ m, 3- to 5 (to 6)-septate, straight. Pycnidia pale throughout, ± immersed within the thallus warts, 0·15–0·3 mm diam. Conidia filiform, ± straight to slightly curved (usually in the upper half) or ± hooked, (25–) 35–55 (–62) × 1–1·2 μ m, 3- to 5-septate. No substances detected by TLC. **BLS 2716**.

On shaded branch of Salix, North London, in association with Catillaria nigroclavata.

The British record was first identified as *Bacidina mendax*, a recently described taxon that was placed into synonymy with *B. assulata* by Ekman (2023). It is likely to have been overlooked in the past. It differs from *B. neosquamulosa* in the lack of a subsquamulose thallus, and from *B. caligans* in its longer and only slightly curved to apically hooked conidia and lack of a granular (sorediate) thallus.

Bacidia assulata auct. br., *non* (Körb.) Vězda (see under the generic account of *Bacidia* above) is an unrelated taxon, and collections may need to be assigned to more than one species. More work is needed.

Bacidina brandii (Coppins & van den Boom) M. Hauck & V. Wirth (2010) *Bacidia brandii* Coppins & van den Boom (2002)

Thallus effuse, composed of scattered to usually confluent granular areoles; areoles convex, 0.15–0.3 mm diam., green-grey or pale brown-grey, matt to slightly shiny, not corticate; photobiont cells 7–14 μ m diam. Apothecia numerous, crowded or dispersed over the thallus surface, sessile and appressed, 0.05–0.5 mm diam.; disc soon becoming convex, pale to dark red-brown, surrounded by a paler margin; true exciple 24–40 μ m thick, colourless, lumina of cells 6–10 μ m diam.; hymenium 30–40 μ m tall, colourless; epithecium colourless, K–; hypothecium dark reddish brown, K+ dull brown; paraphyses few, aseptate, 1.5–2 μ m diam., apices clavate-capitate, to 5 μ m diam., colourless. Asci 30–35 × 5–7 μ m, cylindrical to slightly clavate. Ascospores acicular, mostly slightly curved, 24–31 × 1–1.3 μ m, 0- to 3-septate. Pycnidia white,

immersed in the thallus; wall colourless; conidia filiform, curved, $23-30 \times 0.8-1 \mu m$, appearing to be narrowly 3-septate in lactophenol-cotton blue. **BLS 2411**.

Found on a root of *Prunus* in Kent and on a roof tile in Suffolk, but doubtlessly overlooked elsewhere. In W. & C. Europe, mainly on tree bases in parks and marshes.

Superficially resembles *B. saxenii* and *B. chloroticula*, but differs in the dark hypothecium. *B. arnoldiana* and *B. egenula* share the same hypothecial pigment (Arnoldiana-brown), but have sorediate thalli. See under *B. adastra* for a comparison with related species in similar habitats.



LC



15

Bacidina caerulea (Körb.) S. Ekman (2023)

Thallus crustose, thin to moderately thick, composed of a warted to granular, sometimes slightly cracked crust, pale grey to grey-green. Prothallus thin, whitish, immersed in the substrate between discontinuous granules. Apothecia biatorine, (0.2-) 0.3-0.6 (-0.7) mm diam., at first flat, finally becoming \pm convex, often confluent and tuberculate; disc pale straw or \pm blue-grey to bluish black, often piebald, the margin often darker than the disc, bluish, excluded in convex apothecia; true exciple 30–60 µm thick, without crystals, \pm blue-green in the upper part; hypothecium unpigmented or very pale yellowish; Hymenium blue-green around paraphyses in the upper part and sometimes in scattered, vertical streaks, without crystals; paraphyses unbranched or sparsely branched in the uppermost part, the apices \pm clavate. Ascospores colourless, without a perispore or ornamentation, acicular, straight or only slightly curved, straight in young asci, $30-53 \times 2-2.8$ µm, mostly 5-septate. Pycnidia infrequent, 30-50 µm diam., immersed with exposed ostiole, colourless except for a blue-green ring around the ostiole; conidia filiform, straight or \pm curved, aseptate, $6-14 \times 0.5-0.7$ µm. Lichen substances not observed by TLC; apothecia and conidiomata with Bacidia-green, apothecia sometimes also with small amounts of Laurocerasibrown. **BLS 2850**.

Known from historical records from NE Yorkshire (Kildale) and N. Ireland (Tyrone, Dungannon Park); in Scandinavia it primarily inhabits coarse, porous bark of old *Sambucus nigra* in semi-shade but can be found on bark of various other trees and even twigs of *Picea*.

Similar to *Bacidina friesiana* (q.v.) in the often piebald apothecia and with a preference for soft bark, but with a blue-green rather than brown exciple, a smoother thallus and much smaller pycnidia with blue-green rather than brown pigmentation.

Bacidina caligans (Nyl.) Llop & Hladún (2002)

Bacidia caligans (Nyl.) A.L. Sm. (1911)

Thallus dull green, grey or fawn-brown, finely scurfy granular-sorediate; soredia often in rather discrete soralia; granules (goniocysts) 20–50 μ m diam.; photobiont cells 5–13 μ m diam. Apothecia 0.2–0.6 (–1) mm diam., flat or later irregularly convex, reddish brown to brown-black, the margin often darker than the disc or becoming excluded; true exciple colourless except for a red-brown K+ purple outer edge, with cellular lumina (to 7 μ m diam.) towards the outer edge and in the lower part; hymenium 45–55 μ m high, colourless or pale purple-brown above, K+ intensifying purple; hypothecium colourless; paraphyses 1–2 μ m diam., unbranched, apices often swollen to *ca* 5 μ m diam. Ascospores 24–48 (–63) × 1.5–2 (–2.5) μ m, narrowly 3- to 7-septate, acicular. Pycnidia immersed, white or pink-brown around the ostiole; conidia 29–35

acicular. Pycnidia immersed, white or pink-brown around the ostiole; conidia $29-35 \times ca \ 1 \ \mu m$, curved. **BLS 0137**.

On sheltered calcareous rocks and stonework, asbestos-cement and mosses on crumbling mortar, more rarely on bark (e.g. *Alnus, Salix, Sambucus, Ulmus*) and rabbit droppings; current records show it to be locally frequent but it is clearly under-recorded and is probably widespread in lowland Britain. Only a single record for Ireland.

Characterized by the often rather discrete soralia. See under *B. adastra* for a comparison with related *Bacidina* species in similar habitats.

Bacidina celtica van den Boom & Llop (2021)

Bacidina squamellosa auct. br., non S. Ekman (1996)

Bacidia squamellosa auct. br., non (S. Ekman) Coppins & Aptroot (2008)

Thallus pale yellowish green, dominated by deeply dissected squamules resembling richly branched coralloid isidia, 18–30 μ m diam. and to 300 μ m tall, corticate, with a shiny surface when dry; photobiont cells 5–12 μ m diam. Apothecia 0.3–0.8 mm diam., usually absent, at first barrel-shaped but soon becoming flat, white or with a pinkorange disc and whitish margin; true exciple colourless, with cellular lumina 4–7 (– 9.5) μ m diam. and to 12 μ m long; hymenium 50–55 μ m high, colourless; epithecium colourless; K–; hypothecium colourless; paraphyses 1.2–1.7 μ m diam., unbranched or a few forked near the apices, apices 2.7–4 μ m diam. Ascospores 47–71 × 1.5–1.7 μ m, narrowly 3- to 5-septate, acicular. Pycnidia rare, immersed in the thallus to sessile. **BLS 1732**.

On bark, often over bryophytes, of a wide range of deciduous trees and shrubs in humid, oceanic woodlands; frequent. W. Britain and Ireland.

LC NS

Nb

LC

Formerly treated as *Bacidia squamellosa* S. Ekman (1996), but the type of this species was described from Florida and has dorsiventral squamules; N.W. European material belongs to a distinct, though related species, now recognized as *B. celtica* (van den Boom & Llop 2021). The delicate, richly branched, coralloid 'isidia' and habitat ecology distinguish *B. celtica* from other members of *Bacidina*. When sterile, most easily confused with sterile, isidiose morphs of *Micarea prasina* s.l. ('isidia' dull, ecorticate and photobiont cells all <8 μ m diam.) and of *Porina rosei* (photobiont *Trentepohlia*). Apothecia are rare, but when mature closely resemble those of *Coenogonium luteum*.

Bacidina chloroticula (Nyl.) Vězda & Poelt (1991)

Bacidia chloroticula (Nyl.) A.L. Sm. (1911)

Thallus dull- or grey-green, thin, scurfy-granular; photobiont cells 5–12 (–14) μ m diam. Apothecia 0.08–0.2 mm diam., often crowded and confluent, flat; disc whitish or pink-orange to pale grey-brown; margin persistent, usually paler than the disc; true exciple colourless, ± entirely composed of hyphae with ellipsoidal to globose lumina to 5 (–7) μ m diam.; hymenium 30–42 μ m high, colourless; epithecium colourless, K–; hypothecium colourless; paraphyses 1.5–2 μ m diam., few, unbranched, the apices often swollen to *ca* 4 μ m diam. Ascospores 21–38 × 1–1.8 μ m, thinly 0- to 3-septate, narrowly acicular. Pycnidia white, immersed; conidia 30–43 × 0.5–1 μ m, curved. **BLS 0140**.



A pioneer species of various shaded substrata, such as tree bases and exposed roots,

dead grasses, tops of cut stumps and fence posts, cement and brick rubble, painted iron-work and tarmacadam. Probably thoroughout much of Britain, but under-recorded and most frequently recorded in E. England; apparently rare in Ireland.

Recognized by the small, pale apothecia without internal pigmentation; pale morphs of *B. saxenii* are distinguished by the large, vesicle-like cells in the true exciple. See under *B. adastra* for a comparison with related species of similar habitats.

Bacidina circumpallens (Nyl.) S. Ekman (2023)

Thallus crustose, thin to moderately thick, irregularly cracked, smooth to warted, pale straw; prothallus thin, whitish, fibrous. Apothecia biatorine, 0.24–0.5 mm diam., flat to moderately convex; disc dark purple-brown to black, sometimes pigment-deficient and then \pm straw-coloured; margin concolorous with or darker than disc, outer lower part often paler, persistent; true exciple without crystals, \pm red-brown in the upper part, often also with some green closest to the hymenium, fading below; hypothecium \pm pale brown-orange above, unpigmented below; hymenium 40–65 µm tall, with a distinct, pigmented epithecium containing blue-green and sometimes also red-brown pigment, often as hoods over paraphyses, without crystals; paraphyses unbranched or sparsely branched above; apices \pm clavate. Ascospores colourless, without a perispore or ornamentation, bacilliform, fusiform or clavate, straight, 17–31 × 2.5–3 µm, 5–10 times as long as wide, mostly 3-septate. Pycnidia abundant, 50–160 µm diam., semi-immersed or superficial, dark brown above around the ostiole, unpigmented below; conidia acicular, straight to moderately and \pm symmetrically curved, the apex wide and blunt and base thin and pointed, 1–3-septate, 22–47 × 1–2 µm. Lichen substances not observed by TLC; apothecia with Bacidia-green and Laurocerasi-brown, conidiomata with Laurocerasi-brown pigments. **BLS 2851**.

According to Ekman (2023), *B. circumpallens* inhabits a variety of substrates such as driftwood, soil, brick, roof tiles and igneous rock; confirmed records from Britain and Ireland are restricted to historical type material on clay soil from Ireland (Clare).

Formerly placed in synonymy with *B. subfuscula* (q.v.), but that species differs by the absence of green pigment in the hymenium, the brown pigment usually forming vertical streaks along paraphyses and young asci, a thicker and usually evenly pale yellow hypothecium, thinner apothecial margin, smaller apothecia that soon become distinctly convex and often appear in dense clusters, and absence (or at least extreme rarity) of pycnidia.

Lecania cuprea (q.v.) is somewhat similar to *B. circumpallens* in having narrowly fusiform or bacilliform, mostly 3-septate ascospores and flattish apothecia that are sometimes red-brown, but can be distinguished by its thin to thick, rimose, areolate thallus with an epineeral layer, and often pinkish \pm unpigmented apothecia; it occurs on calcareous rocks.

Bacidina delicata (Larbal. ex Leight.) V. Wirth & Vězda (1994)

Bacidia delicata (Larbal. ex Leight.) Coppins (1980)

Thallus pale green to fawn, usually thin, finely granular (sorediate); granules (goniocysts) (15–) 20–35 (–50) µm diam.; photobiont cells 5–10 (–12) µm diam. Apothecia (0.2–) 0.3–0.6 (–0.7) mm diam., flat, marginate, white, beige or orangepink; true exciple colourless, cells with lumina to 7 µm diam. towards the outer edge and in the lower part; hymenium 35–50 (–55) µm high, colourless; hypothecium colourless; paraphyses 1.5–2 µm diam., unbranched or a few forked above, apices often swollen, to *ca* 5 µm diam. Ascospores (21–) 24–48 × 1–1.5 (–2) µm, narrowly 3- to 7-septate, acicular. Pycnidia ± immersed, white; conidia 21–40 × *ca* 1 µm, curved. **BLS 0144**.

On shaded substrata, including \pm calcareous rock and stonework (often on mosses) and basic bark, occasional. Throughout most of Britain, commoner in the south and absent from N. Scotland, rarely recorded in Ireland.

Records from bark may be misidentified; they should be re-examined. Distinguished from *B. phacodes* by the distinctly granular thallus, larger cellular lumina in the outer exciple and curved conidia. Morphs with small apothecia differ from *B. chloroticula* in the more numerous paraphyses. See under *B. adastra* for a comparison with related species in similar habitats. Sometimes confused with *Lecania cuprea* and *B. subfuscula*, which have shorter, narrowly fusiform to bacillar ascospores and usually at least some apothecia with pinkish brown, $K\pm$ purplish, N+ red pigmentation.

Bacidina egenula (Nyl.) Vězda (1991)

Bacidia egenula (Nyl.) Arnold (1870)

Thallus dull yellow-green, fawn or fawn-brown, finely granular; granules (goniocysts) 15–60 (–90) μ m diam.; photobiont cells 5–12 μ m diam. Apothecia (0.15–) 0.3–0.6 (– 0.75) mm diam., grey-brown, blue-grey or black, flat, marginate; true exciple colourless except the upper outer edge which is olive-brown, K± purple in part (especially above), cellular lumina to 7 (–10) μ m diam. towards the outer edge and in the lower part; epithecium pale to dark olive- to blue-green, K–, N+ red-violet (often with blue crystals); hymenium (35–) 40–55 μ m high, colourless; hypothecium reddish brown, K+ dull olivaceous brown in the upper part, colourless below; paraphyses 1–1.5 μ m diam., unbranched, apices swollen to *ca* 6 μ m diam. and often pigmented.

Ascospores 25–40 (-45) × 1.5–2 (-2.5) μ m, narrowly 3 (-7)-septate, acicular. Pycnidia 0.1–0.2 mm diam., rare, ± immersed, white; conidia 20–35 × *ca* 1 μ m, 0- to 3-septate, curved-sigmoid. **BLS 0145**.

On shaded rocks, stonework (e.g. red brick, sandstone), flints, sometimes on mosses, rarely on shaded bark (*Salix*, wound tracks on *Fagus*) and tops of fence-posts, also on rabbit droppings in sand dunes, occasional. Throughout Britain but apparently commoner in eastern areas. Very rarely recorded from Ireland.

Distinguished from *B. arnoldiana* by the green epithecium, from *B. indigens* by the dark upper hypothecium and more finely granular thallus and from *B. adastra* by the dark upper hypothecium and shorter conidia. The same hypothecial pigment (Arnoldiana-brown) is shared by *B. brandii*, but that has a more coarsely granular thallus and lacks any greenish apothecial pigmentation.

Neocoleroa inundata (Vain.) Diedrich (1999) (syn. Wentiomyces lichenicola subsp. bouteillei auct. brit.) has been recorded on its thallus.

Bacidina flavoleprosa Czarnota & Guzow-Krzem. (2012)

Thallus sulphur-green, almost completely sorediate and forming large cracked patches of goniocysts, or sometimes thinner aggregations resembling punctiform soralia; sometimes portions of the thallus close to apothecia crust-like or minutely granular, thin and olive-tinged. Photobiont chlorococcoid. Apothecia rather rare, scattered or often forming small groups, 0.1–0.45 mm diam., beige to pale brown, at first constricted at the base with a shallow, darker pigmented disc and a thick, distinctly paler, whitish beige margin; when mature slightly convex with a pale, thin, almost invisible margin, but in cross-section remaining well-developed; exciple well-developed, colourless throughout, composed of thin radiating and branched hyphae, swollen to 3-5 (–7) µm diam. towards the outermost edge, in a gel matrix that swells

in K; hymenium colourless throughout, 30-40 µm tall; hypothecium brown, at least in the upper part, pigment

LC







Arnoldiana-brown, K+ dulling; paraphyses numerous, unbranched or forked above, 1.5–2.5 µm diam., the apices slightly swollen to 3.5 mm; asci clavate to cylindrical, $25-35 \times 5-7 \mu$ m; apical dome amyloid, K/I+ blue, apical cushion absent, ocular chamber varied in development; as cospores acicular, not curved, $25-30 \times 1-1.5 \mu m$, 1to 3-septate. Pycnidia unknown. Chemistry: No substances detected by TLC. BLS 2682.

Known in Britain only from a collection without apothecia and pycnidia, from the bole of the ornamental tree Cladrastis sinensis in Essex, and from a collection on Salix from Suffolk (Ekman 2023). An ITS sequence from the *Cladrastis* specimen appears to be identical to that of the type. *Bacidia latebricola* Wheldon & Travis (1915) may provide an earlier name for *B. flavoleprosa*.

Similar to *B. adastra* and *B. arnoldiana* but with a lighter apple-green thallus (when fresh) and less granular in appearance. The former species has apothecia with a pale hypothecium, which lacks the Arnoldiana-brown pigment seen in B. flavoleprosa.

Bacidina friesiana (Hepp) S. Ekman (2023)

Bacidia friesiana (Hepp) Körb. (1860)

Thallus grey-green, partly immersed, mostly thin and minutely granular; photobiont cells 6-14 µm diam. Apothecia 0.2-0.6 (-0.8) mm diam., flat and marginate to convex and immarginate, pale yellowish, blue-grey or bluish black, often piebald; true exciple \pm colourless within, without crystalline inclusions, outer edge (especially above) and upper parts dark brown, K+ purple, hyphae with swollen cells to 6 µm diam. towards the outer edge; epithecium pale grey-green to dark blue-green, K-, N+ red or violet (often with blue granules); hymenium 60–65 µm high, colourless or pale green; hypothecium colourless or pale straw; paraphyses $1-1.5 \ \mu m$ diam., unbranched or a few forked above, apices often swollen to ca 5 μ m diam. Ascospores 30–55 × 2–3 μm, 3- to 7 (-9)-septate, acicular. Pycnidia 80-360 μm diam., brown-walled around the ostiole. BLS 0147.

On nutrient-rich bark of trees and shrubs (especially Sambucus); rather rare. Throughout most of Britain, but sparse especially to the north and west, and thinly recorded in Ireland. The distribution map includes records of B. caerulea, which has only been recently distinguished from B. friesiana.

Easily recognised by the characteristically bluish or greyish, often piebald apothecia. Bacidina caerulea Körb. (q.v.) is similar but lacks dark brown pigmentation ("Laurocerasi-brown" in the exciple; it has recently been recognized from Britain and Ireland. Likely to be confused with shade forms of B. absistens, which have crystalline inclusions in the exciple and longer, 7- to 14-septate ascospores. It has also been confused with Bacidia endoleucoides (q.v.).

Bacidina indigens (Vain.) S. Ekman & J. Gerasimova (2017)

Bacidia viridescens auct. br., non (A. Massal.) Norman (1868)

Thallus grey- or green-white or pale fawn, finely granular-warted; warts 80-120 µm diam.; photobiont cells 6-12 µm diam. Apothecia (0.2-) 0.3-0.6 (-0.8) mm diam., pale brown, grey or black, flat and marginate or becoming convex and immarginate; true exciple purple-brown, K+ intensifying purple in outer and uppermost part, sometimes also with green pigment in upper parts, ± colourless below, cellular lumina to 7 µm diam. towards the outer edge; hymenium 30-50 µm tall, upper part and epithecium olivaceous or green, K-, sometimes discoloured brown; hypothecium colourless; paraphyses unbranched or rarely branched above, $1.5-2 \mu m$ diam., apices often swollen to *ca* 5 μ m diam. and pigmented. Ascospores 25–50 (–58) × 1.5–2 μ m,



Nb

3- to 7-septate, acicular. Pycnidia rare, ± immersed, black, the wall brown, K+ purple and olive in parts; conidia $15-25 \times 1-1.3 \,\mu\text{m}$, curved. **BLS 1623**.

Mostly on soil (on bryophytes, plant debris or rabbit droppings) in lead mine spoil, in sand dunes or over limestone, rarely directly on soft limestone stonework or crumbling mortar, occasional. Throughout Britain, the patchy distribution suggesting that it is under-recorded; a few records from Ireland.

Referred to as Bacidia viridescens by Coppins & Aptroot (2009), but that name is now considered to be a synonym of Toniniopsis bagliettoana (Gerasimova & Ekman 2017, Ekman et al. 2019), which differs by its redbrown hypothecium. Resembles *Bacidina egenula*, but differing in its colourless hypothecium and larger thallus granules. Most British specimens are poorly developed.



Nb

Bacidina inundata (Fr.) Vězda (1991)

Bacidia inundata (Fr.) Körb. (1855)

Thallus grey-green or green-fawn, cracked, the surface granular-warted, usually with a conspicuous white bordering prothallus; photobiont cells 5–12 µm diam. Apothecia 0.2–0.6 (–1) mm diam., flat to convex, pale to dark red-brown, margin usually paler but often becoming excluded; true exciple colourless or pale straw or brown, usually dark brown above, cells with lumina 2.5–5 (–7) µm diam. in outer and lower parts; hymenium 45–55 µm high, colourless or pale pink or purple-brown, K± purple; hypothecium colourless or pale straw, sometimes pink-brown in the upper part; paraphyses 1–1.5 (–2) µm diam., unbranched or a few forked above, apices often swollen to 3.5 (–5) µm diam. Ascospores 24–43 × 2–2.5 µm, narrowly 3 (-7)-septate,

acicular. Pycnidia \pm immersed, of two types: (a) 0.1–0.2 mm diam., white; conidia 23–47 (–55) × 0.5–1 µm, faintly 3-septate, curved; (b) 0.2–0.3 mm diam., dark brown, the wall brown (K \pm purple); conidia 11–15 (–19) × *ca* 1 µm, aseptate, curved. **BLS 0154**.

On hard siliceous rocks (rarely bark or wood) in streams and rivers, more rarely lake margins, often where shaded by overhanging trees; frequent in upland areas. S.W. to N. England, Wales, Scotland, upland Ireland.

A conspicuous species, often seen as orbicular patches surrounded by a white prothallus. The only British and Irish *Bacidina* known to have two conidial types. *B. arnoldiana* can occur in similar habitats on calcareous rocks; it has a more granular thallus and a darker hypothecium.

Neocoleroa inundata (Vain.) Diedrich (1999) has been recorded on its thallus.

Bacidina modesta (Zwackh ex Vain.) S. Ekman (2019)

Bacidia sulphurella Samp. (1924)

Bacidina sulphurella (Samp.) M. Hauck & V. Wirth (2010)

Thallus, apothecia and ascospores as in *B. arnoldiana*. Pycnidia always present, 0.15–0.3 mm diam., white, \pm immersed, sometimes lobate and seemingly multilocular; conidia filiform, 26–47 × 1–1.5 µm, 0- to 5-septate, curved or not, but always with at least one extremity strongly hooked (like a walking stick) and slightly enlarged. **BLS 2502**.

On bark (especially *Sambucus*), often at the base of a tree; tolerant of urban conditions; occasional. Throughout Britain, most frequent in lowland and polluted areas, not yet recorded from Ireland.

Treated as *Bacidia sulphurella* by Coppins & Aptroot (2009), but that name is considered a synonym of *Bacidina modesta* by Ekman *et al.* (2019).

See under *B. adastra* for a comparison with related species in similar habitats. Differs from poorly developed material of *B. neosquamulosa* in the shorter and less conspicuously septate conidia. An identical hypothecium pigmentation (Arnoldiana-brown) is shared by *B. brandii* (thallus with larger granules) and *B. egenula* (greenish, N+ red-violet pigment in epithecium). *B. arnoldiana*, which is mostly saxicolous, has conidia that are never hooked.

Bacidina neosquamulosa (Aptroot & van Herk) S. Ekman (2004)

Bacidia neosquamulosa Aptroot & van Herk (1999)

Thallus corticolous, indeterminate, sometimes covering extended areas, green-grey to olive, dull, corticate, isidiate, consisting of granular microsquamules, without a prothallus; microsquamules variably developed, deeply incised, crenate, convex to flat or slightly concave, sometimes gnarled, to 0.4 mm diam. bearing globose, isidium-like granules mostly along the margin, but sometimes covering the squamules, $50-100 \,\mu\text{m}$ diam.; in thalli with poorly developed microsquamules the granules are smaller and form pale soredia. Apothecia sometimes present, adnate, round to irregularly deformed, 0.2–1.0 mm diam., pink-buff to flesh-coloured, with blackened (piebald) areas when mature; margin persistent, grey above, pink-buff at the sides, with dark brown pigment outside; true exciple well-developed, colourless within, dark brown at

the outer edge, the cells with somewhat expanding lumina $6-12 \times 4-8 \mu m$ in size towards the periphery and in the lower parts; pigmentation brown, K+ purple, N+ purple-brown, without crystals or granules; hypothecium





LC

LC



colourless; epithecium partly colourless, partly dark brown above; pigment as in exciple, without crystals or granules; hymenium 40–55 (–60) μ m tall; paraphyses septate, unbranched, with tips swollen to 3–5 μ m diam. and partly covered by the same coloration as the exciple. Asci cylindrical to clavate, 8-spored, 45–60 × 8–12 μ m. Ascospores coiled in the ascus, needle-shaped to slightly clavate, 3- to 7-septate, (35–) 40–55 (–58) × 1.3–1.7 μ m; one end not pointed, the other attenuated. Pycnidia often abundant, mostly laminal on the microsquamules, globose, erumpent, 70–130 μ m diam., colourless but the upper part often dark above, with olive-grey, K–, N+ purple-red pigment; ostiole always pale; conidia filiform, curved, 3- to 7-septate, (35–) 40–57 × (1.2–) 1.5–2 μ m. No lichen substances detected by TLC. **BLS 0130**.

Mostly on trees with deciduous bark, mainly on half-shaded, \pm sheltered sites, moderately to strongly eutrophicated, usually on dusty rough bark; rarely on rock, e.g. brick and granite boulders. Tolerant of urban conditions. Probably widespread in lowland areas of the British Isles but overlooked, especially common in southern and eastern England, apparently rapidly expanding. There are numerous recent records in Scotland on coniferous bark and lignum; possibly a separate species is involved.

See under *B. adastra* for a comparison with related species in similar habitats. Well-developed material has a very characteristic thallus, but poorly developed material is sometimes difficult to separate from *B. arnoldiana*, from which it differs by the colourless hypothecium and longer and more clearly septate conidia.

Neocoleroa inundata has been recorded on its thallus.

Bacidina phacodes (Körb.) Vězda (1991)

Bacidia phacodes Körb. (1860)

Thallus white to grey-green, thin to irregularly warted or scurfy but never with discrete granules; photobiont cells 7–10 µm diam. Apothecia 0.2–0.5 mm diam., flat to convex, often confluent and clustered, white, beige or pale orange-pink, the margin often paler than the disc; true exciple colourless, K± pale yellowish, of radiating hyphae with sometimes ellipsoidal (<2 µm diam.) cells, but some cells to 4 µm diam. at the outer edge; hymenium 35–50 µm high, colourless or with the upper part pale yellow-brown, K± yellow; hypothecium colourless; paraphyses unbranched, 1–1.5 µm diam., the apices sometimes clavate, to 3 µm diam. Ascospores 29–45 × 1.5–2 µm, 3- to 7-septate, acicular. Pycnidia immersed, the walls colourless; conidia 28–50 (–60) × 1–1.5 µm, narrowly 3- to 7- septate, thread-like, ± straight. **BLS 0161**.

On nutrient-rich bark of mature trees (especially *Acer, Fraxinus, Fagus* and *Ulmus*), often in shaded, sheltered habitats; frequent, but rarer northwards. Throughout Britain, but with a S.W. bias and in N. England and Scotland mainly near the west coast. Widespread in Ireland but rare in the central plain.

Distinguished from *B. rubella* and *B. assulata* by the paler apothecia and from the former also by the nongranular thallus, and thinner hymenium and ascospores. *B. delicata* has a finely granular thallus, outer exciple with larger lumina (to 7 μ m diam.) and strongly curved conidia. In the field it can be confused with *Lecania chlorotiza* and pale morphs of *L. cyrtellina*, both of which have shorter, 0- to 1-septate ascospores.

Bacidina saxenii (Erichsen) M. Hauck & V. Wirth (2010)

Bacidia saxenii Erichsen (1941)

Thallus inconspicuous or thin, green-grey or fawn, scurfy-granular; photobiont cells 7–14 (–19) μ m diam. Apothecia 0.1–0.3 (–0.45) mm diam., flat or convex, usually indistinctly marginate, pale to dark brown. True exciple indistinct, often paler than the disc, colourless except for a dark brown K+ purple upper part in dark apothecia, hyphae 1.5–2 μ m diam., lax in K, terminating in large ovoid or globose vesicle-like cells to 20 × 12 μ m; hymenium 40–45 μ m high, pale brown (K ± purple) or olivaceous (K–, N+ red), especially in the upper part; hypothecium colourless; paraphyses 1.5–2 μ m diam., unbranched or forked above, the apices often capitate, to 5 μ m diam., rare, immersed, the wall colourless; conidia 21–48 × 0.5–1 μ m, curved, thread-like. **BLS 1593**.

A pioneer species of shaded calcareous or dust-enriched substrata, including bones, stones and boulders by farm tracks, dead grass, decaying mosses on tops of fence posts and old leather in sand dunes, also on old iron railings and lead mine spoil; frequent. Probably throughout most of Britain and Ireland, apparently most common in E. England and S.E. Scotland but probably affected by recorder bias.



LC





LC

Easily identified microscopically by the remarkable exciple structure with its large vesicle-like cells; these distinguish pale morphs from B. chloroticula. B. brandii also has large exciple cells, but differs in having a brown upper hypothecium and lacking any purplish or greenish pigmentation in K.

Bacidina subfuscula (Nyl.) S. Ekman (2023)

Lecania subfuscula (Nyl.) S. Ekman (1996)

Thallus granular, green-white to pale buff, granules 40-200 µm diam., coalescing to form a granular-warted, effuse crust; photobiont cells 6-12 (-16) µm diam. Apothecia crowded, in nodular clusters, 0.2-0.6 mm diam., at first flat but soon convex, pink- to grey-brown or black, the margin sometimes remaining pale; true exciple colourless except for the upper outer edge and apex which may be brown and K+ purple, mostly 'cellular' with radiating ellipsoidal lumina $5-13 \times 2.5-4.5$ (-7) μ m; hymenium 40-50 (-65) µm high, colourless or with the upper part (epithecium) olivaceous grey to pinkbrown, K- or purple, N+ red; hypothecium colourless or pale straw, K+ yellow; paraphyses 1.5-2 µm diam., the apices to 5 µm diam., swollen, often pigmented. Ascospores $14-28 \times (2-) 2.5-3 \mu m$, 3(-5)-septate, narrowly fusiform to cylindrical. Pycnidia rare, immersed, walls colourless; conidia $31-55 \times 1-1.5 \mu m$, mostly curved. BLS 0167.



On rocks, turf or clay soil in nutrient-rich situations (e.g. bird colonies), even upon bird-lime; very local but widespread. Scattered throughout Britain with a few records from Ireland.

Resembling Bilimbia sabuletorum in the field. Pale morphs on calcareous rocks are distinguished from Lecania cuprea by the more swollen, often coloured apices of the paraphyses and longer conidia; also Bacidina subfuscula seems to be absent from under dry overhangs.

Bacidina circumpallens is very similar, but has a greenish hymenium and epithecium and a paler hypothecium, and it may be that all British and Irish records of B. subfuscula should be redetermined. See that species for further distinctions.

BELLICIDIA Kistenich, Timdal, Bendiksby & S. Ekman (2018)

As this is a monotypic genus, the description below (B. incompta) constitutes the generic description.

Until recently included within Bacidia, Bellicidia was shown by Ekman (2001) to occupy an isolated position, and Kistenich et al. (2018) placed it as a sister group to a broad assemblage including Bacidina and Toninia.

Bellicidia may be characterized by a dark red-brown pigment in the apothecia and pycnidia, cylindrical ascospores and \pm ellipsoidal conidia. It is included in the key to *Bacidia* and similar genera above.

Literature

Coppins & Aptroot (2009), Ekman (2001), Kistenich et al. (2018).

Bellicidia incompta (Borrer) Kistenich, Timdal, Bendiksby & S. Ekman (2018) VU (A)

Bacidia incompta (Borrer) Anzi (1860)

Thallus dull green, grey-green, white or fawn, granular-verrucose; photobiont cells 5-12 (-14) μ m diam. Apothecia (0.2-) 0.3-0.8 (-1) mm diam., dark purple-brown to black, sometimes becoming convex; margin thin, paler than the disc. True exciple and hypothecium dark red-brown, K+ purple, the outermost edge of the exciple sometimes colourless; hymenium 35–45 (–50) μ m high, colourless or pale red; paraphyses 1.5–2 (–2.5) μ m diam., unbranched or rarely forked above, not or only slightly swollen at the apices (to *ca* 3 μ m diam.). Ascospores 15–25 (–27) × 2–2.5 μ m, (0-) 3 (-5)-septate, cylindrical. Pycnidia \pm immersed, to 200 μ m diam., black, walls red-brown, K+ purple; conidia 5–9 × 2–2.5 μ m, 0 (-1)-septate, cylindric-ellipsoidal. **BLS 0153**.

On trunks of trees with basic bark (especially *Ulmus*), often forming extensive dark green-grey uneven vertical streaks along rain or wound seepage tracks, sometimes on exposed roots of *Ulmus* on cliff faces. Recently much declined owing to demise of *Ulmus* and now mainly found on the bark or lignum of wounded trunks of *Acer*,



Aesculus, Carpinus, Fraxinus, Fagus and *Ilex.* Originally throughout S. England, extending N. through mid Wales to Scotland (to Skye in the west and N. Aberdeenshire in the east); rare in Ireland, now largely lost from the north and west of this area, with no recent Irish records, and now most frequent in S.W. England.

Recognized by the granular-vertucose thallus and dark internal pigmentation of the apothecia. Occasionally found sterile, although the inconspicuous pycnidia are usually present.

BIATORA Fr. (1817)

Thallus crustose, effuse, sometimes membranous in part and mostly rimose, the moss-associated species usually granular to granular-verrucose, creamy white, dull green, glaucous green or greengrey; ± ecorticate, sometimes sorediate; prothallus absent. Photobiont chlorococcoid. Ascomata apothecia, biatorine, sessile or appressed, usually weakly to strongly convex and immarginate, or at first with a flat disc and a shallow margin, occasionally tuberculate, light beige to dark reddish brown, green-grey, bluish green or khaki, rarely black, but then always with a green or blue tinge when wet, most species not pruinose. True exciple soon reflexed, well-developed (easily visible in sections), composed of radiating hyphae with lumina $1-3 \mu m$ diam., with terminal cell lumina to 5 μm diam., tightly bound in a gel matrix that does not dissolve or markedly swell in K; outer edge sometimes covered by a narrow gel layer. Hymenium 30-80 (-100) µm tall, most species without a well-defined epithecium (sometimes with pale pigmentation in the upper part), granules or oil droplets, I+ redbrown when young, blue in older herbarium material. Subhymenium distinct, somewhat opaque due to the presence of ascogenous hyphae, often slightly darker than the hymenium. Hypothecium of interwoven hyphae with lumina 1–2 µm diam. in a dense gel matrix. Hamathecium of coherent (in K) paraphyses, with lumina $0.5-2.5 \ \mu m$ diam., unbranched or sparingly branched, only rarely anastomosed, the apices slightly swollen (lumina to 5 µm diam.), rarely surmounted by a distinct apical 'cap' or 'hood'. Asci 8-spored, cylindric-clavate, lateral walls 0.7-1 µm thick, Biatora-type with K/I+ blue apical dome penetrated from below by a narrow, K/I- apical cushion surrounded by a narrow, deeply K/I+ blue zone, wall K/I- but surrounded by a I+ red-brown, K/I+ blue outer layer, ocular chamber relatively small. Ascospores colourless, ellipsoidal or cylindrical to filiform, or cylindric-fusiform, aseptate or 1- to 7-septate, smooth, without a distinct perispore. Conidiomata pycnidia, globose to pyriform, immersed in the thallus, wall unpigmented or weakly pigmented like the hymenium. Conidia aseptate, bacillar. Chemistry: gyrophoric acid, argopsin, rarely other depsides, depsidones, xanthones or usnic acid, some species without secondary metabolites detectable by TLC. Ecology: on somewhat acidic, organic substrata but avoiding extreme acid or calcareous conditions and in relatively undisturbed habitats. Some species on bryophytes over rocks or treetrunks, bark of old trees or rotten bark at the base of old trees, some on detritus and at the base of shrubs in alpine habitats. Many species growing on bark are characteristic of old woodlands.

Mycobilimbia is similar to *Biatora* in outer appearance but differs in apothecial ontogeny, and in section, apothecia of *Mycobilimbia* usually appear slightly stipitate. The separation is also supported by molecular genetic data. The mostly subtropical to tropical genus *Phyllopsora* is sister in phylogenetic terms (Kistenich *et al.* 2018) and can be very similar to *Biatora* but the British species

of *Phyllopsora* is distinguished by a subsquamulose thallus, a mostly conspicuous hypothallus, stouter paraphyses and excipular hyphae and a hymenium that reacts weakly blue with iodine. For differences between *Biatora* and *Herteliana* (Lecanorales: Squamarinaceae) see under the latter genus.

Although some inter-relationships at species level are not fully understood, the genus is monophyletic and most species are homogenous in phylogenetic terms (Printzen 2014, Kistenich *et al.* 2018). *Biatora beckhausii* has been transferred from *Bacidia*, where it resided in edition 2 of this work, and *Catillaria alba* is now placed in *Biatora* under the name *B. veteranorum* (Sérusiaux *et al.* 2010). Those authors also confirmed the presence of *B. ligni-mollis* in Britain and Ireland.

Literature

Kistenich et al. (2018), Kondratyuk *et al.* (2019), Printzen (1995, 2014), Printzen & Coppins (2009), Printzen *et al.* (2001, 2016), Printzen & Otte (2005), Printzen & Palice (1999), Printzen & Tønsberg (1999), Sérusiaux *et al.* (2010).

Key to the species of Biatora and Mycobilimbia

1	Thallus with effuse, pale greenish or yellowish soralia; often sterile	2
	Thallus without soralia; mostly fertile	.5
2 (1)	Soralia Pd+ orange-red, thallus containing argopsin	3
	Soralia Pd-, thallus without argopsin	.4
3 (2)	Apothecia bluish-grey, containing grey to turquoise pigment in hymenium and hypothecium; in western parts Britain and Ireland	са
	Apothecia pale beige to red-brown, without blue-green pigmentation in section; apparently restricted to E. Scotland	ns
4 (2)	Soralia C+ red Biatora chrysant.	ha
	Soralia C	es
5 (1)	Ascospores mostly 0- to 1-septate (rarely a few 2- to 3-septate)	6
	Ascospores at least mostly multiseptate	13
6 (5)	Thallus Pd+ red, containing argopsin	7
	Thallus Pd–, without argopsin	.8
7 (6)	Apothecia reddish to dark brown; ascospores (10–) 13–17.5 (–20) µm long; on montane soil (no recent records)	ea
	Apothecia grey-black to blue-black; ascospores 7.5–14 µm long; on bark in oceanic situations <i>Biatora ocelliformis</i> auct.	br.
8 (7)	On dry bark or lignum; ascospores <3.5 µm broad	9
	On mosses overgrowing bark or detritus; ascospores >3.5 µm broad	11
9(8)	Apothecia pale to reddish brown, not pigmented in section; pycnidia stalked or sessile, conspicuous, concolorous with the apothecia or white-pruinose	10
	Apothecia grey- to black-brown, often darkly pigmented in section; pycnidia immersed,	
	Inconspicuous, blackBiatora globulo	sa
10 (9)	Thallus UV–; pycnidia stalked, white-pruinose; conidia bacillar, 2.8–3.5 (–3.8) μm long;	
	Thallus UV+ white; pycnidia sessile, pale orange to brown; conidia bacillar, 3.5–5.5 µm long	m
	(ovoid conidia may also be present; ascospores 1- to 2- (to 3-) septateBiatora ligni-mol	lis

- 12(11) On mosses and detritus in alpine and subalpine situations; thallus whitish; inner part of exciple and hypothecium often (not always) orange-brown to dark brown; ascospores $9.5-15.2 \times 3.5-5 \,\mu$ m Biatora subduplex On mossy tree trunks in old woodlands or on sheltered, mossy rocks; thallus greenish grey; apothecia without brown pigmentation in section; ascospores $12.5-19.5 \times 4.3-5.8 \,\mu\text{m}$. Biatora vernalis
- 13(5) Ascospores $1.5-2.5 \,\mu\text{m}$ broad, (1-) 3 (-7)-septate, \pm cylindrical and sometimes curved
- 14(13) Apothecia grey- to dark greyish brown, with greyish to pinkish brown pigment in the

Biatora beckhausii (Körb.) Tuck. (1888)

Bacidia beckhausii Körb. (1860)

Thallus white or pale grey, \pm immersed or thin and varnish-like or slightly warted; photobiont cells 8–14 μ m diam. Apothecia 0.5–1.5 mm diam., at first ± flat but soon convex, immarginate, pale grey in shade to bluish black in well-lit conditions, often thinly white-pruinose or with a bluish 'bloom' when wet; true exciple thin, colourless or partly pale green, K+ violet; hyphae 1.5-2 µm diam., more distinct in K but not separating; epithecium usually with minute granules dissolving in K; hymenium 35-50 µm high, upper part (and often vertical streaks) dull green K+ violet, N+ red; hypothecium colourless; paraphyses 1-1.5 µm diam., unbranched or sparingly branched, apices not or only slightly widening to ca 2 µm diam. Ascospores 17-26 (-29 × 1.5–2.5 µm, (1-) 3 (-7)-septate, bacilliform or slightly curved. Pycnidia 50–100

 μ m diam., immersed, black, the wall olive, K+ violet; conidia 3–3.5 × 1–1.5 μ m, cylindric-ellipsoidal. **BLS 0135**. On bark or rarely wood of trunks of mature deciduous trees (especially Fraxinus, Quercus, Ulmus), mainly in old woodlands; frequent. N. Scotland (C. & E. Highlands), older records from S.E. Scotland and N.E. England (Northumberland, N.E. Yorks).

Placed in *Bacidia* in Edition 2 of this work due to the elongate ascospores, but molecular data align this species with Biatora, with its closest relatives probably B. globulosa and B. ligni-mollis. The large-celled photobiont, epithecial granules and coherent exciple hyphae distinguish this species from Micarea globulosella and M. longispora. It is often difficult to distinguish in the field from Biatora globulosa, which has a green, K-, nongranular epithecium and shorter, 0- to 1-septate ascospores.

Biatora britannica Printzen, Lumbsch & Orange (2001)

Thallus smooth to slightly rimose, sorediate, pale greenish, matt; soralia punctiform, greyish green, paler and more vividly coloured than the thallus, 0.15–0.30 mm diam. Apothecia 0.5–1.0 mm diam., weakly convex, sessile with a weakly constricted base or appressed, bluish grey; margin not prominent, pale grey, slightly glossy, soon excluded; true exciple colourless, ca 35 µm thick; hymenium ca 45 µm high, colourless in apical parts, grey to turquoise in basal parts; subhymenium ca 80 µm high; hypothecium ca 100 µm high, weakly greyish blue, in parts with a brown tinge; epihymenium 5–10 µm high, yellowish green; paraphyses extending as parallel hyphae far into the subhymenium. Ascospores $8-20 \times 3-4.5 \,\mu\text{m}, 0$ (-1)-septate, narrowly ellipsoidal. Pycnidia not observed. Thallus C-, K-, KC-, Pd+ orange-red (argopsin, norargopsin). BLS 2314.

On base-rich bark in sheltered locations, mainly in old growth stands, but may also colonise younger more disturbed woods as well, in the south and west of Britain and in Ireland, probably widespread but under-recorded in these areas.







Nb

Nb

Sterile specimens of *B. britannica* and *B. efflorescens* seem to be morphologically indistinguishable. *B. efflorescens* is a slightly eastern species with a preference for more acidic substrata. *B. britannica* is easily overlooked as *Lecanora jamesii*, but the punctiform soralia have a much greener hue than those of *L. jamesii*, which are yellow, and are also Pd –.

Biatora chrysantha (Zahlbr.) Printzen (1994)

Thallus granular-verrucose, sorediate, grey- to dark green, matt; areoles 0.1–0.25 mm diam., soralia confluent, pale, yellowish green, paler than the thallus, 0.25–0.7 mm diam. Apothecia 0.4–1.1 mm diam., moderately to strongly convex, sessile with a constricted base, pale pink to reddish brown; margin not prominent, slightly paler than the disc, glossy, soon excluded; true exciple colourless, $50–95 \ \mu m$ broad; hymenium 40–55 $\ \mu m$ high, colourless; subhymenium 50–85 $\ \mu m$ high; hypothecium 85–300 $\ \mu m$ high, colourless. Ascospores (10–) 12–16 (–20) × (3–) 4–6 (–7.5) $\ \mu m$, 0 (–1)-septate, ellipsoidal. Thallus C+ red, K–, KC+ red, Pd– (gyrophoric acid). **BLS 1830**.

Over bryophytes or on bark of deciduous trees and conifers, mostly in old woodlands. Frequent in the E. Scottish Highlands, rarer in N. England. Central Wales and S.W. England (Exmoor, Dartmoor, E. Cornwall).

The only British *Biatora* species with a C+ red thallus, due to the presence of gyrophoric acid. Resembles *Mycobilimbia epixanthoides*, which is C-. *Loxospora elatina* has a K+ bright yellow thallus owing to the presence of thamnolic acid. *Ochrolechia androgyna* s.l. has a pale grey, usually much thicker thallus. When the soralia are very confluent, it can be overlooked as a *Lepraria* species, but the yellowish green colour and C+ red spot test are distinctive. Rare morphs of *Trapeliopsis flexuosa* and *T. pseudogranulosa*, when growing on mossy bark, can be distinguished by the photobiont cells, which divide by binary fission into two or four daughter cells.

Biatora cuprea (Sommerf.) Fr. (1831)

Thallus warted to almost squamulose, not sorediate, whitish; areoles 0.2–0.9 mm diam. Apothecia 0.35–1.1 mm diam., moderately to strongly convex, sessile with a weakly constricted base or appressed, reddish brown to dark brown; margin not prominent, paler than the disc, soon excluded; true exciple colourless or with brown pigmentation, 50–120 μ m broad; hymenium 55–75 μ m high, colourless, sometimes with brown spots; subhymenium 50–100 (–170) μ m high; hypothecium 120–360 μ m high, colourless, sometimes with brown spots; paraphyses extending as parallel hyphae into the subhymenium. Ascospores (10–) 13–17.5 (–20) × (3.5–) 4.5–5.2 (–6) μ m, 0 (-3)-septate, narrowly ellipsoidal. Thallus C–, K–, KC–, Pd+ orange-red (argopsin, norargopsin). **BLS 0713**.

On soil at *ca* 1000 m. C. Scotland (Perthshire, Ben Lawers); no records since the 19th century.

A useful distinguishing feature of *B. cuprea* is its extremely hard thallus. It is basically impossible to stick preparation needles or even razor blades into a dry thallus. The superficially similar *B. subduplex* is Pd–, has a hymenium of 35–60 μ m and slightly narrower ascospores. *Protomicarea limosa* has a similar Pd+ red thallus (pannarin), but the apothecia are black.

Biatora efflorescens (Hedl.) Räsänen (1935)

Thallus rimose, sorediate, whitish to greyish green; soralia punctiform, yellowish or greyish green, paler than the thallus, 0.2-0.5 (-0.7) mm diam. Apothecia absent in British material, 0.3-1 mm diam., flat to strongly convex, sessile or appressed between soralia, pale beige to red-brown; margin not or weakly prominent, mostly paler than the disc, soon excluded; true exciple colourless, 35-80 (-110) µm broad; hymenium 30-60 µm high, colourless; subhymenium 50-70 µm high; hypothecium 20-120 µm high, colourless. Ascospores (9–) 12-18 (-22.5) × 3-5 µm, 0 (-1)-septate, narrowly ellipsoidal. Thallus C–, K–, KC–, Pd+ orange-red (argopsin, norargopsin). **BLS 0718**.

A few localities in eastern Scotland (Easterness, Moray, Perthshire and S. Aberdeenshire), where it grows on *Juniperus* and *Quercus*.

Sterile specimens are indistinguishable from *B. britannica* and sequencing is needed to confirm identity of the Scottish material.



Ex

Biatora globulosa (Flörke) Fr. (1846)

Thallus effuse, pale white-fawn, thin, smooth to powdery, \pm rimose or endoxylic; photobiont cells 7–14 (–18) µm diam. Apothecia sessile, numerous, 0.15–0.4 mm diam., at first flat, soon convex to subglobose, usually grey-brown or grey- to greenblack, rarely pale in shade morphs, occasionally white-pruinose when young; proper margin indistinct from above, colourless except the upper edge which is often concolorous with the epithecium, the hyphae coherent in K, lumina ellipsoidal, 2–4 µm diam.; epithecium mostly slate-grey to dark olive-green, K+ green intensifying, N+ red; hymenium 30–40 µm tall, colourless; hypothecium colourless; paraphyses 1.2–2 µm diam., unbranched or forked above; the apical one or two cells often grey-or green-walled and swollen to *ca* 6 µm diam. Ascospores 7–12 (–16) × 2–2.5 µm, 0-

to 1-septate, cylindrical to cylindric-fusiform. Pycnidia inconspicuous, partly immersed, 40–100 μ m diam., black; the wall dark green; conidiogenous cells in a single layer, short-ampulliform; conidia of two types (a) cylindrical or ± curved, 3.5–5 (–6) × 0.5–0.7 μ m (commoner), or (b) ellipsoidal, 2–2.8 × 1–1.5 μ m; the two types not in the same pycnidium. **BLS 0310**.

On rough bark or lignum of *Quercus* and *Alnus* trunks in woodlands or other sheltered situations; local. Scotland (C. & E. Highlands), rare in N.E. England, one record in central Wales.

The usually black discs and apothecia lacking photobiont cells distinguish this species from *Lecania chlorotiza* and *L. cyrtellina*. It is often difficult to distinguish in the field from *Biatora beckhausii*, with which it often grows.

Biatora ligni-mollis T. Sprib. & Printzen (2009)

Thallus thin, continuous, whitish to pale green, distinctly granulose or farinose, partly immersed, prothallus absent. Photobiont chlorococcoid, algal cells 8–14 μ m diam. Apothecia usually present, scattered over the thallus or in groups, sometimes contiguous but not agglomerated, 0.15–0.40 μ m diam., with a slightly constricted base; disc dark orange to pale reddish brown, flat and becoming slightly convex in old apothecia; margin distinct in young and mature apothecia but hardly present in old ones, slightly paler and sometimes slightly sinuose; exciple colourless, 40–45 μ m thick; hypothecium colourless; hymenium colourless, 40–60 μ m high, sometimes with vertical rows of tiny colourless crystals especially in the upper parts; paraphyses rather few, usually shorter than the asci, unbranched, not swollen at the apices, *ca* 1 μ m

diam.; asci $25-35 \times 7-10 \mu$ m, clavate or sometimes slightly turbinate. Ascospores $8-12 \times 2.0-3.5 \mu$ m, narrowly ellipsoidal with rather rounded ends, straight or slightly curved, thin-walled, 1-2 (-3) septate. Pycnidia always present, sessile, conspicuous but quite small (*ca* 0.1 mm diam.), globose, usually with a wide open ostiole, of the same color as the apothecia but paler and thus pale orange to brownish; conidia of two types, not produced in the same pycnidia: (a) bacilliform, $3.5-5.5 \times 0.8-1.5 \mu$ m; (b) ovoid with a slightly pointed end, $2.5-3.0 \times ca$ 2 mm. Thallus C–, K–, KC–, Pd–, UV+ brilliant white (lobaric acid (major) and roccellic acid (major)). **BLS 2536**.

On the underside of a large *Ouercus* trunk, Easter Ross; dry bark on veteran *Ouercus*, Mid Wales (Elan Valley).

Similar to *B. veteranorum*, but with darker and more frequently developed apothecia and sessile pycnidia that are not pruinose; the combination of orange apothecia and pycnidia and the UV+ brilliant white thallus is very distinctive.

Biatora ocelliformis auct. brit, non (Nyl.) Arnold (1870)

Thallus smooth to cracked-areolate, pale to dirty green-grey, very thin and sometimes partly immersed, often wrinkled, irregularly corticate, not sorediate. Hypothallus dark grey. Apothecia scattered or in small groups, sessile and \pm flat when young and with a constricted base when older, 0.3–0.6 mm diam., when tuberculate to 1.15 mm diam. Disc dark grey to black, in young apothecia the edge sometimes lighter than the disc, becoming excluded. True exciple colourless to pale brown outside, the inner part and near the hymenium olive-brown, 30–85 µm thick. Hypothecium and subhymenium dirty olive ("Bagliettoana-green") with dark brown patches, N+ violaceous, HCl+ violaceous. Hymenium 30–40 µm tall, the epithecium not well differentiated, sometimes mottled pale brown. Paraphyses 1–1.5 µm diam., slightly swollen at the apex. Ascospores narrowly ellipsoidal, aseptate or rarely 1-septate, (10–) 11–12 (–14) × (3.0–) 3.5–4 (–5.5) µm. Pycnidia unknown. Thallus C–, K–, Pd+ red. **BLS 2567**.

On branches of Corylus and Ulmus on oceanic ravines, West Inverness.

The grey-black apothecia, sometimes with a shallow, paler margin, may resemble *Lecidella elaeochroma* or *Biatora globulosa*, but the thallus is C– and Pd+ red, the hypothecium is mottled green-black and the ascospores



NT



are narrowly ellipsoidal and usually aseptate.

The British species resembles *Biatora ocelliformis* and also *B. hypophaea* Printzen & Tønsberg (2000), but the turquoise apothecial pigment in these species contains Cinereorufa-green and does not turn violaceous in HCl.

Biatora subduplex (Nyl.) Printzen (1995)

Thallus smooth, rimose, not sorediate, whitish to pale ochre; areoles 0.15–0.55 mm diam. Apothecia 0.2–1.0 mm diam., flat to strongly convex, sessile with a constricted base, orange- to red-brown; margin weakly prominent and soon excluded, paler than the disc; true exciple colourless outside, yellowish to mahogany-brown within and near the hymenium, 25–100 μ m broad; hymenium 35–60 μ m high, colourless or yellowish brown; subhymenium 20–95 μ m high; hypothecium 35–300 μ m high, yellowish to mahogany-brown, rarely colourless. Ascospores 8–15 (–21) × 3–5 (–6) μ m, 0 (-1)-septate, narrowly ellipsoidal. Lichen substances not detected by TLC. **BLS 0162**.

Overgrowing mosses, detritus and bases of shrubs in (sub)alpine localities. Scottish Highlands (Mid-Perthshire).

Distinguished from *B. cuprea* by the lack of lichen substances, and a thinner and more fragile thallus. Phylogenetic studies show that two cryptic taxa are currently hiding under this name, one of which is closely related to *B. vernalis*, the other to *B. meiocarpa* (Printzen 2014). It is possible that both species occur in Britain and Ireland.

Biatora vernalis (L.) Fr. (1831)

Thallus irregularly wrinkled to granular-verrucose, rarely forming a \pm smooth crust on mosses, not sorediate, green to grey-green (turning beige to brownish in the herbarium); warts 0.1–0.25 mm diam. Apothecia 0.35–1.2 (–1.4) mm, weakly to strongly convex, sessile with a constricted base, orange- to red-brown; margin not or only weakly prominent, soon excluded, paler than the disc; true exciple colourless or yellowish to orange-brown inside and near the hymenium, 50–100 µm broad; hymenium 45–65 (–95) µm high, colourless or pale orange-brown; subhymenium 40–70 (–120) µm high; hypothecium 95–300 µm high, like the hymenium in colour. Ascospores (10–) 12–20 (–25) × 4–6 (–7) µm, 0 (-1)-septate, ellipsoidal. Lichen substances not detected by TLC. **BLS 0791**.

In old woodlands on mildly acidic mossy tree trunks (especially *Quercus*); rare on sheltered mossy rocks. Upland Wales, N.W. England, Scotland.

Distinguished from *Mycobilimbia sphaeroides* by its more coarsely granular thallus and mainly aseptate ascospores. British material is often sterile but the absence of soralia separates it from *B. epixanthoides*, *B. chrysantha* and *Megalaria pulverea*, and the Pd– thallus separates it from *Phyllopsora rosei*. *Megalospora tuberculosa* has a softer, usually greenish yellow thallus and contains usnic acid and zeorin. The most difficult split is with occasional sterile thalli of *Bryobilimbia sanguineoatra*, which grows in similar habitats. The thalli of *Biatora vernalis* are conspicuously wrinkled to verrucose and are quite bright grey-green with yellow tinges; *Bryobilimbia sanguineoatra* has a smooth membranous and varnish-like continuous thallus which is darker grey-green with no yellow tinges. The so far undescribed "*B. orientalis*" (Printzen 2014) is extremely similar to *B. vernalis* and has recently been found in Norway. It may occur in Britain as well.

A useful key to species of the *B. vernalis* group can be found in Printzen et al. (2016).

Biatora veteranorum Coppins & Sérus. (2010)

Catillaria alba Coppins & Vězda (1993)

Thallus effuse, thin, pale, indistinct. Apothecia 0.16–0.4 mm diam., white, becoming pale brown; true exciple with conglutinate radiating hyphae, poorly developed; epithecium pale orange with minute crystals dissolving in K; hymenium *ca* 30 μ m high, colourless; paraphyses rarely branched, 1–1.5 μ m diam., broadening at the apex to *ca* 3 μ m diam. Asci clavate, *Biatora*-type. Ascospores ellipsoidal, 1-septate, (6.5–) 8–10 (–11.5) × 2.3–3 μ m. Pycnidia sessile to short-stalked, white-pruinose, 80–120 μ m diam., 80–150 μ m high; conidia aseptate, bacilliform, colourless, 2.8–3.5 (–3.8) × 0.8–1 (–1.2) μ m. Chemistry unknown. **BLS 1911**.







Nb



On lignum or dry bark of ancient trees (mostly *Quercus*, also *Salix*); rare. Scattered records from E. England, E. Scotland (Oxfordshire & Bedfordshire to Ross & Cromarty).

The stalked pycnidia and habitat on lignum of ancient trees are diagnostic. *B. ligni-mollis* differs in having a UV+ white thallus, 1- to 2 (-3)-septate ascospores and sessile, globose pycnidia, with longer bacilliform (3.5– $5.5 \times 0.8-1.5 \mu$ m) or ovoid conidia (2.5– $3 \times ca \ 2 \mu$ m). Other species with white stalked pycnidia are *Micarea pycnidiophora* (pycnidia C+ red), and *M. stipitata* (conidia $6-8 \times 1-1.8 \mu$ m). The stalked pycnidia of *Micarea hedlundii* are also white-pruinose but have a brownish tone from the colour of the pycnidial wall. It grows on damp wood in western forests.

Placed in the new genus *Coppinsidea* by Kondratyuk *et al.* (2019), but the molecular phylogenetic evidence for this does not appear to be strong.

BIBBYA J.H. Willis (1956)

Thallus immersed, crustose, squamulose, bullate, warted or granular, often pruinose, cortical pores absent, pseudocyphellae occasionally present; the **upper cortex** with an often thick epinecral layer and often containing calcium oxalate crystals. **Soredia** and **isidia** absent. **Apothecia** flat to shallowly convex and thinly marginate, sometimes becoming convex and immarginate or tuberculate, dark purple-brown to black, sometimes weakly pruinose. **Thalline margin** absent. **True exciple** dark red-to purple-brown, K+ intensifying purple. **Epithecium** red- to purple-brown, K+ reddish, N–. **Hymenium** sometimes pale brown-purple below. **Hypothecium** colourless or pale brown. **Paraphyses** unbranched or forked above, the upper part sometimes pigmented with the apices swollen. **Asci** *Bacidia*-type. **Ascospores** ranging from aseptate and ellipsoidal to acicular and multiseptate. **Pycnidia** immersed, black, the wall mainly purple-brown but sometimes green around the ostiole. **Conidia** cylindrical to elongate, often curved. **Chemistry**: lichen compounds absent in most species. **Ecology**: on bark and wood, on soil or in rock crevices in non-British species.

Contained within *Toninia* according to the treatment by Timdal (1991), but demonstrated to be a distinct genus by Kistenich *et al.* (2018) and including two species included in *Bacidia* by Coppins & Aptroot (2009). It is distinctive particularly for the red- to purple-brown K+ red pigments in the exciple and epithecium.

Literature

Coppins & Aptroot (2009), Kistenich et al. (2018), Timdal (1991).

1 Ascospores 18–28 × 1.5–2 μm, (0-) 3-septate, short-acicularsubcircumspecta Ascospores 21–40 × 2–3 (–4) μm, 3- to 7-septate, short-acicular or worm-likevermifera

Bibbya subcircumspecta (Coppins) S. Ekman (2018)

Bacidia subcircumspecta Coppins (1992)

Thallus immersed or scurfy-granular; granules, when discrete, 60–100 μ m diam. Apothecia 0.2–0.5 (–0.8) mm diam., mostly flat and thinly marginate, sometimes becoming convex and immarginate or tuberculate, dark purple-brown to black; true exciple dark purple-brown, K+ intensifying purple along the outer edge, pale purple within, hyphae with lumina *ca* 1 μ m diam. except at the outer edge where they are often expanded to *ca* 4 μ m diam.; hymenium 30–35 μ m tall, pale brown-purple below, becoming dark purple brown above, K+ intensifying purple; hypothecium colourless; paraphyses 1.5–1.8 μ m diam., unbranched or forked above, the apices swollen to 3 (–4) μ m diam. Ascospores 18–28 × 1.5–2 μ m, (0-) 3-septate, short-acicular. Pycnidia 60–80 μ m diam., immersed, black, the wall mainly purple-brown but green around the



Nb IR

ostiole; conidia $20-38 \times 0.5-1 \mu m$, curved. **BLS 1651**.

On hard wood, usually fence posts or rails, very rarely on *Populus* bark. Scotland, mostly N. of Clyde-Forth valley.

Scutula circumspecta differs in its greenish epithecium and Bibbya vermifera in its longer, often worm-like ascospores and bacilliform conidia.

Bibbya vermifera (Nyl.) Kistenich, Timdal, Bendiksby & S. Ekman (2018) *Bacidia vermifera* (Nyl.) Th. Fr. (1874)

Thallus immersed to irregularly warted, white; photobiont cells 5–14 µm diam. Apothecia 0.16–0.5 µm diam., flat and thinly marginate, or occasionally convex, black; true exciple brown-red or brown-purple, darker towards the outer edge, K+ intensifying purple; epithecium brown-red to purple-brown, K+ intensifying purple; hymenium 35–50 µm high, ± colourless; hypothecium colourless or pale red-brown; paraphyses 1–1.5 µm diam., unbranched, pigmented in the upper 12–15 µm, apices clavate, widened to *ca* 5 µm diam. Ascospores 21–40 × 2–3 (–4) µm, 3- to 7-septate, short-acicular or worm-like. Pycnidia 40–50 µm diam., ± immersed, black; wall brown-purple in K; conidia 7–9 × 0.5–1 µm, bacilliform or slightly curved. **BLS 0149**.



On bark of *Betula*, *Juniperus*, *Populus tremula* and *Ulmus* in wounds, in old Caledonian pine forest areas. Local in N.E. Scotland (mainly Speyside).

Similar to *B. subcircumspecta* in pigmentation, but with different ascospores and conidia. Its known range has increased in recent years, and while still threatened it may no longer merit an "endangered" conservation assessment.

BILIMBIA De Not. (1846)

Thallus crustose to effigurate, effuse, whitish grey to grey; not sorediate; prothallus absent. Photobiont chlorococcoid. Ascomata apothecia, sessile, usually weakly to strongly convex and immarginate, or at first with a flat disc and a shallow margin, occasionally sublobulate, light ochre to dark brown to black, not pruinose. True exciple soon reflexed, well-developed and easily visible in sections, chondroid, usually at least in parts with a dark brown or pinkish brown, K+ intensifying, N+ purple pigmentation, composed of stout, radiating hyphae tightly bound in a gel matrix that does not dissolve or markedly swell in K. Hymenium 50–90 (–110) µm tall, mostly without a well-defined epithecium (sometimes with pale olive or brown pigmentation in the upper part), granules or oil droplets, I+ red-brown when young, blue in older dried material. Subhymenium usually darker than the hypothecium. **Hypothecium** of interwoven hyphae in a dense gel matrix. **Paraphyses** $1.5-3 \mu m$ diam., coherent (in K), unbranched or sparingly branched, only rarely anastomosed, the apices slightly swollen (to 6 µm diam.). Asci 8-spored, cylindric-clavate, with a K/I+ blue apical dome penetrated from below by a narrow, K/I- apical cushion surrounded by an indistinct, apically often tapering, wall K/I- but surrounded by an I+ red-brown, K/I+ blue outer layer. Ascospores colourless, ellipsoidalfusiform, fusiform or clavate, (0-) 2- to 7 (-9)-septate, often with a rough perispore. Conidiomata not known. **Chemistry**: zeorin, or usually without secondary metabolites detectable by TLC. **Pigments**: uncharacterized olive-green and brown pigments in the hymenium, subhymenium, hypothecium and exciple. Ecology: on calcareous soil or bryophytes over basic substrata.

Separated from *Bacidia, Biatora* and *Mycobilimbia* by a slightly different tholus structure, the relatively stout paraphyses and ascospores surrounded by a finely warted perispore. The two British species are hosts to *Muellerella lichenicola* (Sommerf.) D. Hawksw. (1979) and *Unguiculariopsis refractiva* (Coppins) Coppins (1990).

Bacidia killiasii (Hepp) D. Hawksw. (1983) was described as a lichenicolous fungus on thalli of *Peltigera* species, causing a grey discoloration; it was reported from Perthshire (Ben Lawers). There

are no recent records and its affinities are unclear, but it may well be closely related or synonymous with *Bilimbia sabuletorum* which is known to overgrow other lichens.

Literature:

Kistenich et al. (2018), Printzen & Aptroot (2009).

1 Thallus minutely squamulose, crenate; ascospores 1- to 3-septate, mostly <5 μm diam.lobulata Thallus crustose, granular-warted or scurfy-granular, often with protruding whitish spines; ascospores 3- to 7-septate, mostly >5 μm diam.sabuletorum

Bilimbia lobulata (Sommerf.) Hafellner & Coppins (2004)

Thallus warted-granular to minutely squamulose; squamules 0.2–1.0 mm diam., mostly contiguous, compacted, horizontal, \pm overlapping, whitish grey to grey or fawn, edges \pm pale, underside pale or white; upper cortex 5–10 µm thick, folded, with an epinecral layer; algal layer with scattered groups of algae 25–100 µm diam., often in anticlinal 'columns', rarely forming a distinct layer to 125 µm thick; medulla 15–50 µm thick. Apothecia 0.3–1 mm diam., discrete or often aggregated, sessile, rounded or occasionally sublobulate; disc convex, black to brown-black, matt or \pm glossy, not pruinose; margin excluded from the beginning, true exciple red-brown, opaque, merging with a similarly coloured hypothecium, K+ intensifying, N+ purple-red; epithecium 5–15 (–20) µm high, \pm pale greenish grey, K–, N+ reddish; hymenium 70–

90 μ m high, colourless or pale red-brown; subhymenium 50–75 μ m high, mostly colourless above and pinkish brown to dark brown below; hypothecium 125–200 μ m high, brown above, mostly slightly lighter below; paraphyses conglutinated, unbranched or weakly branched, 1.5–3.0 μ m diam., apically to 5 μ m diam. Ascospores 14–20 (–26) × 3–5 (–6) μ m, (0-) 2- to 3-septate, ellipsoidal-fusiform or clavate. Thallus C–, K–, KC–, Pd– (zeorin). **BLS 1422**.

On soil associated with limestone, epidiorite, chalk and mortar, also on consolidated calcareous dunes, shell sand, mica-schist, upland and some downland areas; local. Throughout Britain, rare and mainly coastal in Ireland.

The squamules often have a characteristic darker centre with a whitish edge. Distinguished from *B*. *sabuletorum* by the \pm squamulose thallus and shorter ascospores.

Bilimbia sabuletorum (Schreb.) Arnold (1869)

Thallus warted-granular or scurfy-granular, sometimes \pm evanescent; granules 50–200 µm diam., scattered, mostly isodiametric, rarely marginally incised, whitish or pale grey; cortex 15–35 µm thick. Algal layer 65–150 µm thick; medulla lacking. Apothecia 0.3–0.8 (–1) mm diam., single, rarely in groups of up to 4, sessile, rounded or slightly deformed; disc mostly markedly convex but sometimes \pm flat when young, pale pinkish brown, pale to dark brown or black, matt, not pruinose; margin scarcely prominent when young and soon excluded, often lacking from the beginning; true exciple usually dark red-brown in upper parts, otherwise pale reddish brown to colourless, composed of hyphae 1.5–2.5 (–3.0) µm diam., apically to *ca* 5 µm diam. bound in a dense gel matrix; epithecium not distinct or patchily pale green to brown;

hymenium 70–110 μ m high, colourless or the upper part pale brown, grey or olivaceous to blue-green, K–, N+ violaceous pink, HCl+ blue; subhymenium 60–75 μ m high, greenish brown to pale golden brown; hypothecium 150–220 μ m high, dark (rarely pale) red-brown, K± reddish or purplish in the upper part, mostly colourless below. Paraphyses 2–3 μ m diam., apically to 5 (–6) μ m diam., unbranched or weakly branched above. Ascospores (16–) 18–40 (–50) × 5–8 (–9) μ m, 3- to 7 (-9)-septate, fusiform, rarely one cell with a longitudinal septum, often with a finely warted perispore (best seen in K). Thallus C–, K–, KC–, Pd– (no substances). **BLS 0165**.

Usually on mosses or on plant debris over calcareous rocks, stonework or turf, rarely overgrowing lichens or directly on rock, occasionally on shaded trunks of old trees (especially *Fraxinus* and *Ulmus*); common, mainly at low altitudes but up to 850 m in Scotland (Highlands). Throughout Britain and Ireland.

Very variable in the colour of the apothecia; intensely pigmented forms with black apothecia have been referred to as *Bilimbia accedens* Arnold. *B. sabuletorum* is easily distinguished from other superficially similar species in similar habitats (e.g. *Bacidia herbarum, Bryobilimbia hypnorum, Mycobilimbia tetramera* and





Toniniopsis bagliettoana) by its large, fusiform ascospores. For the distinction from *B. lobulata* see above. Host to *Lichenochora paucispora* Etayo & Nav.-Ros. (2008) and *Stigmidium mycobilimbiae* Cl. Roux, Triebel & Etayo (1994).

CLIOSTOMUM Fr. (1825)

Thallus crustose, \pm smooth to cracked-rimose or areolate to granular-vertucose, sometimes sorediate, whitish, pale grey, straw- or sulphur-yellow, effuse or bordered by a dark prothallus. **Photobiont** chlorococcoid. Ascomata apothecia; disc concave to flat, rarely convex, white, pink, brown or black, sometimes faintly pruinose. Thalline margin sometimes present. True exciple well-developed, persistent, \pm colourless but appearing straw-coloured due to densely interspersed minute granules; hyphae 1.7–2 µm diam., branched and radiating. Epithecium straw-coloured to dark brown, often minutely granular, granules dissolving in K. Hymenium 35–50 µm tall, I+ blue. Hypothecium colourless, I-. Hamathecium of numerous unbranched or sparingly branched paraphyses, the apices gradually clavate or capitate, sometimes pigmented. Asci 8-spored, clavate, Bacidia- or Biatora-type. Ascospores colourless, smooth, narrowly ellipsoidal to bacilliform, (0)- 1- or 3-septate, without a distinct perispore. Conidiomata pycnidia, in some species numerous, 100-500 µm diam., conspicuous, stromatic, unilocular or multilocular, wall dark or colourless, if dark, purplish-brown (K+ purple intensifying) above, becoming thinner and \pm colourless below. Conidiogenous cells cylindrical. Conidia colourless, smooth, aseptate, drop-shaped, ellipsoidal, bacilliform or bottleshaped. Chemistry: atranorin, chloroatranorin, zeorin, fumarprotocetraric, stictic, usnic and fatty acids. Ecology: on bark or wood, more rarely rocks.

Research by Spjut *et al.* (2020) suggests that *Cliostomum* is polyphyletic, with *C. griffithii* occupying a separate clade from the type *C. corrugatum* that is related to *Ramalina* and other fruticose members of the Ramalinaceae. *Sporoblastia* Trevis. (1851) is available for the *C. griffithii* clade, but more work is needed before changes are made at generic level.

Tylothallia is similar to *Cliostomum*, but has more coherent, more branched and anastomosed paraphyses and immersed pycnidia with colourless walls, except for a green, not purple, pigment around the ostioles.

Literature:

Ekman (1997), Fryday & Coppins (2012), Gilbert & Fox (2009), Kantvilas & Fryday (2010), Kistenich *et al.* (2018), Spjut *et al.* (2020).

1	Thallus sorediate; apothecia often few or absent 2 Thallus without soralia; apothecia normally present 4
2 (1)	Thallus Pd
3 (2)	Thallus yellow-green, entirely farinose-sorediate; on bark of deciduous trees, mostly southern <i>flavidulum</i> . <i>flavidulum</i> Thallus white to grey with initially delimited soralia; on schistose rock <i>subtenerum</i>
4 (1)	Apothecia, at least when young, \pm with a thalline exciple; thallus Pd+ red; saxicolous <i>tenerum</i> Apothecia with a true exciple only; thallus Pd-; corticolous, lignicolous, rarely on sheltered rocks
5 (4)	Apothecia pinkish brown to black, sometimes piebald, occasionally pruinose; pycnidia 0.1–0.2 mm diam., smooth; roccellic acid present

Cliostomum coppinsii Fryday & Kantvilas (2010)

Thallus crustose, effuse, in small patches 1-2 cm diam., delimited by a black prothallus where adjacent to other lichens, white to pale cream, \pm smooth, continuous or rimose to somewhat granular, sometimes patchy or very thin and inconspicuous, mostly $30-50 \mu$ m thick, not corticate; photobiont chlorococcoid with cells 9-12 (-15) μ m diam. Apothecia 0.4-0.8 mm diam., scattered, with a wide base; disc pale yellow, becoming brown when overmature, often lightly pruinose especially towards the margin, flat or slightly convex with age; margin indistinct, paler than the disc but not raised above it; true exciple extending beneath the hypothecium, composed of thin, radiating hyphae, sparingly branched and anastomosing towards the outer edge, end cells not enlarged or differentiated; hypothecium colourless to pale yellowish, K+

yellowish, 50–90 μ m thick; hymenium 60–75 μ m thick, colourless, IKI+ blue, overlain and inspersed in the upper part with a layer of minute pale yellow-brown crystals, K+ yellowish and dissolving; paraphyses 1.5–2.5 μ m diam., unbranched or sparsely branched in the lower part, becoming more branched and anastomosing and unevenly moniliform in the upper part; apices swollen to 2–5 μ m diam., not pigmented; asci clavate, 35–45 × 12–18 μ m, *Biatora*-type; ascospores ellipsoidal, colourless, 12–14 (–16) × 4.5–5 (–6) μ m, invariably 1-septate, \pm polarilocular, with the septum usually 2–3 μ m thick. Pycnidia not observed. Thallus containing atranorin, usnic acid and stictic acid; K+ yellow, KC–, C–, Pd+ orange. **BLS 2560**.

On old stems of Calluna, N.W. Scotland (Wester Ross).

Similar to *C. corrugatum*, but with a much thinner thallus. Only known from a single collection, but could well be under-reported.

Cliostomum corrugatum (Ach.) Fr. (1831)

Like *C. griffithii* but the thallus, although sometimes \pm evanescent, is usually thicker and more irregular, with areoles becoming \pm convex and irregularly vertucose-warted, often with a distinct greasy shine. Apothecia very rare, larger, 0.4–0.9 (–1) mm diam., pale to creamy yellow; exciple edge with a \pm faint purplish tinge, \pm granular, K \pm violetpurple; ascospores ellipsoidal, 1-septate, straight or slightly curved, 10–13 × 2–2.5 µm. Pycnidia very conspicuous, numerous, single or sometimes 2- to 3-clustered, 0.2– 0.5 mm diam., \pm conical at first, black, often with a pale apex, becoming roughenedverrucose to \pm ulcerose when mature; conidia ovoid to shortly cylindrical, 2–4 × *ca* 1 µm. Thallus K+ yellow (atranorin, caperatic acid), apothecia K– (usnic acid); roccellic acid absent. **BLS 0428**.

On wood of old farm buildings, coastal jetties and fence rails; very rare and decreasing. E. England (E. Anglia) & S. coast, S. Wales; formerly N. to the Yorkshire coast. Apart from one recent fertile sample on old pine from Glen Affric, all modern collections lack apothecia, and are probably *C. griffithii* with large pycnidia.

Cliostomum flavidulum Hafellner & Kalb (1992)

Thallus forming small patches, <2 cm diam., thin, continuous, sulphur-yellow to greenish-yellow, delimited by a whitish to black hypothallus. Surface ecorticate, totally farinose-sorediate with soredia 12–20 (–25) μ m diam. Apothecia scarce, 0.3–0.5 mm diam., concave when young, becoming flat, disc light brown with a thick non-sorediate margin, disc and true exciple may be irregularly stained dark grey; hymenium 40–50 μ m high, colourless, I+ blue. Asci 8-spored, ascospores (0-) 1-septate, ellipsoidal, guttulate, 8–13 × 2.5–3.5 (–4) μ m. Pycnidia rare, colourless; conidia drop-shaped. Thallus C–, K–, KC–, Pd+ red, UV–; atranorin (trace) and fumarprotocetraric acid. **BLS 1393**.

On the trunks of deciduous trees in sheltered situations, on mildly acidic to acid







VU (B)

Nb

bark, commonest in old growth woodland but found in disturbed younger woodland as well. Most frequently recorded from S. & S.W. England and Wales but it is also recorded from W. & E. Scotland and Ireland; widespread but much under-recorded.

Similar in appearance to *Lecanora expallens* but brighter yellow and C–, Pd+ red; the finely farinose soredia and brighter colour separate this species from *L. conizaeoides*.

Cliostomum griffithii (Sm.) Coppins (1980)

Thallus variable, whitish to pale grey or blue-grey, matt or slightly glossy, continuous, smooth to warted-areolate. Apothecia 0.2–0.6 (–0.8) mm diam.; disc concave-flat or slightly convex, often thinly white-pruinose, pink-brown to dark brown-grey or blackish, sometimes \pm piebald; true exciple thin, paler or concolorous, in section colourless or brown (K+ purplish tinge) at the upper outer edge, \pm densely granular internally; hymenium 55–60 µm high, paraphyses with \pm clavate apices. Ascospores 8–16 × 2.5–3.5 µm, (0-) 1 (-3)- septate, narrowly cylindric-ellipsoidal. Pycnidia 0.1–0.2 mm diam., usually present as black dots, the wall K+ purple; conidia 3.5–4.5 × 1.5–2 µm, ovoid to ellipsoidal. Thallus K+ yellow (atranorin, roccellic acid). **BLS 0429**.

Most frequent on the dry sides of the bark of mature trees including conifers and wood, often in rather dry, well-lit situations, more rarely on sheltered, \pm vertical rock faces or walls, *Calluna* stems and low shrubs, also decaying *Armeria* tufts; abundant. Throughout Britain and Ireland.

Very variable. The thallus is commonly smooth and thin, but is sometimes thick, irregularly warted or corrugate; the latter morphs are often confusing but usually bear the characteristic dark pycnidia, the walls of which are K+ purple. Apothecia are often notably variable in colour on the same thallus. When on rocks it can be separated from *Tylothallia biformigera* by the pigmentation of the pycnidia, the generally thinner thallus and the chemistry.

Sterile material with large pycnidia at or above the range given here and found on hard worked timber and rarely dead wood needs futher investigation; it has been recorded as *Cliostomum corrugatum*, but is very unlikely to be this species, which is a veteran tree specialist.

Cliostomum leprosum (Räsänen) Holien & Tönsberg (1992)

Thallus whitish to pale green, often with a yellowish tinge, mainly superficial, forming extensive patches, mainly sorediate, the margin diffuse and prothallus absent; soralia numerous, irregular in size and outline, bursting through the surface, sometimes leaving scars where the soredia have been shed, discrete and minute at first, becoming \pm confluent to form \pm continuous patches; soredia fragile, 20–100 µm diam. Apothecia rare, usually few in number per thallus, <0.6 mm diam.; disc pale yellow, turning orange-brown in dried collections; internal structure similar to that of *C. corrugatum*. Pycnidia frequent, black, K–, N+ reddish- violet; conidia subglobose to tear-drop-shaped, (2–) 2.5–3 × 1.5–2 µm. Thallus C–, K+ yellow, KC+ yellow, Pd– (atranorin, caperatic acid), apothecia with usnic acid. **BLS 2414**.

On the dry side of sloping trunk of ancient pine; a single record. Scotland (Mid-Perth, Black Wood of Rannoch).

C. leprosum is closely related to the non-sorediate *C. corrugatum* and may be a secondary sorediate species of that taxon. Although the thallus appearance and its structure are dissimilar, the apothecia are almost identical in structure and in, significantly, containing usnic acid.

Cliostomum subtenerum Coppins & Fryday (2012)

Thallus effuse, thin and discontinuous, occasionally thicker (to *ca* 0.4 mm), white, non-corticate. Soralia pale green, covering most of the thallus, 0.1–0.3 mm diam., soon confluent and effuse; soredia farinose, *ca* 20 μ m diam. Photobiont chlorococcoid, cells 8–12 mm diam. Apothecia scattered, sessile, 0.4–0.8 mm diam., becoming tuberculate and then to 1.2 mm diam.; disc pinkish brown to pale brown with a paler margin, slightly convex and soon becoming tuberculate with an excluded margin; true exciple composed of conglutinate radiating hyphae *ca* 5 μ m diam., internally colourless to yellow-brown with grey-brown granular intrusions not dissolving in K, outer cells with brown pigment, becoming colourless in K; hymenium colourless, I+ blue, 40–45 mm tall, epithecium brown, granular, becoming colourless in K; paraphyses 1.5–2.0 μ m diam., moderately branched and




anastomosing, apices to 3 mm diam., pigmented cap absent; hypothecium colourless. Asci *ca* $30 \times 12 \,\mu\text{m}$, clavate, *Bacidia*-type. Ascospores colourless, 0- to 1-septate, narrowly ellipsoidal to fusiform, often slightly curved, (10–) 12–15 (–20) \times 3–4 µm. Pycnidia rare; flesh-coloured to pale brown, immersed in thicker areas of the thallus. Conidia ellipsoidal-bacilliform, 7-8 × 1.5-2 µm. Thallus and soredia C-, K+ yellow, Pd+ orange, UV+ dull yellow; atranorin, stictic acid and zeorin by TLC. BLS 2573.

In shaded underhangs on schistose rocks, Anglesey, N.E. Yorkshire and Stirlingshire.

Similar to C. tenerum and in the same habitat, but with larger apothecia and ascospores, and a sorediate thallus.

Cliostomum tenerum (Nyl.) Coppins & S. Ekman (1997)

Thallus of minute, scattered to \pm contiguous irregular areoles, areoles flat to somewhat warted with age, creamy, whitish grey or green-grey, paler towards the margins; prothallus, when evident, white. Apothecia inconspicuous, 0.1-0.2 (-0.5) mm diam., dispersed or sometimes contiguous, initially immersed and then emergent, becoming sessile, the base slightly constricted; with a thin thalline margin with a thicker, irregularly smooth-crenulate edge, later becoming excluded; discs white to pale green, pinkish brown or pale brown, becoming strongly convex, often slightly pruinose; epithecium \pm colourless, interspersed with coarse granules dissolving in K; hymenium 25-40 µm tall; paraphyses 1.5-2 µm diam., unbranched or sparsely branched, apices to ca 5 μ m diam. Asci ca 30 \times 10 μ m, broadly clavate. Ascospores 7–10 (–15) \times (1.5–) 2-3 µm, aseptate, rarely 1- to 3-septate, fusiform-ellipsoidal, the apices pointed, often curved. Pycnidia

frequent, half-immersed, colourless; conidia $4-5.5 \times 1-1.5 \mu m$, narrowly ellipsoidal to bacilliform. Thallus C-, K+ yellow, Pd+ red (atranorin, chloratranorin, stictic and ± norstictic acids, unidentified compounds). BLS 0689.

Confined to dry, sheltered crevices and under overhangs of coastal siliceous rocks in the xeric-supralittoral zone; locally abundant but easily overlooked. Frequent in coastal W. Britain and Ireland, rare in E. Scotland.

Often forms extensive patches; with C. subtenerum, the only British species in the genus which can develop a thalline margin. See under that species for comparative data.

KILIASIA Hafellner (1984)

Lichenized or lichenicolous. Thallus, when present, crustose or rarely squamulose, with chlorococcoid photobionts. Ascomata apothecia, black, \pm sessile. Thalline margin absent. True exciple dark with the cellular structure obscure. Hymenium colourless. Epithecium dark green, not crystalline, K+ green intensifying, N+ purple-red. Hypothecium reddish brown, K+ purplish and N+ orange-red. Hamathecium of unbranched or branched paraphyses with clavate, often pigmented apices. Asci Bacidia-type, clavate to saccate, with a large tholus blueing in iodine with a pale central column, and an outer I+ blue gelatinous layer, 8-spored. Ascospores ellipsoidal to \pm cylindrical, 1- to 3-septate, colourless, without a perispore. Conidiomata not known. Chemistry: lichen chemicals not recorded. Distribution: nine species, widely distributed.

Recently resurrected by Kistenich et al. (2018), mostly containing species treated in Toninia by Timdal (1991). In phylogenetic terms, Kiliasia is a sister group to Bibbya and Thalloidima. Catillaria scotinodes (Nyl.) Coppins was transferred to Kiliasia by Gilbert et al. (1998), but although the species belongs to the Ramalinaceae rather than Catillariaceae, it is placed elsewhere within the family and does not currently have an appropriate generic placement.

Only one species is known to occur in Great Britain and Ireland; it is included in the key to Toninia and similar species in this publication.



Literature

Gilbert et al. (1988), Kistenich et al. (2018), Timdal (1991).

Kiliasia episema (Nyl.) Hafellner (1984)

Toninia episema (Nyl.) Timdal (1991)

Thallus absent, vegetative tissues immersed in the host and not visible at the surface. Apothecia 0.2–0.4 (–0.6) mm diam., mostly in small clusters, at first immersed, soon emergent, black; true exciple well-developed, raised, becoming excluded, brownblack, usually with a green tinge, K–, N+ violet (green pigment), lacking crystals; disc concave to convex; epithecium green-black, lacking crystals, K+ green intensifying, N+ purple-red plus formation of blue granules; hymenium 35–40 µm tall, colourless or pale greenish above; hypothecium pale red-brown, K+ purple, N+ orange-red; paraphyses unbranched, 1.7–2 µm diam., the apices swollen to *ca* 5 µm, most coated in dark pigment. Ascospores (9–) 10–14 × 3.5–4.5 µm, ellipsoidal, persistently 1-septate. Pycnidia not seen. Lichen products not examined. **BLS 1904**.



On thallus of *Circinaria (Aspicilia) calcarea* on hard limestones, commensal; local. S. England (frequent in Dorset and Somerset, occasional in surrounding counties), Morecambe Bay, Scotland (Jura, Ardnamurchan, Lismore), S. & W. Wales, N. Wales (Great Orme), scarce but widespread in Ireland.

K. episema could be confused with poorly developed specimens of *Toniniopsis aromatica* having exclusively 1-septate ascospores. *K. episema* never produces its own thallus.

LECANIA A. Massal. (1853)

Thallus crustose, thin to thick, continuous or of scattered granules, warted or areolate, rarely nodulose, papillate or somewhat lobed. Upper surface smooth to nodulose or papillate, occasionally with soralia or minute granule-like outgrowths ('blastidia' or 'goniocysts'), grey-white, white-yellow to brown-black, sometimes pruinose. Upper cortex cellular but occasionally densely crystalline or covered by a dead (epinecral) layer. **Photobiont** chlorococcoid. **Ascomata** apothecia, sessile, at first flat, often becoming convex; disc 0.4–0.6 (-1) mm diam., pale- to black-brown, to orange, sometimes pruinose. Thalline margin usually present, rarely excluded. True exciple sometimes well-developed. **Hymenium** colourless, I/KI+ blue, widening at the apex, lax in K. **Epithecium** often with unevenly distributed pigments giving a piebald appearance when the disc is wetted. **Hypothecium** colourless or pale. Hamathecium of paraphyses, thick, aseptate, conglutinated, sometimes sub-moniliform or with one to two terminal cells with a dark-pigmented cap. Asci Bacidia- or Biatora-type, 8(-16)spored; outer part of ascus wall K/I+ dark blue, remainder colourless within, with a K/I+ blue apical dome with a central apical cushion. Ascospores (0-) 1- to 3(-7)-septate, ovoid to elongate-ellipsoidal, thin-walled, colourless, without a thickened perispore, longer spores often bent. Conidiomata pycnidia, frequent in species on trees, very rare in rock species, conidia curved. Chemistry: most species lack a distinctive thallus chemistry; atranorin and unidentified terpenes are sometimes present. As yet uncharacterized K+ and N+ pigments may occur in the apothecia. Ecology: most frequently associated with nutrient-enriched or base-rich substrata in inland and coastal sites, especially old mortared walls, ragstone and Sambucus.

Distinguished from *Bacidia, Halecania, Lecanora* and *Catillaria* mainly by the different ascus type, ascospores, epithecium and paraphyses; the presence or absence of a photobiont-rich thalline margin is of less importance. In *Halecania* the ascus has a K/I+ blue apical dome lacking an apical plug, and the ascospores have a thickened outer wall layer (perispore).

Lecania polycycla (Anzi) Lettau (1912) (syn. *L. genevensis* (Müll. Arg.) Lettau) has been incorrectly reported from Britain and Ireland, and *L. subfuscula* (Nyl.) S.Ekman was transferred to *Bacidina* by Ekman (2023).

A notoriously difficult genus whose species tend to predominate in oceanic areas. Some of the

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species currently recognized can be very difficult to separate, particularly where thickness of the thallus or epinecral layer (dead cortical cells) are critical. Several saxicolous species, i.e. those in which the discussion centres on the occurrence on a specific type of rock, may turn out to be ecotypes of the same, polymorphic species; more comprehensive molecular studies would be useful. Thallus morphology, presence of blastidia and structure of the thalline exciple provide important diagnostic features.

Literature:

Fletcher *et al.* (2009a), Fryday & Coppins (2012), Kondratyuk *et al.* (2019), Mayrhofer (1988), Reese Naesborg (2008), Reese Naesborg *et al.* (2007), Sérusiaux *et al.* (2012), van den Boom (1992), van den Boom *et al.* (1996), van den Boom & Brand (2005).

1	Thallus on rock, cement, shells, bone or soil
2 (1)	Ascospores with a distinct perispore; ascus tip <i>Catillaria</i> -type <i>Halecania</i> Ascospores lacking a perispore; ascus tip <i>Bacidia</i> - or <i>Biatora</i> -type
3 (2)	Thallus with soredia or blastidia
4 (3)	Thallus sorediate, of dull matt blue- or green-grey granules <70 μ m diam
5 (4)	Soralia round at first, delimited, mottled blue-grey-indigo; usually sterile
6 (4)	Ascospores 1-septate, 9–16 µm long; blastidia sparse, often confined to thalline margins <i>erysibe</i> Ascospores 3- or more septate, >19 µm long; blastidia predominating7
7 (6)	Disc red-brown to black; ascospores 4–4.5 µm diam., 3-septate; on inland mortar <i>coeruleorubella</i> Disc pinkish to pale brown; ascospores 2–3 µm diam., 3- to 7-septate; on peaty soil, maritime, northern
8 (3)	Thallus papillate, hairy or nodulose
9 (8) 10 (9)	Thallus and apothecial margin covered with minute granular hairs
11 (10)	Thallus initially weakly areolate, warted to knobby papillate, usually pale to dark grey, slightly effigurate; often with a dark brown-black prothallus; with two unknown triterpenesaipospila Thallus initially warted, bullate areolate to subsquamulose, greyish to brown, not effigurate; prothallus not seen in European material; without lichen substancesfructigena
12 (8)	Ascospores 0- to 1-septate
13 (12)	White pruina present on apothecia or thallus 14 Pruina absent 15

14 (13)	Thallus and apothecia densely white-pruinose; apothecia ± crowded; cortex white-grey; areoles compressed, usually effuse
	Thallus not pruinose but disc pruinose; apothecia scattered, not compressed; cortex yellow-brown; thallus often delimited, ± orbicular
15 (13)	On calcareous substrata; thallus immersed, inconspicuous
16 (15)	Thalline margin persistent with a rich photobiont layer, cortex thick, containing ovoid cells; disc uniformly dark brown, red-brown when wet
17 (16)	Apothecial disc translucent and brown-speckled when wet; spores 4.5–6 µm diam.; in coastal rock crevices, rarely on treated timber
18 (12)	Disc not pruinose, thalline margin absent
19 (18)	On hard limestone; apical cells of paraphyses to 3 µm diam., unpigmented <i>cuprea</i> On soil or plant detritus, spreading onto calcareous or siliceous rock, apical cells of paraphyses swollen to 5 µm diam., often dark-pigmented <i>Bacidina subfuscula</i>
20 (18)	Ascospores 3- to 7-septate, 4–6 µm diam.; thalline margin with thick-walled, netted hyphae
	Ascospores 3-septate, usually <4–5 µm diam.; thalline margin netted or pseudoparenchymatous21
21 (20)	Ascospore apices pointed; thalline margin pseudoparenchymatoussuavis Ascospore apices blunt; thalline margin of thick-walled, netted hyphaenylanderiana
22 (1)	Ascospores predominantly 3-septate
23 (22)	Ascospores 8-16 per ascus [probably extinct in our region] <i>fuscella</i> Ascospores 8 per ascus
24 (23)	Thallus white to pale brown, granular; on soil or plant detritus
25 (24)	Thallus thickly granular to blastidiate, thalline margin of apothecium crenate or granular; disc pale brown to pinkish
26 (22)	Ascospores markedly crescent-shaped, 4–6 µm diam <i>dubitans</i> Ascospores ellipsoidal or only slightly curved, 2–6 µm diam27
27 (26)	Ascospores 4–6 µm diam. 28 Ascospores <3 µm diam. 31
28 (27)	Thallus and apothecial margin covered in minute hairs

29 (28)	Thallus thin and filmy to scurfy; disc pale pink to red-brown; on nutrient-rich bark
30 (29)	Ascospores 8 per ascus; in <i>Xanthorion</i> communities, especially on <i>Sambucus</i> or <i>Fraxinuscyrtella</i> Ascospores 16 per ascus; in old woodland or on <i>Populus</i> barksambucina
31 (27)	Thalline margin absent, white-pruinose when young; disc grey-blackBiatora globulosa Thalline margin present when young, containing photobiont cells, not pruinose; disc pink-brown32

Lecania aipospila (Wahlenb.) Th. Fr. (1867)

Thallus usually forming extensive coalescing patches, pale grey to grey-brown, often blue- or mauve-tinged, of contiguous coarse knobbly papillae and warts >1 mm diam., often somewhat lobed at the margin, prothallus usually dark grey-brown. Apothecia 0.5–1 mm diam., usually frequent, sessile or somewhat immersed, apical on the warts or papillae and hence appearing long-stalked; disc red-brown to brown-black, redbrown when wet, concave to weakly convex, not pruinose; thalline margin concolorous with the thallus, becoming excluded, the outer edge anatomically distinctive and similar to the cortex of the papillae, with a colourless superficial amorphous layer above a single outer layer of isodiametric cells with brownpigmented thickened walls, within composed of compact short-celled somewhat

radiating pseudoparenchyma intermixed with photobiont cells; epithecium brown, red-brown to orange, without granules; hymenium 65–90 μ m high; paraphyses slightly swollen and short-celled towards the apices, sometimes sub-moniliform. Ascospores 9–14 (–16) × 4–6 μ m, 1-septate. May contain two unidentified terpenes. **BLS 0609**.

On weakly basic rock or on siliceous rocks subject to bird-manuring, and seepage tracks, in rocky coastal areas, often in the xeric-supralitoral zone; locally frequent throughout western and northern regions of Great Britain, also around Irish coasts.

Readily distinguished by the coarsely warted or papillate thallus which is often indistinctly lobed and with apothecia apparently on stalks, with a distinctive cellular structure in the thalline margin. The stalked apothecia can resemble those of *Lecanora poliophaea*. In shade, the thallus can be pale fawn, but in exposed sites it is browner or tinged deep blue or mauve.

The closely related *L. fructigena* has smaller, densely crowded warts and lacks terpenes. Terpenes may be recognized by their leaving a white, crystalline evaporate from an acetone extract. The two species occur in the same habitat, but have so far not been found side-by-side. *Moelleropsis nebulosa*, when young, has a thallus forming nodular extensions on a dark basal thallus that can resemble *L. aipospila*.

Lecania atrynoides M. Knowles (1913)

Thallus even or granular, rimose-areolate, the surface smooth, sometimes following cracks and almost disappearing, dirty white to pale brown, often partly darkened by the invasive hyphae of other commensalistic fungi. Apothecia 0.3-1 mm diam., usually scattered, somewhat irregular in shape; disc dark red-brown to almost black, roughened, pale brown, translucent and speckled darker brown when wet (×20 lens), flat to slightly convex, not pruinose; thalline margin becoming excluded, concolorous with or darker than the disc, with a thin cortex, occasionally also with a poorly developed inner true exciple with thicker, brown-walled cells at the external edge; epithecium brown or black-green; hymenium (60–) 70–90 µm high; paraphyses rather sparse upbranched gradually widening to 3.5 µm at the anices and there often con

sparse, unbranched, gradually widening to $3-5 \ \mu m$ at the apices and there often conglutinated, forming dark-mottled patches on the disc. Ascospores 0- to 1-septate, $10-14 \ (-16) \times 4.5-6 \ \mu m$. **BLS 0611**.

On siliceous rocks in exposed situations on the sea coast, abundant in the submesic and xeric-supralittoral zones in crevices and below overhangs; rarely on worked timber in similar habitats; rather local, especially western regions of Great Britain.

Nb

Nb

Often confused with *Catillaria lenticularis* which differs in having paraphyses with uniformly dark apical caps. *Lecania turicensis* differs in the thicker, pruinose thallus and often pruinose apothecia, not speckled when wet.

Lecania baeomma (Nyl.) P. James & J.R. Laundon (1980)

Thallus wide-spreading, forming extensive patches to several cm diam., mostly indeterminate, white or yellow-grey, thin to medium thick, scaly or scurfy, irregularly coarsely rimose-areolate; surface with scattered delimited irregular erose or pustular soralia, coalescing when old; soralia finely speckled indigo-blue, $10-20 \mu m$ diam. (×20 lens), forming a confluent crust on the surface, uniformly pale within. Apothecia very scarce, 0.9–1.5 mm diam., sometimes deformed, scattered, rarely 2 or 3 contiguous; disc dark brown to black, densely mauve-grey pruinose, concave or flat to somewhat convex; thalline margin persistent, prominent, raised, usually sorediate, concolorous or paler than the thallus; epithecium black-brown, sometimes with an olivaceous tinge, densely granular; hymenium $60-100 \mu m$ high; paraphyses 2–2.5 μm diam. with apices not or slightly thickaned. Accompares 12, 16 (18) × 4, 55 um 1 s



diam., with apices not or slightly thickened. Ascospores $12-16 (-18) \times 4-5.5 \mu m$, 1-septate. K-, C-, Pd-, UV- (atranorin, gangaleoidin, unknowns). The indigo-blue pigment is within the mycobiont cell wall. **BLS 0612**.

On shaded sheltered, often north- or east-facing outcrops and below overhangs on siliceous rocks, predominantly coastal but extending inland; locally frequent. Channel Islands, Britain northwards to Scotland (Shetland), widespread in coastal areas of western Ireland.

Distinguished by the abundant diffuse indigo-speckled soralia and pruinose apothecia with an erodedsorediate thalline exciple. It is usually sterile. Reese Naesborg *et al.* (2007) claimed that this species is more closely related to *Ramalina* rather than *Lecania*, but that link needs confirmation.

Lecania chlorotiza (Nyl.) P. James (1992)

Thallus scurfy-leprose, bright to glaucous-green, becoming dirty grey, continuous, uneven, often wide- spreading. Apothecia 0.1–0.3 mm diam., occasional, semiimmersed, rarely becoming sessile, becoming convex, rounded or tuberculate, bright pink-orange to piebald brown; thalline margin thin, becoming excluded; hymenium 25–40 µm high, with photobiont below. Ascospores 8 per ascus, 0 to 1- septate, (9–) 10–12 (–18) × 2–3 µm. Pycnidia of two sizes: (a) minute, to 50 µm diam.; microconidia 7–10 × *ca* 0.5 µm, curved or hook-shaped; (b) 70–160 µm diam., pale with gaping ostioles; macroconidia 3–6 × 1–2 µm, cylindrical. **BLS 0307**.

On very shaded, base-rich bark and inside old hollow trees, especially *Ulmus*, *Fraxinus*, *Salix* or very old *Quercus* in sheltered wayside and woodland sites and by

water; rare but widespread in S.W. England and Wales, very rare beyond in N.E. England, W. Scotland, Ireland. Reese Naesborg *et al.* (2007) found that *L. chlorotiza* was not closely related to the core *Lecania* group, but did not suggest a more appropriate generic placement. Kondratyuk *et al.* (2019) included this species in the new genus *Vandenboomia*, but more molecular data are needed to confirm the placement.

The ascospores are exceptionally narrow, like those of *L. cyrtellina*, but the brighter pink apothecia and semiimmersed apothecia are distinctive. *Biatora globulosa* has black, sessile apothecia. The somewhat similar *Mycobilimbia sphaeroides* has apothecia 4–8 mm diam., and broader ascospores.

Lecania coeruleorubella (Mudd) M. Mayrhofer (1988)

Thallus thick, determinate, coarsely rimose-cracked, thickly and densely covered in flattened or spherical blastidia 45–65 μ m diam., forming chains, yellow-brown to brown-grey. Apothecia 0.5–1.2 mm diam., sessile or sometimes partially obscured by blastidia, single or in small clusters, often deformed; disc red-brown to black, densely grey-pruinose, convex to flat; thalline margin well-developed, irregular, swollen, irregularly cracked to incomplete and partially hidden, surface densely and minutely granular with blastidia; epithecium brown, densely granular; hymenium 60–70 μ m high; paraphyses short-celled towards the apices, becoming sub-moniliform, the cells often noticeably vacuolate. Ascospores 19–25 × 4–4.5 μ m, 3-septate. **BLS 1869**.

On old, crumbling mortar; very rare. N. England (Cleveland, there apparently no





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longer present) and Hertfordshire. Assessed as Extinct in the UK by Woods & Coppins (2012), but since rediscovered on a church wall in Hertfordshire.

This species has a thick thallus of abundant shiny, corticate blastidia closely resembling sterile but exuberantly blastidiate forms of *L. erysibe*. It has possibly been overlooked in the sterile state.

Lecania coerulescens Mudd (1861)

Thallus thick, of gnarled, warted areoles, ascending at the edges, with a smooth surface, to 20 mm diam., grey-brown to black-brown. Apothecia crowded, sessile, to 1.5 mm diam.; disc black-brown, red-brown when wet, flat to weakly convex, undulating, disc and thalline margin densely pruinose, constricted at the base, flexuose when old; thalline margin swollen, irregularly crenulate, concolorous with the thallus, with a cartilaginous cortex with a radiating network of hyphae with elongated, thread-like, narrow cells with very thick walls, like a netted matrix; true exciple absent; epithecium black-brown to green-black; hymenium 65–95 μ m high, with photobiont cells below; paraphyses mostly unbranched, the apical 1 to 2 cells swollen. Ascospores 16–29 × 4–6 μ m, 3- to 7-septate, elongate, slightly curved, ends somewhat attenuated to abruptly rounded. Conidia 12–13 × *ca* 0.7 μ m, curved, thread-like, aseptate. **BLS 1759**.

On calcareous sandstone of walls; rare. N.E. England (Cleveland; there probably extinct) & East Anglia (E. Norfolk). Endemic.

Rarely collected but distinguished by the 3- to 7-septate ascospores, large apothecia and the unique netted structure of the hyphae in the thalline margin.

Lecania cuprea (A. Massal.) van den Boom & Coppins (1992)

Thallus pale grey-green, often overgrown by green algae, thin, uneven, of finely rimose areoles <0.2mm diam. or minutely and irregularly granular-warted, but granules never discrete; photobiont cells 5–12 μ m diam., sparse below the hymenium. Apothecia 0.3–0.5 mm diam., sessile, flat or convex, pale pink-brown; thalline margin excluded, proper exciple colourless, or upper outer part pale to dark pink-brown and K+ purple, hyphae narrow but cells with expanded, ellipsoid lumina, to 5 μ m broad towards the outer edge; hymenium (35–) 40–45 (–50) μ m high, colourless, or pale grey and K+ purple in dark apothecia; hypothecium colourless or pale straw; paraphyses 1–1.5 μ m diam., the apices to 3 μ m. Ascospores 14–28 × 2–3 μ m, 1- to 3(-5)-septate, narrowly fusiform. Pycnidia immersed, white; conidia 10–19 × 0.8–1.2 μ m, strongly curved. **BLS 0143**.

On deeply shaded, hard limestone rocks, mainly under dry overhangs and deep crevices; localized. Throughout Britain and Ireland, but rather local.

Very variable in appearance. Most likely to be confused with *Bacidia delicata*, *Bacidina subfuscula* or other *Lecania* species with 3-septate ascospores. *Bacidina subfuscula* is usually on open rocks, turf or soil.

Lecania cyrtella (Ach.) Th. Fr. (1871)

Thallus very thin, filmy, smooth, occasionally finely scurfy, effuse or immersed, white to pale grey. Apothecia 0.25–0.5 mm diam., very numerous to crowded, emergent to sessile, the disc flat to markedly convex, pale pink to red-brown, translucent when wet, white inside with a brown epithecium; thalline margin very thin, smooth to crenulate, becoming incomplete and excluded, white or pale grey; true exciple often visible, thin, dark brown. Asci 8-spored. Ascospores $10-16 \times (3-) 4-5 \mu m$, narrowly ellipsoidal, 1 (-3)-septate, generally bent when mature. Microconidia $17-20 \times ca 0.5 \mu m$, curved. **BLS 0613**.

On nutrient-rich bark in the *Xanthorion*, especially on *Sambucus*, *Fraxinus* and *Acer*; often common. Throughout Britain and Ireland.

The broader ascospores distinguish *L. cyrtella* from *L. cyrtellina* and *Biatora globulosa*. The very similar *L. sambucina* has predominately 12- to 16-spored asci. The occasional presence of 3-septate ascospores may lead to confusion with *L. suavis* which is always on rock. *Lecania chlorotiza* and *L. cyrtella* have smaller apothecia and narrower ascospores than *Mycobilimbia sphaeroides*. The common *Lecanora persimilis* has aseptate ascospores.



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Host to the lichenicolous fungi *Dacampia cyrtellae* Brackel (2010), *Echinodiscus lesdainii* (Vouaux) Etayo & Diederich (2000) and the plurivorous *Intralichen christiansenii* (D. Hawksw.) D. Hawksw. & M.S. Cole (2002) and *Lichenodiplis lecanorae* (Vouaux) Dyko & D. Hawksw. (1979).

Lecania cyrtellina (Nyl.) Sandst. (1912)

Thallus thin, filmy, continuous, smooth, pale grey. Apothecia pale pink to brown or piebald, translucent when wet, sessile, convex, 0.1–0.2 mm diam., often clustered; thalline margin thin, white when young, true exciple dark; hymenium 30–35 μ m high. Ascospores 8 per ascus, 8–12 (–15) × 2–3 (–4) μ m. Microconidia (12–) 14–16 (–18) × *ca* 0.5 μ m, curved; macroconidia 10–15 (–18) × 1.5 (–2) μ m, 0- to 1-septate, curved, crescent-shaped. **BLS 0614**.

On shaded, base-rich bark in old woodlands, typically in wound tracks, but not associated with the *Xanthorion*; local. Throughout Britain, but under-recorded in some areas, probably predominantly eastern and lowland; rare in Ireland.

Very similar to the common L. cyrtella which has consistently broader ascospores

and is mostly confined to Xanthorion communities. L. chlorotiza also has narrow spores but deeper pink discs and semi-immersed apothecia.

Host to the lichenicolous fungus *Echinodiscus lesdainii* (Vouaux) Etayo & Diederich (2000) as well as the plurivorous *Muellerella lichenicola*.

Lecania dubitans (Nyl.) A.L.Sm. (1918)

Like *L. naegelii* or *L. cyrtella* which have straight, 1- or 3-septate ascospores, but with extremely curved, crescent-like or 'U'-shaped ascospores, $12-14 \times 4-6 \mu m$. **BLS 2388**.

Known only on bark of old Populus tremula; rare. Scotland (E. Highlands).

Lecania erysibe (Ach.) Mudd (1861)

Thallus thin, scurfy, rimose-cracked-areolate, the areoles sharply angled, scattered or contiguous, delimited, not pruinose, margins blastidiate, sometimes very sparsely so; blastidia 70 μ m diam., pale grey to dirty green-brown. Apothecia usually present, to 0.4 mm diam., sessile, scattered, disc orange-brown to brown-black, moderately to strongly convex; thalline margin with granule-like blastidia; true exciple often differentiated; epithecium yellow-green-brown to black-brown; hymenium 50–70 μ m high; paraphyses mostly not widened or slightly clavate at the apices. Ascospores 9–16 × 3–5 μ m, 1-septate, ellipsoidal. **BLS 0616**.

In nutrient-enriched habitats, often near domestic habitation in urban sites, on brick, damp base-rich rocks, asbestos-cement, agriculturally polluted limestones, gravestones, very rarely on decaying wood and bark; often abundant. Throughout Britain and Ireland.

Although frequently fertile, *L. erysibe* is very variable and can form extensive sterile colonies (*e.g.* on gravestones) and is then distinguished by the minutely blastidiate, non-pruinose thallus. Sparsely blastidiate forms occur in which the hymenium and ascospores are similar to *L. inundata*, which has a thicker thallus, or *L. rabenhorstii* which is dark grey-brown with pruinose apothecia. The distinctions between this and sterile forms of *L. coeruleorubella* need further examination. Probably much confused with *L. turicensis* which has a very pruinose thallus.

Lecania fructigena Zahlbr. (1914)

Thallus greyish, light yellowish brown, pale to dark brownish, weakly areolate, usually divided into secondary warts; warts \pm bullate, dispersed, becoming crowded, papillate to \pm subsquamulose, roundish to elliptical, often irregularly constricted at the base; upper surface matt to somewhat shining; prothallus not seen in European material. Apothecia broadly sessile to almost substipitate, 0.5–1 (–1·4) mm diam.; disc \pm flat to slightly concave, red-brown to dark brown; thalline margin entire or more often flexuous or crenulate, 0.1–0.2 mm broad, \pm concolorous with the thallus; hymenium 40–70 µm high; epithecium reddish brown to dark brown; ascospores (0-) 1-septate, 10–15 (–18) × (3–) 4–5 (–5·5) µm, cylindrical to ellipsoidal. Pycnidia numerous, immersed, 75–





DD NR

LC



Nb NR

150 μ m diam., brown near the ostiole; conidia filiform, slightly to strongly curved, 14–24 × *ca* 0.8 μ m. **BLS 2445**.

Coastal, scattered from Cornwall and Wales to Cumbria, S.E. Scotland and the Inner Hebrides, a single record on the E. coast (S. Essex).

Lecania fructigena is easily mistaken for *L. aipospila* especially if the warts or papillae are not well-developed. Both species have a very variable habit with a thallus that may be reduced and rather thin- to thick-papillate. The thallus is typically greyish brown, and terpenoids are absent (see under *L. aipospila*).

Lecania fuscella (Schaer.) Körb. (1855)

Thallus thin, granular, effuse, pale grey-white, containing numerous coarse crystal clusters. Apothecia 0.5–0.8 mm diam., flat, sessile; neatly rounded, disc pale brown to brown-black, naked or patchily white- or blue-pruinose, aggregated into groups; thalline margin thin, persistent; epithecium pale to deep red-brown, K± deep purple-brown, N–; hymenium (45–) 65–70 μ m high; paraphyses 2–2.5 μ m diam., unbranched or forked, apices slightly swollen. Asci 8- to 16-spored. Ascospores 12–22 × 4–6 μ m, 3-septate, straight or slightly bent, fusiform-ellipsoidal with abruptly rounded ends. **BLS 0618**.

On smooth, rarely roughened bark, especially *Acer campestre* and *Populus tremula*; very rare, possibly extinct in Britain. S. England (Gloucester, Kent).

This lichen superficially resembles small-fruited specimens of Lecanora chlarotera.

Lecania granulata Coppins & Fryday (2012)

Thallus whitish to pale buff, densely granular-blastidiate, to 1.5 mm thick; granules 30–80 (–100) μ m diam. Apothecia (0.2–) 0.3–0.7 mm diam., flat or becoming convex and then up to 0.9 mm diam., each developing within a thalline wart and then becoming urceolate with a crenulate thalline margin and concave disc, later expanding further with the thalline margin becoming granulate or receding to reveal a true exciple, and with the disc becoming flat to convex. Disc pale, pinkish or pallid, often with patchy brown pigment towards the margin in older apothecia, with a paler true exciple. Thalline margin 40–60 μ m thick. True exciple 35–60 μ m thick, but not clearly delimited from the hypothecium below, colourless or dilute reddish brown, in the outer half composed of ± radiating hyphae with lumina to 5 × 2.5 μ m, cortical cells 5–6 mm

diam. Hymenium 50–65 μ m tall, colourless or tinged dilute reddish brown in part in older apothecia; epithecium colourless or with patchy dilute reddish brown pigment, especially towards the margin; subhymenium 20–35 μ m tall, K+ dilute yellow; paraphyses unbranched, *ca* 1.5 μ m diam., the upper 2–4 cells gradually widening to 4 (– 6) μ m diam. Hypothecium massive, of irregularly orientated, slender hyphae 1–1.7 μ m diam. Asci narrowly clavate, 53–60 × 9–11 mm, *Bacidia*-type; ascospores narrowly clavate-fusiform to shortly acicular, 20–33 × (2–) 2.5–3 μ m, 3- to 5- (to 7-) septate. Conidiomata not seen. Thallus C–, KC–, K–, Pd–, UV–; no substances detected by TLC. **BLS 2575**.

On peaty soil in coastal habitats, Orkney, Shetland, the Outer Hebrides and E. Inverness-shire.

Lecania granulata has somewhat similar ascospores to *Bacidina subfuscula*, which can also inhabit nutrientenriched coastal turf. *L. granulata* differs in having a thickly granular (blastidiate) thallus and a crenate to granular thalline margin.

Lecania hutchinsiae (Nyl.) A.L. Sm. (1918)

Thallus thin, wide-spreading, continuous or rimose-areolate, \pm effuse or irregularly delimited, the edges white, surface dirty grey, tinged brown. Apothecia 0.3–0.6 mm diam., sessile, mostly single and discrete or in small groups; disc pale pink-brown to dark brown, translucent when wet, at times piebald or paler in shaded habitats, strongly convex even when young, thalline margin becoming excluded, with few photobiont cells with the cortex restricted to the lower edge of the apothecium; true exciple wide, almost colourless; epithecium yellow-brown to colourless; hymenium 40–70 µm high. Ascospores 1-septate, (9–)10–16 × 3–4.5 µm, ellipsoidal. **BLS 1625**.

On siliceous rocks, stones, scattered boulders, etc., often in moderate to deep shade,







Nb

also in old woodlands or scrub especially near the coast; locally frequent. Most records from S.W. and E. England, but recorded widely from the rest of Britain and Ireland.

Very variable but notable for its very convex apothecia, the soon excluded, well-developed true exciple and much reduced thalline margin. Most material is difficult to separate from *L. sylvestris* which occurs on calcareous rock. See also *L. olivacella*.

Host to the plurivorous Intralichen christiansenii.

Lecania inundata (Hepp ex Körb.) M. Mayrhofer (1988)

Thallus of uneven subsquamulose areoles to 2 mm diam., separated by deep cracks, the surface with small pale nodules $50-100 \,\mu$ m diam., more conspicuous when moist, white- to grey-brown, at times becoming green. Apothecia 0.3–0.5 mm diam., sessile, often clustered in small groups, rarely crowded and deformed; disc orange- to blackbrown, becoming translucent when wet, flat to moderately convex, at times strongly convex when old, rarely white-pruinose; thalline margin usually conspicuous, pale grey to pale brown, swollen when young, often fissured, 'pie-crust'-like, with an algalrich medulla and algal-free cortical zone particularly well-developed towards the base of the apothecia, sometimes transformed into an epinecral layer; true exciple sometimes present, the outer cell walls of which may be concolorous with the

epithecium; epithecium pale orange, red-brown to dark brown, rarely black-brown, spotted; paraphyses hardly or slightly swollen towards the apices but with at least some usually swollen, the apical cell distinct, externally brown-pigmented. Ascospores $12-18 \times 5.5-6$ (-7.5) µm, 1-septate. **BLS 1707**.

On limestones, ragstones and other calcareous rocks, also on concrete; common and overlooked until recently. Throughout lowland Britain; few records from Ireland.

Characterized by the uneven areoles with small nodules on the surface. The individual nodules are larger than blastidia, not in chains, and have a smooth upper surface and well-developed algal-free zone which may in part be transformed into a layer of dead cells, rendering them translucent when wet. The papillae of *L. aipospila* are much larger (>1 mm diam.), are not translucent when wet and bear terminal apothecia.

Lecania naegelii (Hepp) Diederich & van den Boom (1994)

Thallus thin, smooth, pale yellow-white to green, usually forming small patches amongst other crustose lichens; photobiont cells $6-16 \mu m$ diam., sparse below the hymenium. Apothecia 0.2–0.6 (–0.8) mm diam., dispersed, flat to convex, disc white, blue- to brown-grey to black, often piebald when wet; thalline margin weakly developed, usually paler than the disc, colourless or with dark brown upper parts, the hyphal cells with expanded, ellipsoidal lumina to 3 μm diam., lined by a darker, persistent true exciple; epithecium colourless or with granules which are pale greybrown to blue-green, K+ intensifying green, N+ red, rarely partly or totally purplebrown and K+ intensifying purple; hymenium 50–65 μm high, colourless; hypothecium colourless; paraphyses 1.5–2 μm diam., unbranched or forked above, the

apices swollen to *ca* 5 μ m diam., often coloured. Ascospores 13–24 (–28) × 4–5 (–6) μ m, (0-)3(-5)-septate, cylindrical to fusiform, often bent. **BLS 0159**.

On nutrient-rich bark and twigs of trees and shrubs, usually in *Xanthorion* communities, very rarely on nutrient-rich rocks; common in areas not polluted with SO₂. Throughout Great Britain and Ireland.

Similar to *L. cyrtella* and in similar habitats, but that species has smaller, usually 1-septate ascospores. The unbranched paraphyses, C– thallus reaction and habitat on nutrient-enriched bark help to separate *L. naegelii* from *Micarea peliocarpa*.

Reese Naeseborg *et al.* (2007) suggested that *L. naegelii* was not part of the main *Lecania* clade, but was perhaps related to *Cliostomum*. More research is needed, but its parasitism by *Echinodiscus lesdainii* supports the placement in *Lecania*.

Host to Echinodiscus lesdainii, Epithamnolia sp. (in apothecia) and the plurivorous Lichenodiplis lecanorae.

Lecania nylanderiana A. Massal. (1856)

Thallus wide-spreading, thin, areolate, the areoles sharply angled, white-grey to pale brown. Apothecia sessile, in crowded heaps, becoming deformed by mutual pressure; disc black, a few red-brown, translucent when wet, with a dark-pigmented pruinose margin; disc mostly flat, rarely convex; thalline margin pale grey, swollen in flat







apothecia, appearing narrow in convex apothecia, inner part algal-rich, cortical zone broad, of netted radiating thread-like hyphae in a gelatinous matrix, particularly well-developed on the lower part and sides of the proper margin; true exciple narrow, the cell walls of the outermost hyphal cells slightly to strongly brown-pigmented; paraphyses swollen towards the apices, the apical 2-3 cells with dark pigmented walls, some with a cap-like deposit of a dark brown pigment. Ascospores 12–16 (–18) × 4–5 μ m, 3-septate, the ends abruptly rounded, thin-walled. **BLS 0619**.

On coastal, mostly vertical or overhanging calcareous rocks, also inland churchyards; rare. A few scattered records from Britain.

Characterized by the flat, black, pruinose apothecia, with a pale persistent margin

and the rather broad ascospores. Often confused with *L. suavis* which also has 3-septate ascospores but differs in having a pseudoparenchymatous outer part to the thalline margin and narrower ascospores, $3-4 \mu m$ diam.

Lecania olivacella (Nyl.) Zahlbr. (1928)

Thallus of scattered scales or areoles, dirty white to yellow-brown, to 0.5 mm diam., resembling squamules. Apothecia to 0.6 mm diam., sessile, numerous to crowded; disc orange-red to dark brown, when moist becoming paler to cinnamon brown, with a dark pigmented edge, flat to moderately convex; thalline margin narrow, regular, white, with an alga-rich medulla and cortical zone of isodiametric cells, overlain by a narrow epinecral layer of dead cells; true exciple narrow, upper part with dark-pigmented walls; hymenium 55–65 μ m high; paraphyses mostly unbranched, the apices slightly swollen and pigmented. Ascospores 11.5–14 × 4.5–6 μ m, 1-septate, thin-walled. **BLS 1870**.

On siliceous rocks; known from a single 19_{th} century collection. S.W. England (Devon, Torpoint).

Morphologically similar to *L. hutchinsiae*, but the thallus is thicker, scaly-areolate, and the apothecia have a persistent thalline margin.

Lecania poeltii van den Boom, Alonso & Egea (1996)

Thallus crustose, consisting of closely scattered to contiguous areoles, the upper surface vertucose or granular-vertucose, the granules $50-100 (-200) \mu m$ diam. and sometimes flattened, grey to greyish-brown, matt. Areoles

angular, 0.3–1 (–1.5) mm diam., covered with minute hairs arising from the granules. Hairs 30–60 \times 5–7 (–8) μ m, sometimes branched, straight or slightly curved, colourless, with a \pm granulate surface, with a distinct, strongly gelatinized wall below, becoming thinner-walled above and tapering to a point. Thallus to 300 μ m thick, the cortex overlain by a colourless epineeral layer. Apothecia roundish to \pm irregular, (0.2–) 0.3–1 mm diam., scattered or three to five together, sessile, constricted at the base, bordered by a relatively thick and conspicuous persistent, mostly finely hairy,

thalline margin; disc pale to dark brown, concave at first, later becoming flat; true exciple pale to reddish brown, K+ purplish; epithecium pale to reddish brown, K+ purplish; hymenium colourless, 45–60 (–70) μ m tall, I+ blue; hypothecium colourless, to 50 μ m tall; paraphyses unbranched or sparsely branched toward the apices, apical cells swollen, to 5 μ m diam., and sometimes with a thin internal reddish brown pigmentation. Asci clavate, 30–40 (–45) × 10–12 um, 8-spored, with an I+ blue outer coat and a blue apical dome (*Bacidia*-type). Ascospores colourless, ellipsoidal, (7–) 9–12 × (3.5–) 4–5 μ m, 1-septate, thin-walled. Pycnidia immersed. Conidia aseptate, 11–17 × 0.8–1 μ m, filiform, curved. Thallus K–, C–, KC–, PD–, I–. **BLS 2549**.

Known from a single collection from siliceous rock on Skellig Michael, off S.W. Ireland. Collections elsewhere have been on branches in dry habitats.

The species is unique amongst the genus in having a minutely hairy thallus and apothecial margin.

Lecania rabenhorstii (Hepp) Arnold (1888)

Thallus usually in orbicular patches, thick, of contiguous, angular areoles, the edges often curling upwards; surface dark, yellow-grey-brown, lumpy, at times with small, scattered angular or lobe-like fragments; cortex of isodiametric cells, overlain by a well-developed epinecral layer. Apothecia to 0.7 mm diam., sessile, in parts numerous and covering areoles, rarely deformed; disc pruinose, orange to warm red-brown and black-spotted

Ex





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NE

when wet, flat or rarely convex; thalline margin yellow-white, strongly contrasting with the disc, not swollen, becoming excluded only in strongly convex apothecia; true exciple poorly developed, narrow, upper part brown; epithecium mottled pale brownorange to dark brown; hymenium 65–85 µm high, with a thick photobiont layer below; paraphyses mostly not or slightly swollen towards the apices, a few strongly swollen to ca 6 µm diam., mostly colourless, a few with an external yellow-brown deposit on the outer cell wall of the terminal 1–2 cells. Ascospores 11–13 (–16) \times 4–7 μ m, 1septate, thin-walled. BLS 1708.

On base-rich rocks, limestone, etc.; common. Throughout Britain, predominately lowland: scarce in Ireland.

L. turicensis is the other common pruinose species on base-rich rocks, but has a white to pale grey, smooth thallus, crowded apothecia and pruina usually restricted to the discs. Lecania inundata has a similar anatomy, but has distinctly nodulose areoles with less numerous pruinose apothecia, usually in groups.

Host to the plurivorous Intralichen christiansenii.

Lecania sambucina (Körb.) Arnold (1884)

Like L. cyrtella but with 16 ascospores per ascus. BLS 2340.

On trunks of mature Populus tremula in Populus-Betula-Juniperus pasture woodland in the E. Highlands (Speyside, Deeside); rare. A single record from N. Ireland (Fermanagh) needs confirmation.

Lecania suavis (Müll. Arg.) Mig. (1926)

Thallus of flat to convex areoles or warts, rarely continuous, areoles raised at the edges, <0.5 mm diam.; upper surface warted, smooth, yellow-white to red-brown or dark brown, becoming paler when moist, at times with a dark pigmented edge, flat, convex to semi-globose, irregular, at times pruinose; thalline margin black, partly swollen, becoming excluded in strongly convex apothecia, concolorous with the disc, with photobiont below and a well differentiated cortex of isodiametric cells, the outer layers with thicker, slightly swollen margins, overlain by an epinecral layer, the cortex particularly well-developed at the sides of apothecia; true exciple of elongate, thickly conglutinate hyphal cells, the cell walls deeply pigmented including those deep within the apothecium; epithecium orange to dark brown, slightly mottled; hymenium 45–65

 μ m high, at times brown; paraphyses strongly swollen towards the apices (to 8–10 μ m diam.), the terminal 2-4 cells with brown-pigmented walls. As cospores $13-20 \times (3-) 4-4.5 \mu m$, 3-septate, thin-walled, fusiform. BLS 1760.

On calcareous or at least nutrient-rich vertical rock surfaces and below overhangs; local. Few records, scattered throughout Britain, most records made in Norfolk.

The commonest Lecania on rock with 3-septate ascospores. Typically of rounded warts with apothecia varying from moderately convex with a distinct thalline margin, to strongly convex with an excluded margin. See also L. nylanderiana.

Lecania sylvestris (Arnold) Arnold (1884)

Very similar to L. hutchinsiae, but the thallus mostly immersed or thin and inconspicuous, granular-uneven or as a few scattered areoles, often following fine crevices. Apothecia orange to dark brown, translucent with a darker excipular zone apparent when wet. BLS 1761.

On shaded chalk pebbles and limestones; widespread but rare in Britain and Ireland. A collection from S.W. Ireland is host to Echinodiscus lesdainii (Vouaux) Etayo & Diederich (2000).

Lecania turicensis (Hepp) Müll. Arg. (1862)

Thallus thin, granular to areolate, white to pink-white or grey, usually pruinose, of rimose areoles separated by deep cracks; cortical zone of isodiametric cells overlain by an epinecral layer, densely white-pruinose. Apothecia to 0.8 mm diam., sessile, plane, numerous, often thickly crowded and deformed; disc red-brown to black, when moist becoming paler, with a dark pigmented edge, pale grey- to white-pruinose; thalline margin narrow, white,

Nb

Nb



LC



often becoming excluded, with photobiont below and in part with a narrow, alga-free cortical zone, at times overlain by a thick crystalline layer; hymenium 55–80 μ m high, occasionally partly pigmented like the epithecium; paraphyses unbranched, strongly swollen to 6 μ m diam. towards the apices, the terminal 1–3 cells with external pigmentation. Ascospores 10.5–13 × 4.5–6 μ m, 1-septate, thin-walled, occasionally slightly pigmented. **BLS 1691**.



On calcareous and non-calcareous rocks, also mortar; frequent throughout Britain especially in the south, rare in eastern Ireland.

On limestone the thallus is mostly continuous, areolate, with a densely pruinose upper surface; on non-calcareous rocks the areoles are often more scattered and may

lack pruina. Well-developed morphs have a tumid, small-lobulate thallus that is often densely white-pruinose. *Lecania atrynoides* has non-pruinose apothecia which are speckled brown, and in *L. rabenhorstii* the pruina is restricted to the disc.

MEGALARIA Hafellner (1984)

Thallus crustose, without a distinct cortex, continuous to granular. **Photobiont** *Dictyochloropsis* and possibly other unicellular genera. **Ascomata** apothecia, sessile, black, relatively large. **Thalline margin** absent. **True exciple** persistent, of anticlinally arranged hyphae, each with a thick gel coat. **Hymenium** colourless to pale brown. **Epithecium** with K+ intensifying greenish to dark purple pigments. **Hypothecium** often also pigmented with K+ intensifying greenish to dark purple but sometimes only pale colours. **Hamathecium** of numerous slender paraphyses, unbranched or sparingly branched; apices clavate, without dark apical caps. **Asci** cylindric-clavate, (2-) 8-spored, *Lecanora-*, *Bacidia-* or *Biatora-*type with a broad, non-amyloid apical cushion and a distinct ocular chamber. **Ascospores** \pm ellipsoidal, 1-septate, colourless, thick-walled, smooth, lacking a distinct outer sheath. **Conidiomata** pycnidia. **Conidia** ellipsoidal to cylindrical, aseptate, colourless. **Chemistry**: products not detected by TLC, or in some species atranorin, zeorin and fumarprotocetraric acid. **Ecology**: on bark, rarely on rock or soil.

Megalaria forms a distinct, well-supported clade within the Ramalinaceae according to Kistenich *et al.* (2018), and was placed in the separate family Megalariaceae by Hafellner (1984). The genus *Catillochroma* was split from *Megalaria* by Kalb (2007) with the new genus distinguished by the presence of a two-layered exciple and the production of zeorin, but the separation has not been universally accepted. *Megalaria pulverea* belongs to this taxon.

Distinguished from *Catillaria* and *Catinaria* by the presence of a well-developed axial body in the ascus tip, absence of dark brown apical caps on the paraphyses and from *Catinaria* also by the green or purple pigments in the epithecium and smooth-walled ascospores.

Literature:

Ekman & Tønsberg (1996), Fryday & Lendemer (2010), Hafellner (1984), Kalb (2007), Kistenich *et al.* (2018), McMullin & Lendemer (2016), Sanderson (2009).

1	Thallus smooth; hypothecium with K+ intensifying green or purple pigments	2
	Thallus granular to sorediate; hypothecium colourless or pale brown, K	pulverea
2 (1)	Exciple black, glossy; ascospores $20-30 \times 10-15$ µm	
-(-)	Exciple grey-black, matt; ascospores $12-18 \times 5-7 \ \mu m$	laureri

Megalaria grossa (Pers. ex Nyl.) Hafellner (1984)

Thallus effuse, \pm smooth or slightly verrucose, often rimose, greenish-white to pale grey; photobiont cells 5–15 µm diam. Apothecia 0.4–1.5 (–2) mm diam.; disc flat to convex, matt; true exciple persistent, black, raised, glossy; inner part colourless, of anticlinally arranged hyphae, each with a thick gel coat; epithecium, hypothecium and outer exciple bluish to greenish black, K+ green intensifying, N+ purple-red; hymenium 120–140 µm tall, usually colourless but this and the hypothecium sometimes with additional reddish (K+ purple-red) pigment (especially in old apothecia); paraphyses 1.5–2 µm diam., tips clavate, 3–4 µm diam. Asci *Lecanora*-type with a broad, non-amyloid apical cushion and a shallow ocular chamber. Ascospores 20–30 × 10–15 µm, ellipsoidal to cylindric-ellipsoidal, often slightly



constricted at the septum, wall 1–2 µm thick. Pycnidia 100–120 µm diam., inconspicuous, immersed; wall colourless or pale greenish in upper parts; conidiogenous cells $10-15 \times 1-1.5$ µm, ± cylindrical; conidia $3-4 \times 1.5-2$ µm. Thallus C–, K–, Pd–, UV–. **BLS 0323**.

On base-rich bark of usually mature trees (especially *Fraxinus* and *Populus tremula*), sometimes on younger or small trees (e.g. *Corylus*), usually in old, humid woodlands, very rarely on basic rocks; rather rare and local. Mainly in N. & W. Britain and Ireland, much declined and now only frequent in the Scottish Highlands and locally in W. Ireland.

Usually recognizable in the field by the contrasting pale thallus and rather large black sessile apothecia with a minutely roughened disc and shiny raised exciple. Like a large form of *Lecidella elaeochroma*, which is C+ orange.

Megalaria laureri (Hepp ex Th. Fr.) Hafellner (1993)

Thallus whitish to grey-green, rimose, thin and smooth, or to 150 μ m thick with a granular-warted surface; prothallus black, delimiting; photobiont cells 6–14 μ m diam. Apothecia 0.4–1.1 mm diam.; disc flat to slightly convex; true exciple shallow, often paler than the disc, colourless or sometimes brownish (concolorous with the epithecium) at the upper outer edge, at base of apothecium often concolorous with the hypothecium, swelling in K, the hyphae distinctly radiating, branched and anastomosing, 1.5–2 μ m diam., without swollen ends; epithecium dark purple-brown, K+ purplish, N+ red, sometimes with additional patches of greenish, K+ green, N+ red pigment; hymenium 65–80 μ m tall, colourless to pale purple brownish; hypothecium purple-red, K+ purple in the upper part (subhymenium); lower part pale golden-brown,

K-; paraphyses $1.3-1.7 \mu m$ diam., unbranched, the apices clavate to $3 \mu m$ diam., cemented by adhering pigment. Asci *Bacidia*-type, with a distinct apical cushion. Ascospores $12-18 \times 5-7 \mu m$, ellipsoidal to fusiform-ellipsoidal. Pycnidia not found. Thallus C-, K+ pale yellow, Pd-, UV-. **BLS 0324**.

On trunks of old *Fagus* in rain tracks in old growth woods, an old record from *Quercus*; very rare. S. England (Hampshire, New Forest), formerly Ireland (Killarney). This species is very rare in Britain and should not be collected.

Superficially resembles some morphs of the common *Lecidella elaeochroma*, which can be readily distinguished using chemical reactions. The pale margin contrasting with the darker disk is distinctive when well-developed, but morphs with less contrasting margins exist and are more difficult to pick out.

Megalaria pulverea (Borrer) Hafellner & E. Schreiner (1992)

Thallus effuse, thin, \pm evanescent; soralia large, effuse, grey-white to glaucous, granular, sometimes coalescing to form an almost continuous sorediate crust; soralia-soredia grey-green, bluish or yellowish green, 40–100 µm diam.; photobiont cells 5–14 µm diam. Apothecia 0.5–2.2 mm diam., rare, flat, sometimes convex and contorted, black; true exciple distinct, colourless or pale brownish in the upper part, sometimes concolorous with the epithecium at the upper outer edge, the hyphae coherent in K, 2–3 µm diam., each with a thick gel coat; epithecium dark green, K+ green intensifying, N+ red, sometimes with additional violet K+ green patches; hymenium 45–75 µm tall, colourless; hypothecium (and exciple) colourless, or pale brown in uppermost and/or lowermost parts, with minute, colourless crystals that do not



dissolve in K or N; paraphyses 1.8-2 (-2.5) µm diam., the apices clavate, 3-4 µm diam., surrounded by dark



pigment. Asci *Bacidia*- or *Biatora*-type, the apical cushion narrow, \pm surrounded by a thin, dark blue zone. Ascospores 10–16 (–19) × 4.5–6.5 µm, broadly to fusiform-ellipsoidal, the walls rather thick; epispore absent. Pycnidia not seen. Thallus K+ yellow, K/UV (dry)+ bright yellow, Pd+ red, often Pd– or faint yellow, UV– (atranorin, zeorin and usually fumarprotocetraric acid). **BLS 0318**.

On generally rather acidic, mossy trunks (rarely branches) in old, moist woodlands, occasionally on mossy rocks and soil (especially near the coast), or old *Calluna*. Western and southern parts of Britain and western Ireland, extending east locally.

Usually sterile, when it can be confused with *Megalospora tuberculosa*, *Phyllopsora rosei* or thickly sorediate morphs of *Violella fucata*. The Pd– forms are especially difficult to separate from *Megalospora tuberculosa*, which contains usnic acid but not atranorin. The new K/UV+ spot test for atranorin, however, solves this problem; *M. pulverea* reacts K/UV (dry)+ bright yellow, even on problematic Pd– thalli, while *Megalospora tuberculosa* thalli react K/UV (dry)–.

A recently collected specimen with an identical thallus and spot tests but with orange-brown apothecia, with the dark green epithecial pigment replaced by an orange-brown pigment, and significantly larger spores, $17-22 \times 7-8 \mu m$, may be an overlooked and normally sterile cryptic taxon.

Host to undidentified species of Capronia and Merismatium as well as Spirographa fusisporella s. lat.

MYCOBILIMBIA Rehm (1889)

Thallus crustose, effuse, sometimes membranous in part, mostly rimose, creamy white, dull green, glaucous green or green-grey; \pm ecorticate, sometimes sorediate; prothallus absent. Photobiont chlorococcoid. Ascomata apothecia, biatorine, sessile or appressed, usually weakly to strongly convex and immarginate, or at first with a flat disc and a shallow margin, light beige to dark reddish brown or khaki, margin soon excluded. True exciple composed of radiating branched and anastomosing hyphae. Hymenium 60-90 µm tall, most (and all British) species without a welldefined epithecium (sometimes with pale pigmentation in the upper part), granules or oil droplets, I+ red-brown when young, blue in older dried collections. Subhymenium distinct, somewhat opaque due to presence of ascogeneous hyphae, often slightly darker than the hymenium. Hypothecium chondroid, of interwoven hyphae, with lumina $1-2 \,\mu m$ diam. in a dense gel matrix. Hamathecium of coherent (in K) paraphyses, with lumina $0.5-2.5 \,\mu$ m diam., unbranched or sparingly branched, only rarely anastomosed, the apices slightly swollen (lumina to 5 µm diam.), never surmounted by a distinct apical 'cap' or 'hood'. Asci 8-spored, cylindric-clavate, lateral walls 0.7-1 µm broad, Biatoratype with a K/I+ blue apical dome penetrated from below by a narrow, K/I- apical cushion surrounded by a narrow, deeply K/I+ blue zone, wall K/I- but surrounded by a I+ red-brown, K/I+ blue outer layer, ocular chamber relatively small. Ascospores colourless, ellipsoidal or cylindrical to filiform or cylindric-fusiform, (0-) 1- to 3-septate, smooth, without a distinct perispore. **Conidiomata** not known. Chemistry: without secondary metabolites detectable by TLC. Ecology: on somewhat acidic, organic substrata but avoiding extreme acid or calcareous conditions and in relatively undisturbed habitats. Some species on bryophytes over rocks or tree-trunks, bark of old trees or rotten bark at the base of old trees.

Biatora has a different apothecial ontogeny and most species have a secondary chemistry. *Bilimbia* is similar but has thick-walled asci, broader paraphyses and ascospores with a warted perispore. Species of *Bryobilimbia* (formerly the *Lecidea hypnorum* group) have a *Porpidia*-type ascus and a dark brown or olivaceous brown hypothecium.

Fryday et al. (2014), Kistenich et al. (2018), Printzen (2014), Printzen et al. (2009), Reese Naesborg et al. (2007).

See also under Biatora for a key to the species of both genera

1	Thallus with effuse, pale greenish or yellowish soralia; often sterile Thallus without soralia; mostly fertile	epixanthoides
2 (1)	Ascospores mostly 0- to 1-septate (rarely a few 2- to 3-septate) Ascospores at least mostly multiseptate	sphaeroides
3 (2)	Apothecia grey- to dark (± reddish) brown, with reddish brown pigment in the hymenium and/or upper exciple in section	tetramera carneoalbida

Mycobilimbia carneoalbida (Müll. Arg.) S. Ekman & Printzen (2004)

Thallus pale greenish, granular-verrucose, not sorediate; areoles 50-200 μ m diam. Apothecia 0.5–1.0 mm diam., flat to ± globose, old ones often tuberculate, sessile with a constricted base, whitish to pale orange-brown, matt; margin not or only weakly prominent, slightly paler than the disc; true exciple colourless, 60–80 μ m thick; hymenium 60–75 μ m high, colourless; subhymenium 35–55 μ m high; hypothecium 120–240 μ m high, colourless. Ascospores 13–22 × 4–6 μ m, (0-) 3-septate, ellipsoidal. Lichen substances not detected by TLC. **BLS 1653**.

On mosses on rock in a gully at 1160 m; rare. C. Scotland (Perthshire, Ben Lawers), the only British locality.

M. sphaeroides and Biatora vernalis differ in the predominantly 0- to 1-septate

ascospores. The two are old woodland species and are widely distributed in W. Britain. *M. tetramera* has slightly larger ascospores and a pigmented inner exciple and hypothecium.

Mycobilimbia epixanthoides (Nyl.) Vitik., Ahti, Kuusinen, Lommi & T. Ulvinen ex Hafellner & Türk (2001)

Thallus granular-verrucose, sorediate, pale grey- or yellowish green; soralia effuse, often confluent and thallus more or less leprose. Apothecia often absent, 0.4–1.0 mm diam., weakly to strongly convex, sessile with a constricted base, grey- to red-brown; margin not or weakly prominent, paler than the disc, soon excluded; true exciple colourless outside, pinkish brown within and near hymenium, *ca* 70 µm thick; hymenium 50–90 µm high, colourless, sometimes with brown spots; subhymenium 30–85 µm high; hypothecium 200–300 µm high, colourless. Ascospores (12.5–) 15– $25 \times (4-) 4.5-7 \mu m$, (1-) 3-septate, ellipsoidal. Lichen substances not detected by TLC. **BLS 0146**.

Over bryophytes and base-rich bark of mossy trunks of old deciduous trees in

ancient woodlands, rarely on mossy rocks in wooded ravines; local. Often found on the same trees as *M. sphaeroides* but is generally more frequent than this species in woods where both are found but is overlooked as usually sterile. N. & S.W. Britain and the more wooded areas of Ireland.

Biatora chrysantha is distinguished by a C+ red reaction of thallus and soralia.

Host to Sclerococcum parasitaster (Nyl.) Ertx & Diederich (2018) and an unidentified Stigmidium sp.

Mycobilimbia sphaeroides (Dicks.) S. Ekman & Printzen (2021)

Mycobilimbia pilularis (Körb.) Hafellner & Türk (2001)

Thallus granular, not sorediate but granules often so fine as to resemble soredia, $25-70 \mu m$ diam., surface greygreen, matt. Apothecia 0.4–0.8 (–1.1) mm diam., moderately convex to \pm globose, sessile with a constricted base, orange-pink to dull ochre, matt; margin slightly prominent when young, paler than the disc, soon excluded; true





LC

exciple colourless, $50-135 \,\mu\text{m}$ thick; hymenium $55-70 \,\mu\text{m}$ high, colourless or weakly orange-brown in apical parts; subhymenium $50-85 \,\mu\text{m}$ high, colourless; hypothecium $100-250 \,\mu\text{m}$ high, colourless; epithecium lacking. Ascospores (9.5–) $11.5-14 \,(-17) \times (3-) \, 4-4.5 \,(-5) \,\mu\text{m}$, (0-)1(-3)-septate, fusiform-ellipsoidal. Lichen substances not detected by TLC. **BLS 0320**.

On sheltered, mature deciduous base-rich tree trunks (especially *Fraxinus* and *Quercus*), often around their bases, in old woodlands, more rarely on mossy rocks in wooded ravines or sheltered mountain gullies; local. Ireland, N. & W. Britain, extending eastwards to S. England (E. Sussex).

Distinguished from *Biatora vernalis* by a more finely granular thallus, predominantly 1-septate ascospores and young apothecia with a conspicuous pale margin. *Lecania chlorotiza* and *L. cyrtella* have smaller apothecia and narrower ascospores. Host to *Sclerococcum parasitaster* (Nyl.) Ertx & Diederich (2018).

Mycobilimbia tetramera (De Not.) Vitik., Ahti, Kuusinen, Lommi & T. Ulvinen ex Hafellner & Türk (2001) VU (D1, 2)

Thallus granular-verrucose, not sorediate, greyish green. Apothecia 0.4–1.3 mm diam., flat to strongly convex, sessile with a markedly constricted base, grey- to red-brown; margin not or only weakly prominent, paler than the disc, excluded in old apothecia; true exciple colourless or in places reddish brown, 65–95 μ m thick; hymenium 70–100 μ m high, colourless or brownish in apical parts; subhymenium 70–85 μ m high; hypothecium 110–240 μ m high, colourless or upper part reddish brown. Ascospores (15.5–) 17–22 (–26) × (4.5–) 5–7 (–7.5) μ m, (0-)3-septate, ellipsoidal to fusiform. Lichen substances not detected by TLC. **BLS 0160**.

On bryophytes, small shrubs and detritus on or amongst rocks in montane situations above 1000 m; rare. Scotland (Highlands).

Distinguished from *M. epixanthoides* by the non-sorediate thallus and from *M. carneoalbida* by the darker apothecia. Pale morphs of *Bilimbia sabuletorum* differ in their stouter paraphyses and often longer, 3- to 7(-9)-septate ascospores with a finely warted perispore. *Bacidia fuscoviridis* has stouter hyphae in the true exciple and grows on rock at low altitudes.

PHYLLOPSORA Müll. Arg. (1894)

Thallus crustose to squamulose, often pubescent, squamules usually corticate; prothallus usually distinct, white or reddish brown. **Photobiont** trebouxioid. **Ascomata** apothecia, convex and often tuberculate, disc often deeply fissured, pale to dark reddish brown, never greenish or purplish in K, not pruinose. **Thalline margin** absent. **True exciple** often inconspicuous except occasionally when young, of radially orientated thick-walled gelatinized hyphae, some extending outwards into the thallus. **Epithecium** poorly differentiated. **Hymenium** I– or faintly blue. **Hypothecium** massive, pale, of gelatinized interwoven narrow hyphae. **Hamathecium** of paraphyses, unbranched or sparingly branched, short-celled, each surrounded by a gel coat, apices not swollen, colourless. **Asci** 8-spored, clavate, *Bacidia*-type. **Ascospores** aseptate or thinly septate, ellipsoidal to narrowly fusiform, colourless, without a thick perispore. **Conidiomata** pycnidia, resembling incipient apothecia. **Conidia** bacillar, colourless, aseptate. **Chemistry**: β -orcinol depsides and depsidones, zeorin and other terpenoids, and fatty acids. **Ecology**: on bark.

Similar to and the phylogenetic sister of *Biatora*, but differing in the pubescent-squamulose thallus, the presence of a usually distinct prothallus and in the slightly different ascus structure. This large, mainly subtropical/tropical genus has recently been shown to be polyphyletic, its apparently diagnostic thallus form having evolved on several occasions. There is only one British and Irish species.

VU (D1, 2)



Literature

Kistenich et al. (2018, 2019a,b), Rose et al. (2009).

Phyllopsora rosei Coppins & P. James (1979)

Thallus of pubescent squamulose granules, or sometimes larger squamules at the thallus edge, forming a \pm thick, uneven pale grey- to blue-green crust to 5 cm or more diam., granules 50–150 µm diam., squamules flattened, crenate to \pm fingerlike, 0.15–0.3 mm broad, weakly corticate; prothallus whitish, cottony, sometimes obscured in thick thalli; photobiont cells 9–15 µm diam. Apothecia 0.3–1.5 mm diam., often absent, convex, often clustered or tuberculate, pale orange- to deep red-brown; true exciple inconspicuous except in some young apothecia, concolorous with or paler than the disc, colourless or red-brownish in section; hymenium 20–30 µm tall, colourless or tinged red to brownish above; hypothecium 200–230 µm tall, colourless or red-brownish in parts; paraphyses mostly aseptate, 2–3 µm diam., apical cell \pm tapered.



Asci $20-26 \times 7-9 \ \mu\text{m}$. Ascospores (7–) $10-13 \ (-15) \times 2-3 \ (-4) \ \mu\text{m}$, aseptate or thinly 1(-3)-septate, narrowly ellipsoidal to shortly fusiform. Pycnidia not known. Thallus C–, K± faintly yellow, K/UV–, KC–, Pd+ red (argopsin). **BLS 1111**.

On mature tree trunks, especially *Quercus*, often overgrowing mosses, characteristic of oceanic, rather 'acidic' *Lobarion* communities in old woodlands and sheltered stream valleys; local. S. England east to Hampshire (New Forest), northwards in W. Britain from Cornwall to C. Scotland (Westerness), very local in Ireland, mainly recorded from the S.W., Connemara and the Wicklow Mountains.

When sterile, it has been frequently confused with *Megalaria pulverea*, from which it can be distinguished by the presence of minute squamules (at least at the edge of the thallus) and the lack of atranorin (the latter can be detected in *M. pulverea* by the K/UV(dry)+ bright yellow spot test). Other similar sterile crusts in such habitats also lack squamules and are all Pd–, e.g. *Biatora chrysantha*, *B. vernalis*, *Megalospora tuberculosa* and *Mycobilimbia epixanthoides*.

RAMALINA Ach. (1809)

Thallus shrubby, often tufted, erect to pendent, lobes sprouting from a restricted or spreading holdfast, rarely unattached and free-living; branches single to numerous, branching dichotomous to irregular, rarely palmate, often markedly compressed and strap-shaped though not dorsiventral, rarely rounded or bilaterally symmetrical in cross section, sometimes channelled, occasionally with fenestrations, papillae and pseudocyphellae, smooth or ridged. Cortex thin, indistinct, overlying a well-developed cylindrical zone of intertwined hyphae (absent in R. lacera), invaded by the photobiont zone on its inner side. **Photobiont** trebouxioid. **Medulla** usually lax and arachnoid, rarely dense and opaque, sometimes completely absent in hollow branches. Soralia frequent, sometimes with isidium-like granules. Ascomata apothecia, shortly stalked, apical or subapical, often on the bends of angled branches, concave to plane or convex with age; disc pale yellow, pale green, brown or pink-yellow, sometimes white-pruinose. Thalline margin present, persistent to almost excluded. Asci elongate-clavate, Bacidia-type, 8-spored. Ascospores 1-septate, broadly ellipsoidal or kidneyshaped, colourless. Conidiomata pycnidia; ostiole pale or blackened. Conidiogenous cells \pm cylindrical. Conidia bacillar, colourless, aseptate. Chemistry: usnic acid, often with depsides, depsidones and aliphatic compounds. Ecology: predominantly corticolous but frequently saxicolous in oceanic climates.

Separated from *Evernia* and *Pseudevernia* which have the photobiont restricted to one (upper) surface of a dorsiventral thallus, and lack cartilaginous tissue in the subcortex. *Ramalina lacera* may occasionally have a paler lower surface, but is never white as in that of *Evernia*.

Literature

Aptroot & Schumm (2008), Fletcher *et al.* (2009b), Gasparyan *et al.* (2017), Kistenich *et al.* (2018), Krog & James (1977), Krog & Østhagen (1980), LaGreca *et al.* (2020), Spjut *et al.* (2020).

1	Thallus thread-like (often <0.5 mm diam.), often detached and entwined; lateral branches with hook-shaped ends; soredia absent
2 (1)	Branches hollow, particularly in older parts
3 (2)	Soredia absent; apothecia usually present
4 (3)	Main branches ± rounded, <1.5 mm wide; soralia apical and lip-shaped, or as laminal ruptures in the cortex; Pd+ orange, K+ orange-red
5 (2)	Soredia or coarse corticate granules present; apothecia rare
6 (5)	With coarse isidium-like smooth corticate spherical granules 60–180 µm diam., singly or clustered in numerous small elliptical laminal pseudocyphellae; thallus prostrate; on rocks
7 (6)	Soralia on tips of upright lobes, umbel-like; thallus very short, <1.5 cm high
8 (7)	Upper and lower cortex not splitting to reveal soredia (soredia superficial in discrete soralia)
9 (8)	Soralia oval or round, strictly delimited
10 (9)	Holdfast spreading, usually forming extensive swards; soredia ± granular in flat or excavate soralia; usually on rocks
11(9)	Branches >1 cm wide, conspicuously compressed, or irregularly divided; surface smooth or with reticulate ridges, especially on the lower surface, matt <i>lacera</i> Branches <0.5 cm wide; sometimes terete; surface without reticulate ridges, cartilaginous, ± shiny <i>pollinaria</i>
12 (5)	On rocks (rarely on wood or bark); chemical reactions various
13 (12)	Main branches often conspicuously compressed; surface often ridged; thallus not or rarely little-blackened at the base; ostioles of pycnidia pale

- 14(12) Branches distinctly channelled, especially towards their base; surface \pm smooth; branches
- 15(14) Thallus in \pm erect tufts, to 5 cm, often obscured by numerous apical apothecia; lobes 3-8 mm wide, rounded, inflatedfastigiata Thallus pendent, to 20 cm; apothecia, if present, lateral; lobes to 1-4 cm wide, strap-likefraxinea

Ramalina calicaris (L.) Fr. (1824)

Thallus 5-8 (-15) cm long, in coarse upright tufts, becoming pendent when old, pale grey-green, stiff and spiky when dry; branches 2-3 (-10) mm wide, usually distinctly channelled, especially towards the base, surface shiny, smooth, texture hard and hornlike; pseudocyphellae variable in frequency, whitish, fusiform to narrowly elliptical. Apothecia frequent, marginal, subterminal, on the bends of angled branches. Ascospores 10–16 × 5–7 µm, broadly ellipsoidal, straight. Medulla C-, K-, KC-, Pd-, UV- (usnic acid; sekikaic acid complex sometimes present). BLS 1231.

On branches and twigs, especially of trees and shrubs with nutrient-rich bark, rarer on tree trunks, often near the coast in well-lit situations; locally abundant. W. Britain and Ireland, extending locally to E. Scotland & S.E. England.

The number and width of branches vary. Specimens restricted to a few broad, poorly developed branches, to 10 mm wide, can be confused with R. fraxinea and straggling morphs may resemble R. fastigiata; the overall tough texture of the thallus, the channelling of the main branches, especially towards their base, and the elliptical to fusiform pseudocyphellae are diagnostic.

Host to an undidentified *Didymocyrtis* sp. and the plurivorous *Marchandiomyces corallinus*.

Ramalina canariensis J. Steiner (1904)

Thallus to 3 cm long, forming pulvinate to ragged tufts, scattered or forming swards; branches 2-8 mm wide, pale grey-green or dull green, matt, markedly broadening from the base, sometimes tapered towards the apices, flattened, internally solid with a lax cottony medulla or hollow in older parts, with a tough cartilaginous subcortex; soralia lateral or sub-terminal, mostly near the apices, in ruptured helmet-shaped vesicles or released from irregular lacerations of the cortex, usually visible through holes; soredia 20-40 µm diam., farinose. Apothecia very rare, marginal or on the lobe surface. Ascospores $15-21 \times ca$ 6 µm, broadly ellipsoidal or kidney-shaped. Medulla and soralia C-, K-, KC-, Pd-, UV± blue-white (usnic and divaricatic acids). BLS 1230.

On nutrient-rich bark in well-lit situations, also on rocks below dry overhangs and sheltered walls, rather common in Britain and Ireland, but in the North predominantly coastal.

A variable species, ranging from a single palmate lobe to a dense eroded ragged cluster of lacerate-contorted branches. Soredia are often in subterminal inflated vesicles. Eroded specimens, especially when on rocks, can resemble R. lacera, a superficially similar but apparently unrelated species (Spjut et al. 2020). R. lacera lacks a cartilaginous subcortex, has soredia on the surface and a different chemistry. See also R. pollinaria.

Host to the lichenicolous fungus Tremella tuckerae Diederich (2007).

Ramalina capitata (Ach.) Nyl. (1879)

Thallus small, erect, 10–15 mm high, arising from a single holdfast, lobes flat, sometimes divided into fan-like branches, 1-3 mm wide, surface tough, horn-like, longitudinally striate with narrow slit-like lacunae, lacking obvious pseudocyphellae; subcortex cartilaginous; medulla solid; soralia granular, discrete, on the underside of lobe ends, appearing at one level on all lobes of the tuft (appearing umbel-like), lobe ends fanning and recurving backwards when exposed to the light. Usnic acid only. BLS 1390.

On gritstone tombs (rarely on Fraxinus) in Lincolnshire and Yorkshire, also a 19th century record from coastal rocks in Aberdeenshire.

The apical soralia on short lobes are distinctive. Much confused with the much





LC

Nb

longer lobes of *R. polymorpha*, which has laminal, spherical isidium-like granules scattered along lines of pseudocyphellae. Recently shown to be genetically distinct from, but closely related to, *R. polymorpha* (Marthinsen *et al.* 2019; Spjut *et al.* 2020).

Ramalina chondrina J. Steiner (1904)

Thalli in dense tufts or scattered fragments to 5 cm long, pendent or decumbent, arising from a narrow holdfast, or often detached and entwined around other shrubby lichens; branches cylindrical, thread-like (0.1–0.3 mm diam.), finely pointed and hook-tipped, mainly richly dichotomously branched, pale green-grey, often discolouring with black patches and black base, smooth, weakly foveolate, with indistinct tiny white pseudocyphellae; cartilaginous subcortex present, medulla solid. Apothecia not observed in British material. Usnic acid only. **BLS 1696**.

On coastal rocks, and also dead tufts of *Armeria*; nationally rare. S.W. Britain and the Isles of Scilly.

Closely resembling an *Alectoria* except for the presence of a cartilaginous \square \square \square \square \square subcortex, hook-tipped lobe ends and absence of chemical products except usnic acid. At one time, not uncommon locally on exposed steep N- to N.W.-facing granite cliffs on the Isles of Scilly, entangled amongst *R. cuspidata* and *R. siliquosa*. However, recent surveys suggest that populations have declined.

Ramalina cuspidata (Ach.) Nyl. (1870)

Like a finer form of *R. siliquosa*, but differing in the more erect, terete, narrower (1-3 mm) main branches which are often markedly shiny-blackened at the base and elsewhere, originating from a wide-spreading holdfast, sometimes forming swards; surface shiny, smooth, brown-yellow or pale green with a yellow tinge. Pycnidia blackened at the ostioles. Chemistry: Three chemotypes all with usnic acid – medulla (a) K+ yellow→red (crystals), Pd+ yellow-orange, UV– (norstictic acid); (b) K+ yellow-orange, Pd+ yellow-orange, UV– (stictic acid, sometimes with minor amounts of norstictic acid); (c) K–, Pd–, UV– (no chemistry). **BLS 1232**.

On wind-exposed siliceous seashore rocks, xeric-supralittoral, often with *Ramalina* [*siliquosa* or somewhat lower on the shore, rarely on wood of fence posts, coastal; local. W. Britain and Ireland, extending locally to E. coasts of Scotland & Ireland.

Molecular phylogenetic analysis (LaGreca et al. 2020) supports the distinctness of *R. cuspidata* from *R. siliquosa* (q.v.) despite their similar morphologies but at the same time suggests that the three chemotypes (historically sometimes recognised as species or subspecies) are conspecific. The two species are usually distinguishable when growing together: *R. siliquosa* has a matt surface, lacks the characteristic \pm blackened areas, especially at the holdfast and around the pycnidial ostioles and usually has more flattened lobes. *R. cuspidata* tends to occur in more exposed situations lower down the shore than *R. siliquosa* – the latter may also occur in inland sites (e.g. Stonehenge, Wiltshire). In addition, the two species can usually be separated with TLC, though both produce a chemistry-deficient chemotype.

Host to the lichenicolous fungi *Stigmidium epiramalina* (Vouaux) Hafellner (1994) and *Tremella tuckerae* Diederich (2007).

Ramalina farinacea (L.) Ach. (1810)

Thallus 3–6 (–10) cm long, tufted, pendent, arising from a strictly delimited holdfast, often subdivided into numerous flattened, occasionally slightly concave branches to 3 mm wide, yellow- to dark grey-green; surface matt, smooth; texture firm; medulla solid, subcortex cartilaginous; soralia numerous, marginal, discrete, circular to elliptical, saucer-shaped, becoming flat; soredia 20–30 μ m diam., pale yellow-green, farinose. Apothecia rare, lateral. Ascospores 8–15 × 5–7 μ m, broadly ellipsoidal. Chemistry: four chemotypes, all with usnic acid – medulla and soralia: (a) K– or orange-brown, Pd+ orange-red, UV– (protocetraric acid); (b) K+ yellow-red, Pd+ yellow-orange, UV– (salazinic acid, ± norstictic acid); (c) K–, Pd–,UV+ blue-white (hypoprotocetraric acid); (d) K–, Pd–, UV– (lichen products not detected). **BLS 1234**.

On a wide variety of substrata and in diverse habitats, ranging from trunks and twigs within shaded deciduous woodland to sunny wind-exposed isolated trees, hedgerows and scrub, and wooden posts, very rarely on rocks,







LC

occasionally free-living on sand dunes; common. Throughout Britain and Ireland.

Specimens in air-polluted habitats are often dark green and tufted, with short decumbent contorted or recurved branches, while in deep shaded woodland, material is often elongated, pale and rather sparingly branched with narrow branches. Here thalli may resemble Evernia prunastri but have a tough, cartilaginous subcortex and are terete with photobiont cells below all surfaces. It is the Ramalina species that is least sensitive to SO₂ pollution (<60 µg m⁻³) and wind-blown inorganic fertilizers. The chemotypes are sometimes given separate names as species or varieties. The corticolous R. pollinaria, as well as the corticolous and saxicolous R. europaea, may closely resemble R. farinacea. The saxicolous R. subfarinacea may also appear similar to R. farinacea, and molecular data suggests that these two taxa are closely related, or perhaps conspecific (LaGreca et al. 2020; Spjut et al. 2020). See also R. portuensis.

Host to the lichenicolous fungi Abrothallus suecicus (Kirschst.) Nordin (1964) that blackens the whole thallus, Asteroglobulus giselae Brackel (2010), Didymocyrtis ramalinae (Roberge ex Desm.) Ertz et al. (2015), Endococcus ramalinarius (Linds.) D. Hawksw. (1979), Lichenopeltella ramalinae Etayo & Diederich (1997), and the plurivorous Lichenoconium erodens and Marchandiomyces corallinus.

Ramalina fastigiata (Pers.) Ach. (1810)

Thallus usually erect, densely tufted and richly branched, pulvinate, lobes 1-5 cm long, 3-8 mm wide, sometimes becoming lax and pendent, pale- to dull grey-green; branches cylindrical or somewhat angular, slightly flattened, hollow, appearing inflated, with a web-like lax medulla and cartilaginous subcortex; surface sometimes longitudinally fenestrate and lacunose. Apothecia terminal, usually numerous, often appearing at one level (umbel-like), sometimes totally obscuring the thallus lobes; disc concave, becoming flat or convex when mature. As cospores $12-15(-18) \times 5-6(-7) \mu m$, mainly kidney-shaped, rarely broadly ellipsoidal. Medulla C-, K-, KC-, Pd-, UV- (usnic and evernic acid complex). BLS 1235.

On trunks or twigs of well-lit, wind-exposed hedgerows or parkland trees with nutrient-rich bark, rarely on rocks, absent from hilly areas; common. Throughout Britain and Ireland.

A polymorphic species; specimens are normally in somewhat globose tufts, with the apothecia facing the light at the same level. In moist sites the thallus is paler, frequently fenestrate and rarely fertile. Very narrow, straggling morphs occur with an almost transparent thallus when wet and numerous angled branches giving the thallus a spiny appearance. Coarse straggling morphs of R. fastigiata could be confused with R. calicaris, which has tougher, channelled branches usually containing sekikaic acid.

The most frequent host for Didymocyrtis ramalinae. Other lichenicolous fungi hosted include Abrothallus suecicus, Endococcus ramalinarius, Tremella ramalinae, an unidentified Polycoccum sp. and the rather plurivorous Illosporiopsis christiansenii and Lichenoconium usneae.

Ramalina fraxinea (L.) Ach. (1810)

Thallus pendent, coarsely tufted, rarely monophyllous, grey-green or olive to greenblack; branches to 20 (-30) cm long and 3-4 cm wide, conspicuously flattened and leaf- like, unbranched or sometimes sparingly branched, often twisted, tapering towards the base and apices, flat or commonly channelled, often with an uneven, reticulately wrinkled surface, sometimes fenestrate or longitudinally lacerate; lateral branches usually arising near the distinct holdfast; medulla solid, subcortex cartilaginous; pseudocyphellae frequent, inconspicuous, appearing as thin pale lines. Apothecia usually frequent, marginal or laminal; disc cup-like, becoming flat or weakly convex. Ascospores 10-17 × 4-7 µm, kidney-shaped. K-, C-, Pd-, UV-(usnic acid only). BLS 1236.

Frequent on nutrient-rich bark in windy, well-lit sites, but rare in woodlands except in the canopy. E. & S. England (once much decreased but now increasing again), N. England, S. & E. Scotland, throughout Ireland.

R. fraxinea is by far the largest species of Ramalina in Britain and Ireland, though it may vary considerably in the size, width and number of branches; narrow-lobed morphs can be confused with R. calicaris especially when it lacks chemistry, but the surface is always finely and irregularly ridged, crumpled, matt, softer in texture, with kidney-shaped ascospores and lichen products have not been detected in its medulla. Extremely sensitive to air pollution (SO₂ not exceeding 35 μ g m⁻³) and agricultural fertilizers.





LC

The most frequent host for *Tremella ramalinae*. Other lichenicolous fungi hosted include *Abrothallus suecicus*, *Didymocyrtis ramalinae* and *Tremella tuckerae*, as well as the plurivorous *Lichenoconium erodens* and *L. usneae*.

Ramalina lacera (With.) J.R. Laundon (1984)

Thallus ranging from a single convoluted lobe, to dense, erect to partly decumbent ragged tufts; branches strap-like, flattened, concolorous, white- to yellow-green, the lower side sometimes somewhat paler, often with indented margins, sometimes with twisted and deformed marginal prolongations; surface matt, often peeling, with a smooth or coarse reticulum of ridges; medulla dense, not hollow, subcortex soft, lacking cartilaginous tissue; soralia laminal and marginal, starting as eroded patches on the cortex, later occupying entire lobe ends, especially the underside; soredia 20–40 µm diam., farinose. Apothecia unknown. Medulla and soredia C–, K–, KC–, Pd–, UV– (usnic and bourgeanic acids). **BLS 1233**.



Mainly on wayside trees, hedgerows and scrub, also on shaded dusty siliceous rock and walls in dry sheltered situations; locally common, especially S. and E. Britain, rarer in the north. Frequent in central Ireland.

A polymorphic species. Branching, narrow-lobed morphs may resemble *Ramalina pollinaria* and its recent segregate *R. europaea*, both of which have evernic acid, a cartilaginous subcortex and usually subterminal or terminal, punctiform or elongate soralia. *R. canariensis*, an apparently unrelated but similar species (Spjut *et al.* 2020), has a cartilaginous subcortex, soredia in vesicles and emanating from the medulla, and produces divaricatic acid. On church walls populations can occur where the upper surfaces of lobes are abraded, white-mottled and thalli are in deformed clusters.

Host to the lichenicolous fungus *Mixtoconidium insidiens* (Vouaux) Etayo & van den Boom (2017), recently recorded from Ireland.

Ramalina pollinaria (Westr.) Ach. (1810)

Thallus 1–2 (–5) cm long, lobes discrete or forming swards, pale green to pale yellow; lobes flattened, 3 mm broad at the base, rapidly proliferating into numerous fine branches which are partially terete and 1–2 mm broad, or more flattened branches with wavy or deeply incised or notched margins; surface smooth, shiny, appearing cartilaginous; medulla dense, not hollow, subcortex cartilaginous; soralia mainly subterminal or terminal, more rarely on branch margins or lamina, from degenerating regions of cortex, starting as excavate soralia, irregularly spreading, often appearing lip-shaped at apices, soredia fine, 30–45 μ m diam. Apothecia unknown. Medulla and soralia C–, K–, KC–, Pd–, UV± blue-white or pale violet grey (usnic acid; evernic acid complex sometimes present). **BLS 1237**.



Reported from below dry sheltered overhangs on siliceous rock or exposed tree roots, also on N- or E-facing church walls and branches of *Ilex* and *Malus*; primarily from S. England.

Previously much confused with *Ramalina lacera*, the *R. pollinaria* aggregate is more finely branched and lobes have a shiny surface. *R. farinacea* and *R. subfarinacea* have neatly rounded, ulcerose soralia on the margins and lamina, and a different chemistry.

R. pollinaria was recently split into three taxa by Gasparyan *et al.* (2017). A segregate that they described as *R. europaea* Gasparyan, Sipman & Lücking may occur in Great Britain and Ireland; it was characterized in morphological terms as having soralia which are initiated terminally as small, punctiform structures on small, spine-like branchlets, and granular soredia 50–70 μ m diam. In contrast, *R. pollinaria* s. str. was described as having soralia which from the beginning are subterminal to laminal-marginal and irregularly elongate, not starting out on small branchlets and with such branchlets absent or rare, and with farinose soredia <50 μ m diam. However, the morphological and molecular differences between these taxa seem marginal and they appear to have more or less coextensive distributions. Further DNA data is needed, especially from British and Irish populations.

Ramalina polymorpha (Lilj.) Ach. (1810)

Thallus 3-6 cm long, usually prostrate, in dispersed flat radiating tufts, often coalescing into extensive swards, dark green-grey; branches strap-shaped, flat, 1-4 (-6) mm wide, sometimes longitudinally dissected, usually tapered towards the ends, surface uneven, scabrid, longitudinally ridged or lacerate, commonly with numerous

NT

scattered or confluent concolorous or paler pseudocyphellae which open into numerous fenestrations; cartilaginous subcortex present; spherical, shiny, corticate, sessile or stalked, isidium-like granules present, $60-180 \ \mu m$ diam., singly or mainly clustered around the rounded-elliptical pseudocyphellae. Apothecia rare, terminal or subterminal in small thalli, lateral and marginal in larger morphs, cup-like, rarely becoming convex; thalline margin scabrid-vertucose. As cospores $12-16 \times 4-6 \mu m$, broadly ellipsoidal. C-, K-, Pd-, UV- (usnic acid only). BLS 1238.

On intensely nutrient-enriched rocks, particularly below bird-roosting or nesting sites on or near sea cliffs; locally abundant on bird-inhabited islands in S.W. Wales, rare in N.E. England and C. & N.E. Scotland.

R. polymorpha is characterized by the nesting-bird perch habitat, and lobes with a scabrid surface and numerous pseudocyphellae, each containing one or several coarse corticate isidium-like granules (often misinterpreted as soredia). Pycnidiate or mite-mutilated thalli of R. siliquosa have sometimes been misidentified as this species. R. siliquosa has a paler green thallus contrasting with the deep, green-grey of R. polymorpha when wet. See also R. capitata.

Ramalina portuensis Samp. (1924)

Thallus similar to R. farinacea with which it sometimes grows, with swollen, straggling, *Cladina*-like lobes, flattened at the base, 0.5–3 cm long, 1 mm wide, pale yellow-grey, convex and weakly foveolate, soon branching into narrow (0.1-0.3 mm wide) dichotomous shiny lobes which are irregular and almost terete; medulla hollow, subcortex cartilaginous; soralia emanating from irregular, longitudinal slits, often visible through tears in the cortex, usually near the tips; soredia white and granular. Chemistry: K+ red, Pd+ orange, UV- (unidentified medullary substance in addition to usnic and salazinic acids). BLS 1239.

On sunny to somewhat sheltered, rather moist tree trunks, twigs, rarely old Calluna stems and rock outcrops, mainly near the coast; rare. S.W. England, Isles of Scilly (common), W. Wales, extending to Scotland (Skye, West Ross), S.W. Ireland.

Distinguished by its small pendent clusters of hollow lobes, scored with irregular, superficial lacerations revealing internally developed soredia.

Ramalina siliquosa (Huds.) A.L. Sm. (1918)

Thallus coarsely tufted, erect to pendent, stiff and tough, branches usually numerous, arising from a wide-spreading holdfast, simple to richly branched, sometimes in swards; main branches 3-7 (-10) cm high, 2-9 mm wide, usually flattened, rarely partly terete, especially towards the base; secondary branching dichotomous; surface pale grey-green to yellow-green, rarely matt and discoloured and blackened at the base or elsewhere; a cartilaginous subcortex present giving a rope-like appearance. Apothecia frequent, lateral, occasionally terminal. Ascospores $11-20 \times 5-6$ µm, broadly ellipsoidal or slightly kidney-shaped. Pycnidia frequent, often clustered and forming coarse, nodulose irregularities, the ostioles pale or flesh-coloured and transparent when wet. Chemistry: four chemotypes, all with usnic acid - medulla: (a)

K-, Pd+ orange-red, UV- (protocetraric acid); (b) K+ red, Pd+ orange, UV- (salazinic acid); (c) K-, Pd-, UV+ blue-white (hypoprotocetraric acid); (d) K-, Pd-, UV- (no chemicals detected). BLS 1240.

On siliceous rocky shores in the xeric-supralittoral zone, often dominant and forming a luxuriant zone on sea cliffs, even in shelter; more rarely extending to 70 km inland on wind-exposed churches, ancient monuments and outcrops, occasionally occurring on seashore fence-posts, rarely on *Quercus* and *Fraxinus*; common and often abundant. Throughout coastal Britain (except the S.E.) and all of coastal Ireland, rare inland on both islands.

A very polymorphic species; on vertical cliff faces, R. siliquosa is often large, pendent and coarse, with a few thick, flattened branches; on sloping rock faces and boulders, the thalli are usually shorter and erect, and the branches less flattened. A common form on western shores (previously recognized as R. incrassata (Nyl.) Mot.) has clusters of decumbent strongly convex downwardly arching lobes that are densely tuberculate or pycnidiate. This form grows on vertical faces and below overhangs, where it avoids direct contact with seawater spray, which causes it to become reddish, presumably because of the invariable presence of salazinic acid; it is uncommonly



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found inland. The four known chemotypes are sometimes given infraspecific or species status, but molecular evidence (LaGreca *et al.* 2020) indicates that they are all conspecific. The closely related *R. cuspidata* has terete lobes that are shiny-black towards the base; it usually occurs closer to the shoreline (i.e. on more exposed rocks) than *R. siliquosa*, and has a diversity of chemotypes similar to that of the latter species. Sometimes thalli of both species are eroded down to a mere holdfast, which can then resemble crustose species such as *Lecanora sulphurea*. The two British *Roccella* species can be distinguished from *Ramalina siliquosa* by the pale mauvegrey (not green-grey) thallus, the large blue-white soralia and the C+ red reaction of the cortex or soralia.

Host to the lichenicolous fungus *Stigmidium epiramalina* (Vouaux) Hafellner (1994), as well as the plurivorous *Lichenoconium erodens* and *Marchandiomyces corallinus*.

Ramalina subfarinacea (Nyl. ex Cromb.) Nyl. (1872)

Similar to *R. farinacea*, but differing mainly in its principally coastal, saxicolous habitat, spreading holdfast and tendency to form swards, a more erect, spiky appearance, generally yellower colour of the thallus and granular ($25-60 \mu m$ diam.) soredia in excavate soralia. Medulla and soralia generally K+ red (usnic and norstictic acids), but other chemotypes may occur as in *R. farinacea*. **BLS 1241**.

On xeric-supralittoral rocks, near bird perches, or rarely on old *Calluna* stems, or free-living on dune soil, predominantly coastal, but sometimes inland by freshwater lakes, on ancient standing stones and church towers; frequent on rocky coasts. Throughout coastal Britain, except the S. E., and all of coastal Ireland, occasional inland on both islands.



Extreme shade morphs may have very narrow branches with hook-shaped ends, resembling compact forms of *R. chondrina*. Most similar to *R. farinacea* (q.v.), which molecular evidence (LaGreca *et al.* 2020; Spjut *et al.* 2020) indicates is closely related or conspecific with it.

Host to the plurivorous Marchandiomyces corallinus.

SCUTULA Tul. (1852)

Thallus present or absent; when present white or pale green-grey, thin, irregularly warted or composed of small irregular globose to flattened granules, the photobiont a green alga, probably micareoid in form. Apothecia sessile, narrowly attached, constricted at the base, round, scattered to \pm aggregated. Disc flat to convex, cream or pale brown to dark purple-brown or black, matt to shiny. Margin distinct, pale dark brown or black. True exciple prominent, composed of parallel, regularly radiating branched and anastomosing strongly agglutinated hyphae; outermost parts colourless or pale to dark reddish brown, apically with an unevenly distributed greenish or purplish brown to greenish black granular pigment; inner parts colourless or greenish to red-brown. Hypothecium composed of loosely intertwined hyphae, colourless to brown. Subhymenium colourless. Hymenium colourless, sometimes pale brownish, orange-brown or greenish black in upper parts. Hymenial gel hemiamyloid. Hamathecium of septate paraphyses, very sparingly branched and with few anastomoses, the apical cells slightly thickened to clavate and sometimes pigmented. **Epithecium** not continuous, with an unevenly distributed granular, greenish brown to greenish black pigment which occasionally follows the paraphyses downwards. Asci 6- to 8-spored, with an amyloid tholus and diffuse non-amyloid apical cushion, and an outer amyloid wall layer. Ascospores variably septate, narrowly to broadly ellipsoidal or cylindrical to cylindric-fusiform, the ends usually attenuated, sometimes with oil droplets, thin-walled, smooth, colourless. Conidiomata containing microconidia pycnidial, globose, semi-immersed to sessile; microconidia aseptate, bacilliform to filiform, sometimes curved, colourless. Conidiomata containing mesoconidia (Libertiella type) pycnidial, globose, semi-immersed to sessile, conidia aseptate, bacillar to falcate, often irregular in shape, colourless. Conidiomata containing macroconidia (Karsteniomyces type) pycnidia, globose,

sessile; conidia 0- to 1-septate, cylindrical to bacillar, often somewhat irregular in shape, colourless, the base truncated.

Scutula is a diverse genus in terms of nutritional strategy, containing species that are lichenized, lichenicolous or initially lichenicolous but developing an independent thallus. The genus was linked with *Bacidina* and *Toninia* by Andersen & Ekman (2005), and the relationship was confirmed by Pino-Bodas *et al.* (2017) and Kistenich *et al.* (2018). There are several other species currently placed in *Bacidia* that show morphological similarities to *Scutula* species, but lack of molecular data means that their transfer would be premature. They are accordingly included within the key below.

Scutula epicladonia (Nyl.) Zopf has been recorded from various sites in Scotland; it has recently been transferred to the genus *Zhurbenkoa* (Malmideaceae) by Flakus *et al.* (2019).

Literature

Alstrup & Hawksworth (1990), Andersen & Ekman (2005), Coppins & Aptroot (2009), Kistenich *et al.* (2018), Pino-Bodas *et al.* (2017), Triebel *et al.* (1997), Wedin *et al.* (2007).

Key to species of Scutula and similar species of Bacidia and Bibbya

1	Thallus present
	Thallus absent (lichenicolous on <i>Peltigera</i> and <i>Solorina</i> spp.)
2 (1)	Ascospores ± filiform or acicular, length/breadth ratio 10:1 or more
	Ascospores cylindric-fusiform, ellipsoidal or clavate, length/breadth ratio 9:1 or less
3 (2)	Epithecium green
4 (3)	Ascospores ± filiform, straight, not markedly tapering at the lower endScutula circumspecta Ascospores acicular, mostly curved or flexuose, tapering towards the lower endBacidia caesiovirens
5 (3)	Ascospores \leq 40 µm long, 3- to 7-septate; hymenium <60 µm high; apothecia mostly 0.2–0.7 mm diam
	Ascospores mostly >45 µm long, 7- to 16 (to 22)-septate; hymenium >60 µm high; apothecia mostly 0.5–1 mm diam
6 (5)	Ascospores $21-40 \times 2-3$ (-4) µm, strongly curved, sigmoid, worm-like, or a few short-acicular; conidia $7-9 \times 0.5-1$ µm, ± bacilliform
7 (5)	Thallus granular or granular-isidiateBacidia biatorina
	Thallus smooth to warted, often cracked, never with distinct granulesBacidia laurocerasi
8(2)	Initially lichenicolous on <i>Peltigera</i> spp., subsequently developing an independent thallus <i>Scutula dedicata</i>
	Not lichenicolous at any stage of the life cycle
9 (8)	Thallus thickly and entirely granular; ascospores (3-) 5- to 6 (-7)-septate
10 (1)	Initially lichenicolous, subsequently developing an independent thallus
11 (10)	Ascospores $18-40 \times 5-8 \mu m$, cylindric-fusiform, sometimes sinuous, 3- to 5- (to 7-) septate
	Ascospores <15 µm long, ellipsoidal, almost all 0- to 1-septate

Scutula circumspecta (Vain.) Kistenich, Timdal, Bendiksby & S. Ekman (2018) VU (C, D1) Bacidia circumspecta (Norrl. & Nyl.) Malme (1895)

Thallus white or pale green-grey, thin, irregularly warted but without distinct granules; photobiont cells 7–14 (–16) µm diam. Apothecia 0.2–0.7 (–1) mm diam., flat, marginate, black; true exciple with upper part and outer edge dark purple-brown, K+ intensifying purple, becoming pale-coloured to colourless below; epithecium blue-green, K–, N+ purple-violet, often with blue crystals; hymenium 45–55 µm high, colourless or pale green above; hypothecium colourless or pale straw; paraphyses 1–1.5 µm diam., unbranched or forked above, the apices often pigmented and swollen to *ca* 4 µm diam. Ascospores (18–) 20–30 (–38) × (1.5–) 2–2.5 µm, ± filiform. Pycnidia rare, 100–160 µm diam., sessile, ± globose, black, the wall with purple-brown and green pigments; conidia 7–9 × 1.5–2 µm, 0 (-1)-septate, cylindrical. **BLS 0142**.

On trunks of mature *Quercus*, *Fagus*, *Ulmus glabra* and old *Juniperus*, typically in small base-rich wound tracks, in old woodlands; rare. S. & N. England, Mid-Wales, E. Highlands of Scotland.

Distinguished from *Toniniopsis separabilis* by the non-granular thallus and pale hypothecium, and from both *Bibbya vernifera* and *B. subcircumspecta* by the ascospores that are not tapered at the base and by the green epithecium. *Bacidia igniarii* has mostly shorter ascospores, and slightly smaller, barrel- to inversely cone-shaped apothecia.

Scutula dedicata Triebel, Wedin & Rambold (1997)

Initially lichenicolous, but developing an independent thallus composed of small noncorticate granules 70–90 µm diam. Apothecia 0.35–0.5 (–0.8) mm diam., scattered or in clusters, varying in colour from almost pale or reddish brown to dark brown or black. Disc flat when young, later convex. Hymenium 45–55 µm high, hemiamyloid. Paraphyses septate, sparingly branched, apical cells slightly thickened, non-capitate. Asci narrowly clavate, 30–46 × 7–8.5 µm. Ascospores colourless, ellipsoidal, (0-) 1septate, (9–) 10–11 (–13) × 3.5–4 µm. Conidiomata containing microconidia globose, subimmersed to sessile, *ca* 60 µm diam. Microconidia colourless, narrowly cylindrical to filiform, 5–9 × 0.5–1 µm. Conidiomata containing mesoconidia of *Libertiella*-type 200–300 (–400) µm diam. Mesoconidia (3.5–) 6–6.5 (–8) × 2–3 (–3.5) µm.

Conidiomata containing macroconidia of *Karsteniomyces*-type \pm globose, sessile, 80–250 µm diam. Macroconidia colourless, bacillar, (7–) 8.5–11 × 2–3.5 µm, 0- (to 1-) septate. **BLS 2394**.

On thalli of *Peltigera didactyla*, Argyll and Moray, initially causing necrosis with the algal layer seriously damaged, and subsequently developing a \pm granular thallus. Other cyanobacterial species of *Peltigera* are affected elsewhere.

Scutula heeri has slightly larger ascospores and conidia; it also occurs on thalli of *Peltigera* and later forms an independent thallus.

Scutula effusa (Rabenh.) Kistenich, Timdal, Bendiksby & S. Ekman (2018)

Bacidia auerswaldii (Hepp ex Stizenb.) Mig. (1929)

Thallus indeterminate, thin, of discrete or continuous, globose or irregular, often slightly flattened granules; granules $40-150 \ \mu m$ diam. Apothecia $0.3-1.1 \ mm$ diam., flat to slightly convex, marginate, normally purple-brown to black, but sometimes (in



Nb



non-British collections) pigment-deficient; true exciple laterally orange to black-brown, K \pm purplish, N \pm orange-red; hypothecium colourless or pale yellowish; hymenium 75–125 µm tall, upper part orange to black-brown, K \pm purplish, N \pm orange-red; paraphyses 1.0–1.6 µm diam., apices \pm clavate, 2.5–5 µm diam. Ascospores 20–26 × 4–5 µm, (3-) 5 to 6 (-9)-septate, cylindric-fusiform with blunt ends. Conidiomata not seen. **BLS 0134**.

On bark of *Fraxinus* and *Quercus*, N. and N.W. Scotland, rare; also a historic record on trunk of *Ulmus* in S.W. England (? in parkland); not recorded there since 1937.

Distinguished from Bacidia biatorina by the cylindric-fusiform ascospores.

Scutula epiblastematica (Wallr.) Rehm (1889)

Thallus absent (lichenicolous). Apothecia 0.1–0.3 (–0.45) mm diam., scattered or in clusters, varying in colour from pale to dark brown or black. Disc flat when young, later slightly convex. Hymenium 35–60 μ m high, hemiamyloid. Paraphyses septate, sparingly branched, apical cells markedly thickened, non-capitate. Asci narrowly clavate, 35–50 × 6–10 μ m. Ascospores colourless, ellipsoidal or rarely ± cylindrical, (0-) 1 (-3)-septate, (8–) 8.5–12.5 (–17) × (2.5–) 3–4 (–4.5) μ m. Conidiomata containing microconidia globose, subimmersed to sessile, 45–95 μ m diam. Microconidia colourless, cylindrical to shortly filiform, often slightly curved, (4–) 5– 8 (–9) × (0.5–) 1–1.5 μ m. Conidiomata containing mesoconidia of *Libertiella*-type 65–160 μ m diam. Mesoconidia ± cylindrical to falcate, (5–) 6–8 (–9) × (1.5–) 2–2.5 μ m. Conidiomata containing macroconidia of *Karsteniomyces*-type not known. **BLS 2198**.



On thalli of *Peltigera praetextata* and *P. rufescens*, Cornwall, Perthshire and Sutherland. Causes necrosis.

Scutula igniarii (Nyl.) S. Ekman (2021)

Bacidia igniarii (Nyl.) Oxner (1968)

Thallus indeterminate, rather thin, discontinuous, of discrete or contiguous convex, sometimes subsquamulose areoles, light brown-grey. Apothecia 0.2–0.4 mm diam., black, barrel-shaped to inversely cone-shaped; true exciple with green and brown pigmentation, strongly developed below hypothecium, mostly consisting of intricately intertwined hyphae; hypothecium pale; hymenium 40–50 µm tall, upper part blue-green. Ascospores 12–19 × 2.5–2.9 µm, 3-septate, cylindrical to clavate. **BLS 1828**.

On trunks of *Populus tremula*, less often on *Fraxinus* and *Quercus*; rare. Scotland (Speyside, Deeside and Glen Lyon, Perthshire).

Most likely to be confused with *Scutula circumspecta*, which has slightly larger, flatter apothecia and longer ascospores.

Scutula miliaris (Wallr.) Trevis. (1853)

Thallus absent (lichenicolous). Apothecia 0.2–0.35 (–0.45) mm diam., scattered or rarely clustered over infected areas, cream to dark brown or black. Disc flat when young, later slightly convex. Hymenium 45–80 µm high, hemiamyloid. Paraphyses septate, sparingly branched, apical cells slightly thickened, non-capitate. Asci clavate, $36-60 \times 9-17$ µm. Ascospores colourless, ellipsoidal, (0-) 1-septate, (10–) 11.5–14 (– $15) \times (4-) 5-6$ (–7) µm. Conidiomata containing microconidia globose, subimmersed to sessile, 80–110 µm diam. Microconidia colourless, narrowly cylindrical to filiform, often slightly curved, (6–) 7.5–9 (–13) × 1–1.5 µm. Conidiomata containing mesoconidia of *Libertiella*-type unknown. Conidiomata containing macroconidia of *Karsteniomyces*-type ± globose, sessile, 80–150 (–200) µm diam. Macroconidia



colourless, ± cylindrical, sometimes curved, (8-) 13.5–19 (–26) × (3–) 4–5 (–5.5) µm, 0- to 1-septate. **BLS 2201**. On thalli of *Peltigera membranacea*, Dartmoor, as the *Karsteniomyces* anamorph. Only a single confirmed British record.

Similar to *S. tuberculosa*, but occurs on *Peltigera* rather than *Solorina* species, with somewhat smaller apothecia and larger ascospores.

Scutula tuberculosa (Th. Fr.) Rehm (1906)

Thallus absent (lichenicolous). Apothecia 0.2–0.7 (–0.8) mm diam., scattered over infected areas, varying in colour from almost white or pale brown to very dark brown or black. Disc flat when young, later convex and





wide. Epithecium reddish brown to greenish black. Hymenium 65–100 µm high, hemiamyloid. Paraphyses septate, sparingly branched, apical cells slightly thickened, non-capitate. Asci narrowly clavate, $50-60 \times 10-18$ µm. Ascospores colourless, ellipsoidal, 1-septate, 10-12 (-14) × 4–6 µm. Conidiomata containing microconidia globose, subimmersed to sessile, *ca* 50 µm diam. Microconidia colourless, narrowly cylindrical to filiform, $8-11 \times ca$ 1 µm. Conidiomata containing mesoconidia of *Libertiella*-type unknown. Conidiomata containing macroconidia of *Karsteniomyces*-type ± globose, sessile, 80–200 µm diam. Macroconidia colourless, ± cylindrical, 11–15 (-18) × 3–4 µm, 1-septate, the septum comparatively indistinct. **BLS 2202**.



On thalli of *Solorina saccata* and *S. bispora*, causing some degradation of the host tissues, rare. Central Highlands (Perthshire and S. Aberdeenshire).

In addition to host preference, *Scutula tuberculosa* is characterized by its relatively large apothecia. Both types of conidiomata are commonly found in addition to the apothecia.

THALLOIDIMA A. Massal. (1852)

Thallus squamulose (rarely absent and lichenicolous), pseudocyphellae absent or indistinct. Upper cortex usually well-developed, with a prominent epinecral layer over a lower layer composed of anticlinally oriented thin- to thick-walled hyphae with rounded to narrowly cylindrical lumina; usually strongly pruinose with calcium oxalate crystals on the surface and sometimes included within the cortex. Photobiont (where present) green, chlorococcoid. Medulla usually well-developed, of loosely interwoven hyphae, lacking crystals. Lower cortex resembling the upper, but thinner and lacking crystals. Ascomata apothecia, black, often white- or grey-pruinose; usually concave to flat when young, later often becoming convex. Thalline margin absent. True exciple distinct when young but later often excluded, pale grey to dark brown throughout or with a dark grey rim, K- and N-, or K+ violet and N+ violet (additional grey pigment). Epithecium grey, usually containing crystals of calcium oxalate, K+ violet, N+ violet. Hymenium I+ blue. Hypothecium colourless to dark brown. Hamathecium of paraphyses, straight, unbranched or sparingly branched and anastomosed, not conglutinated, thin-walled, the apical cell distinctly swollen and covered by a \pm well-developed gelatinous pigment cap. Asci Bacidia-type, 8-spored, clavate, surrounded by a gelatinous K/I+ blue sheath, with a well-developed K/I+ blue tholus containing a deeper-staining tube and pronounced ocular chamber. Ascospores 1-septate (rarely 3-septate), colourless, acicular to ellipsoidal, without a distinct perispore. Conidiomata not seen. Chemistry: fatty acids, terpenoids and unknown compounds occur occasionally through the genus. Ecology: most species are initially associated with cyanolichens and possibly parasitic, mostly later free-living, mainly on \pm base-rich rock and soil in exposed habitats.

A segregate from *Toninia*; see under that genus for further explanation. According to Kistenich *et al.* (2018), *Thalloidima* contains species that (with few exceptions) have the characteristic greyish pigment Sedifolia-grey (Meyer & Printzen 2000), a thallus partly or entirely covered by white pruina formed by calcium oxalate, and fusiform, 1-septate ascospores. Most species are lichenized (with the exception of the non-British lichenicolous *T. collematicola* (Timdal) Timdal and *T. leptogii* (Timdal) Timdal) but begin their development in close association with cyanobacterial lichens and may well be initially parasitic. This is a lifestyle found elsewhere in the Ramalinaceae, for example in *Kiliasia, Scutula* and *Toninia* s. str.

Thalloidima alutaceum Anzi (1911) and *T. candidum* (Web. ex Wigg.) Th. Fr. (1867) are both known from single collections, made last century, reputedly from near the summit of Ben Lawers. Their presence in Britain and Ireland is in need of confirmation.

Literature

Hitch et al. (2009), Kistenich et al. (2018), Meyer & Printzen (2000), Timdal (1991).

1	Hypothecium pale brown to colourless. + transparent	2
-	Hypothecium reddish brown, \pm opaque	
2 (1)	Squamules bullate to columnar, marginal squamules not elongated; pseudocyphellae ± inconspicuous, white, not to moderately pruinose, pruina farinose	physaroides
	absent; usually densely pruinose, pruina granular	rosulata
3 (1)	Squamules irregularly convex to bullate, not to entirely pruinose; pruina finely farinose . Squamules \pm convex but not bullate, usually entirely white-pruinose; pruina granular	4 diffractum
4 (3)	Squamules strongly convex to extended bullate-nodulose and partly vertically flattened, often imbricate; considered extinct in our region	opuntioides
	imbricate	sedifolium

Thalloidima diffractum (A. Massal.) A. Massal. (1853)

Toninia diffracta (A. Massal.) Zahlbr. (1901)

Squamules to 3 mm diam., scattered when young, later contiguous, weakly convex to hemispherical; upper surface grey, densely white-pruinose or more rarely irregularly granular-pruinose, dull, smooth or with shallow fissures, lacking pseudocyphellae, the edges concolorous with upper side, the underside white to pale brown; upper cortex 40-70 µm thick, lacking an epinecral layer but overlain by an amorphous layer of calcium oxalate crystals; lower cortex resembling upper cortex, but thinner and without crystals; photobiont zone continuous; medulla without crystals. Apothecia to 2 mm diam., weakly concave to weakly convex, partly to entirely granular, usually white-pruinose; true exciple ± persistent, brown, K- and N-, or K+ violet and N+ violet (Sedifolia-grey pigment); epithecium grey, containing crystals of calcium

oxalate, K+ violet, N+ violet; hymenium 70-80 µm tall, colourless to pale brown; lower part of hypothecium brown, upper part dark brown. Ascospores $14-20 \times 3-5 \mu m$, 1-septate, fusiform. Unidentified terpenoids detected by TLC in some instances. BLS 1903.

On calcareous rock, mainly in fissures on steep to overhanging rock faces, or soil, associated with cyanolichens when young. N. Wales (needs confirmation), Scotland (Perthshire).

Three chemical races of T. diffractum occur in Britain, one without lichen products, and two with a differing series of terpenoids. British material of T. diffractum has often been incorrectly identified as T. candidum which has not been correctly recorded for our region, a species which forms rosette-shaped thalli with a continuous, densely pruinose upper surface and always without regular fissures in the cortex.

Thalloidima opuntioides (Vill.) Kistenich, Timdal, Bendiksby & S. Ekman (2018)

Toninia opuntioides (Vill.) Timdal (1991)

Squamules to 4 mm diam., strongly convex to bullate when young, later vertically flattened and often imbricate; upper surface olivaceous brown to dark brown, usually partly white-pruinose (especially in convex parts), slightly shiny, with shallow fissures in the cortex (when well-developed), lacking pseudocyphellae; edge usually more densely white, farinose-pruinose; lower surface white to pale brown; upper cortex 40–90 µm thick, including a thick epinecral layer to 50 µm deep, sometimes containing or overlain by calcium oxalate crystals; lower cortex resembling the upper, thinner and lacking crystals; photobiont layer continuous; medulla lacking crystals. Apothecia to 4 mm diam., weakly concave to weakly convex, usually moderately farinose, white-pruinose; true exciple distinct when young but later often excluded,

medium to dark brown throughout or with a dark grey rim, K- and N- or K+ violet and N+ violet (Sedifoliagrey pigment); epithecium grey, usually containing crystals of calcium oxalate, K+ violet, N+ violet; hymenium



Nb



Ex

70–80 μ m tall, colourless; hypothecium medium brown in the lower part, dark brown in the upper part. Ascospores 15–25 × 3–5 μ m, 1-septate, fusiform. Unidentified terpenoid detected by TLC turning bright yellow on charring. **BLS 1905**.

On calcareous soil and rock, mainly among mosses or in fissures on rock walls, apparently always associated with cyanolichens when young, also on shell sand; very rare in Great Britain, recent records from Scotland (Ayrshire, E. Lothian, Berwickshire). Previously recorded from S.W. England (Somerset, Cleve Hill) and W. Scotland (Mull, Lismore). Some collections identified as *T. sedifolium* might belong here.

T. sedifolium differs in the more regularly bullate, irregularly sausage-shaped, often imbricate squamules with a more cracked upper surface and usually with a more distinct white margin. Special care is required when identifying this species solely on morphology; however, the unknown terpenoid is diagnostic.

Thalloidima physaroides (Opiz) Opiz (1857)

Toninia physaroides (Opiz) Zahlbr. (1926)

Squamules to 2 mm diam., scattered or contiguous, hemispherical when young, later bullate to columnar, sometimes branched; upper side dark olivaceous green to dark brown, usually sparingly pruinose, rarely densely pruinose, dull to shiny, smooth, with punctiform to irregular but often indistinct pseudocyphellae; the edge concolorous with the upper side; underside paler than the upper side, not usually pruinose; upper cortex 20–50 μ m thick, including an epinecral layer to 20 μ m thick, partly disintegrating into pseudocyphellae, sometimes containing or overlain by calcium oxalate crystals, especially in the pseudocyphellae; lower cortex resembling the upper, thinner and lacking crystals; photobiont layer continuous (sometimes broken under pseudocyphellae); medulla without crystals. Apothecia to 3 mm diam., flat to weakly

CR (B2, C2)

convex, not pruinose; true exciple raised when young, later often excluded, pale grey to colourless in the inner part, dark grey in the rim, K+ violet, N+ violet; epithecium grey, not containing crystals, K+ violet, N+ violet; hymenium 70–80 μ m tall, colourless; hypothecium pale brown to colourless. Ascospores 12–18 × 3.5–5 μ m, 1-septate, fusiform. Lichen products not detected by TLC, or with traces of fatty acids. **BLS 1906**.

On calcareous soil, usually associated with cyanolichens when young; very rare. E. England (Northants, Suffolk).

Distinguished from *T. sedifolium* by the more regularly bullate to columnar thallus, presence of pseudocyphellae (which are often inconspicuous) and \pm colourless hypothecium and inner part of the exciple.

Thalloidima rosulatum Anzi (1868)

Toninia rosulata (Anzi) H. Olivier (1911)

Squamules to 4 mm diam., plane to bullate, marginal squamules often elongated; upper surface grey, densely white-pruinose, dull, with shallow fissures, without pseudocyphellae; the edge concolorous with the upper side; underside white to pale brown; upper cortex 40–100 μ m thick, lacking an epinecral layer, overlain by an amorphous layer of calcium oxalate crystals; lower cortex resembling the upper, thinner and lacking crystals; photobiont layer continuous; medulla without crystals. Apothecia <3 mm diam., weakly concave to weakly convex, often lobed, usually faintly white-pruinose; true exciple \pm persistent, pale grey to colourless in inner part, medium grey in the rim, K+ violet, N+ violet; epithecium grey, containing crystals of calcium oxalate, K+ violet, N+ violet; hymenium 70–80 μ m tall, colourless;

hypothecium pale brown to colourless. Ascospores $14-22 \times 3-5 \mu m$, 1-septate, fusiform. Lichen products not detected by TLC. **BLS 1814**.

On calcareous soil and rock, apparently always associated with cyanolichens when young, montane; rare. Scotland (Perthshire, Ben Lawers range).

Differs from *T. diffractum* and *T. sedifolium* in the more rosette-shaped thallus and the colourless to pale brown hypothecium and inner part of the exciple.

Thalloidima sedifolium (Scop.) Kistenich, Timdal, Bendiksby & S. Ekman (2018)

Toninia sedifolia (Scop.) Timdal (1991)

Thallus squamulose; squamules to 3 mm diam., scattered to contiguous, sometimes irregularly imbricate, rounded or irregularly lobed, weakly convex to swollen; upper surface dull olive-green to brown, usually \pm



EN(D)

LC

densely white- or blue-pruinose, dull to slightly shiny, sometimes appearing greasy, smooth or sometimes with shallow fissures in the cortex, without pseudocyphellae; the margin concolorous with the upper side or often more densely white-farinose pruinose; underside white to pale brown; upper cortex $20-60 \mu m$ thick, including a $20 \mu m$ thick epinecral layer, often containing (or overlain by) calcium oxalate crystals; lower cortex resembling the upper, but thinner and lacking crystals; photobiont zone continuous; medulla without crystals. Apothecia to 3 mm diam., weakly concave to weakly convex, not to densely farinose, white-pruinose; true exciple raised when young, often later becoming excluded, medium to dark brown throughout, K– and N–, or K+ violet and N+ violet (Sedifolia-grey pigment); epithecium grey, often containing crystals of



calcium oxalate, K+ violet, N+ violet; hymenium 70–80 μ m tall, colourless; hypothecium medium brown in the lower part, dark brown in the upper part. Ascospores 14–25 × 2.5–5 μ m, 1-septate, fusiform. Lichen products not detected by TLC or with traces of fatty acids or unidentified substances. **BLS 1416**.

In fissures in calcareous rocks, on old mortar of walls, or on calcareous soil, especially dunes, usually associated with cyanolichens, at least when young; locally frequent. Throughout Great Britain and Ireland.

Very variable and easily confused with the much rarer *T. physaroides* and *T. opuntioides*. Specimens with fatty acids are less frequent than the non-fatty acid race but are more widely distributed.

Frequently parasitized by Stigmidium tabacinae (Arnold) Triebel (1989).

TONINIA A. Massal. (1852)

Thallus (where present) squamulose, often proliferating and forming a \pm continuous crust, sometimes nodular or granular, without fissures or pseudocyphellae. Upper cortex poorly to well differentiated, sometimes with an epinecral layer, lacking crystals. Lower cortex poorly developed or absent. Photobiont green, chlorococcoid (when present) forming a continuous layer or of scattered groups of cells. Medulla usually lacking crystals. Ascomata apothecia, black, not pruinose; usually flat when young, later often becoming convex. Thalline margin absent. True exciple raised and usually distinct at first but often finally excluded, of radiating thick-walled conglutinated hyphae with rounded to narrowly cylindrical lumina, colourless within, with a dark outer margin or uniformly dark brown throughout, sometimes with a green tinge, lacking crystals, K-, N-, or N+ violet (Bagliettoana-green pigment). Epithecium olivaceous to green, rarely brown or colourless, lacking crystals, K-, usually N+ violet. Hymenium I+ blue. Hypothecium colourless to dark brown, not containing crystals. Hamathecium of paraphyses, straight, unbranched or sparingly branched and anastomosed, not conglutinated, thin-walled, the apical cell distinctly swollen and covered by a \pm well-developed, gelatinous pigment cap. Asci Bacidia-type, 8-spored, clavate, surrounded by a gelatinous, K/I+ blue sheath, with a well-developed, K/I+ blue tholus containing a deeper-staining tube and pronounced ocular chamber. Ascospores aseptate to 7-septate, colourless, ellipsoidal to narrowly fusiform or acicular, smooth, without an epispore or gelatinous sheath. Conidiomata pycnidia, black, immersed to partly protruding. Conidia bacilliform to thread-like. Chemistry: terpenoids in a non-British species, stictic acid and/or xanthones occasionally present in two species that need exclusion from the genus. Ecology: lichenicolous or on calcareous or siliceous rock, sometimes overgrowing bryophytes.

The treatment of *Toninia* in previous editions largely followed the monograph of Timdal (1991), which included several infrageneric groups that have now been recognized (at least in part) as separate genera (Kistenich *et al.* 2018). However, the differences in apothecial pigments emphasized by Timdal in his analysis of the genus do not appear to be diagnostic for these groups. In Great Britain and Ireland, *Toninia* sensu stricto is now a much reduced genus, with most species being transferred to *Thalloidima* and *Toniniopsis*. However, the key below includes all of these segregates to aid

continuity from the last edition.

According to Kistenich *et al.* (2018), species of *Toninia s. str.* have a green, K–, N+ violet "Bagliettoana-green" pigment (Meyer & Printzen 2000) or brown, K–, N– pigment in the epithecium and exciple, ellipsoidal to acicular 0-, 1- or multiseptate ascospores; and are either lichenicolous or have a thallus varying from flattened-squamulose to bullate.

Of species placed provisionally in *Toninia* by Hitch *et al.* (2009), *T. squalescens* and *T. thiopsora* have \pm conglutinated paraphyses without a swollen apical cell and pigmented cap and asci without an ocular chamber. Molecular data contributed by Kistenich *et al.* (2018) demonstrate that neither belong in the Ramalinaceae, and the former has now been moved to *Gilbertaria* [Lecanorales: Sphaerophoraceae] by Svensson *et al.* (2022); see also Cannon *et al.* (2022). An appropriate generic placements has not yet been suggested for *T. thiopsora* and it is retained here pending further research. A third species in this category, *T. tumidula*, was transferred to *Porpidinia* by Timdal (2010), a genus placed in the Lecideaceae by Lücking *et al.* (2017).

Toninia tristis (Th. Fr.) Th. Fr. (1874) is erroneously reported from Britain and Ireland.

Literature

Cannon *et al.* (2022), Hitch *et al.* (2009), Kistenich *et al.* (2018), Meyer & Printzen (2000), Svensson & Fryday (2022), Timdal (1991, 2010).

1	Lichenized thallus present, or \pm associated with cyanolichens, at least when young, but not lichenized out	2
	Lichen thallus absent, lichenicolous	22
2 (1)	Paraphyses \pm lax, not conglutinated, each with a distinct swollen apical cell covered by a pigmented cap; asci with a well-developed ocular chamber	3
	Paraphyses \pm conglutinated, not lax, with or without a swollen apical cell and pigment cap; asci with or without an ocular chamber	17
3 (2)	Epithecium grey, K+ violet (<i>Thalloidima</i>) Epithecium green or brown, K–	4 8
4 (3)	Hypothecium pale brown to colourless, ± transparent Hypothecium reddish brown, ± opaque	5 6
5(4)	Squamules bullate to columnar, marginal squamules not elongated; pseudocyphellae ± inconspicuous, white, not to moderately pruinose, pruina farinose	oides ulata
6 (4)	Squamules irregularly convex to bullate, not to entirely pruinose; pruina finely farinose Squamules ± convex but not bullate, usually entirely white-pruinose; pruina granular	7 <i>ctum</i>
7 (6)	Squamules strongly convex to extended bullate-nodulose and partly vertically flattened, often imbricate; considered extinct in our region	oides olium
8 (3)	Hypothecium and inner part of exciple pale brown to colourless	alida 9
9 (8)	Ascospores mostly 3- to 7-septate, length/breadth ratio $> 8:1$, acicular or narrowly cylindrical Ascospores mostly 1- to 3-septate, length/breadth ratio $< 6:1$, cylindrical to ellipsoidal	10 13

10 (9)	Ascospores $11-19 \times 1.9-2.3 \mu m$, (0-) 3 (-5) septate at maturity (the septa developing at a late stage); on acid rock	
	Ascospores >20 µm long, 3- to 7-septate; on bark, soil or plant debris	
11 (10)	On trunks of mature trees in ancient woodlands; thallus granular	
12 (11)	Hymenium 40–55 µm tall; ascospores 2–2.5 (–3) µm broad; widespread <i>Toniniopsis bagliettoana</i> Hymenium 70–80 µm tall; ascospores 3–4 µm broad; montane, very rare <i>Toniniopsis coelestina</i>	
13(9)	Epithecium brown, N–	
14 (13)	Thallus crustose, areolate to rimose; areoles without maculae	
15 (14)	Thallus finely warted to ± granular; on limestone, montane	
16 (14)	Ascospores narrowly ellipsoidal to cylindrical with blunt rounded ends; lowland habitats <i>Toniniopsis aromatica</i> Ascospores persistently cylindrical with pointed ends; montane habitats <i>Toniniopsis fusispora</i>	
17 (2)	Thallus yellow-brown to buff, C+ orange; ascospores (5-)7-septate" <i>Toninia" thiopsora</i> Thallus pale to dark grey, C–; ascospores simple to (1-)3-septate	
18 (17)	Hypothecium pale brown to colourless 19 Hypothecium reddish brown to dark brown 21	
19 (18)	Thallus K+ yellow; epithecium olive-green, K	
20 (19)	Thallus often reduced, cream to pale grey, often following cracks in rock; ascospores (8–) 9–11 (–13) × 3.5–4.5 μm	
21 (18)	Thallus thin, effuse; apothecia 0.2–0.4 mm diam.; epithecium indistinct	
22 (1)	Ascospores consistently 1-septate, ellipsoidal	
23 (22)	On <i>Circinaria calcarea</i> ; epithecium greenish	
24 (22)	Ascospores <17 μm; on <i>Lecanora campestris</i> , elsewhere on <i>Protoparmeliopsis muralis</i> and <i>Lecidella scabra</i>	

Toninia plumbina (Anzi) Hafellner & Timdal (1991)

Thallus immersed in host tissue, not distinct. Apothecia to 0.6 mm diam., not pruinose, with a prominent margin and flat disc when young, becoming immarginate and convex with age; true exciple blackish brown on the rim and dark brown internally, sometimes with a green tinge, lacking crystals, K-, N-, or N+ violet (green pigment); epithecium dark olivaceous green to bright green, lacking crystals, K-, N+ violet; hymenium 50-60 µm tall; hypothecium dark brown, lacking crystals. Ascospores (1-) 3 (-5) septate, $18.5-29 \times 3-4.5 \mu m$, narrowly fusiform to cylindric-fusiform. Pycnidia immersed; conidia filiform. Lichen products not examined. BLS 1907.

On thallus of *Pectenia plumbea* s. str. in both corticolous and saxicolous communities. England (Lake District), W. Scotland.

Similar to Toniniopsis aromatica in internal apothecial anatomy, but parasitic and with longer, (1-) 3 (-5) septate ascospores.

Toninia squalida (Ach.) A. Massal. (1852)

Squamules to 3 mm diam., often proliferating and forming a ± continuous crust, weakly concave to weakly convex; upper surface brown to dark brown, sometimes with a grey tinge, not pruinose, dull, often with shallow fissures, lacking pseudocyphellae; edges concolorous with the upper surface; upper cortex 25-100 µm thick, including a 20–30 µm thick epineeral layer, lacking calcium oxalate crystals; lower cortex pale brown, poorly developed; photobiont layer discontinuous; medulla lacking crystals. Apothecia to 1.5 mm diam., flat to weakly convex, not pruinose; true exciple indistinct, dark brown in the rim, sometimes green, pale brown to colourless in the inner part, K-, N± violet (green pigment); epithecium green, lacking crystals, K-, N+ violet; hymenium 70-80 µm tall, colourless; hypothecium colourless to pale

brown. Ascospores $17-45 \times 3-5 \mu m$, 3- to 7-septate, acicular. Lichen products not detected by TLC. BLS 1427. On calcareous rock, mainly amongst mosses in seepage tracks, in alpine areas; rare. N. Scotland (Highlands).

A rather variable species characterized by the green epithecium, pale hypothecium and 3- to 7-septate acicular

ascospores. Could be confused with Toniniopsis aromatica and T. coelestina, however both these species have a dark hypothecium.

Toninia subfuscae (Arnold) Timdal (1991)

Thallus immersed in host tissue, not distinct. Apothecia to 0.6 mm diam., not pruinose, with a persistent margin and flat to weakly convex disc; true exciple dark, red-brown with a green tinge, K-, N+ violet, lacking crystals; epithecium olivaceous green to dark green, K-, N+ violet, lacking crystals; hymenium 50–60 µm tall; hypothecium red-brown, lacking crystals. Ascospores ellipsoidal to shortly cylindrical, often slightly curved, (1-) 3-septate, 9.5-16 × 4.5-5 µm. Pycnidia not known. Lichen products not examined. BLS 2419.

Lichenicolous on Lecanora campestris. S. England, Wales (Ceredigion), Scotland (Ardnamurchan Peninsula).

Abroad, this species has also been reported on Lecanora muralis and Lecidella scabra. Close to Kiliasia episema, with 1-septate spores, on the thallus of Circinaria calcarea and to Toniniopsis aromatica, lichenized with its own thallus.

Toninia thiopsora (Nyl.) H. Olivier (1911)

Thallus of small squamules to 4 mm diam., weakly to strongly convex, sometimes nodulose, composed of aggregations of proliferating granules; upper surface pale to brown-yellow, not pruinose, dull, lacking fissures and pseudocyphellae; upper cortex 30-50 µm thick, poorly differentiated from the photobiont layer, lacking an epinecral layer, with crystals which dissolve in K; lower cortex absent; photobiont layer continuous; medulla with crystals dissolving in K. Apothecia occasional, to 1 mm diam., weakly to strongly convex, shiny, not pruinose; true exciple indistinct when young, confluent with the hypothecium, brownish black, K-, N-; epithecium colourless, lacking crystals, K-, N-; hymenium 60-80 µm tall; hypothecium brownish black.

NT



Nb



Paraphyses \pm conglutinated, without a swollen apical cell and pigmented cap. Asci without an ocular chamber. Ascospores 20–38 \times 3–5 μ m, mainly 7-septate, acicular. Thallus C+ orange, UV– (two unidentified lichen products, possibly xanthones). **BLS 1425**.

Overgrowing mosses or in fissures on siliceous, \pm vertical rock and boulder faces, often on or near the coast; rare. England (Dartmoor, Lake District), Scotland (W. Highlands), N. & W. Wales, Ireland.

The pale brown, \pm closely granular, C+ orange thallus is diagnostic. Molecular data place this species outside of the Ramalinaceae, but its closest neighbours are not clear and there is apparently no appropriate genus in which it may be placed.

Toninia verrucariae (Metzler ex Nyl.) Timdal (1992)

Thallus absent, lichenicolous. Apothecia *ca* 0.5 mm diam., dark brown to black, with a flat disc and a narrow margin that is eventually excluded. True exciple, epithecium and hypothecium dark red-brown, sometimes tinged greenish or violet. Hymenium I+ vinaceous. Paraphyses conglutinated, frequently branched above, the apices brown-pigmented. Asci 8-spored. Ascospores $13-20 \times 4-6 \mu m$, ellipsoidal to cylindrical, 1-septate. **BLS 2550**.

On thalli of *Bagliettoa baldensis*, not discolouring the thallus; S. England (Portland, Dorset), Ireland (County Clare).

Much resembles *Kiliasia episema*, which grows on *Circinaria calcarea*, but differs in having a red-brown (not greenish) epithecium.

TONINIOPSIS Frey (1926)

Thallus granular-crustose, sometimes rimose-cracked, to squamulose, sometimes with maculae or fissures, usually not or weakly pruinose, pseudocyphellae absent or indistinct. Upper cortex usually poorly developed, an epinecral layer usually absent, usually not crystalline. Photobiont (where present) green, chlorococcoid. Medulla usually well-developed, of loosely interwoven hyphae, lacking crystals. Lower cortex absent. Ascomata apothecia, dark brown to black, not or faintly pruinose; usually \pm flat when young, later often becoming convex. Thalline margin absent. True exciple distinct when young but later often excluded, pale grey to dark brown throughout or with a dark grey rim, K- and N- or N+ violet. Epithecium greenish to olivaceous or brown, not containing crystals of calcium oxalate, K- and usually N+ violet. Hymenium I+ blue. Hypothecium dark reddish brown. Hamathecium of paraphyses, straight, unbranched or sparingly branched and anastomosed, not conglutinated, thin-walled, the apical cell distinctly swollen and covered by a \pm well-developed, gelatinous pigment cap. Asci Bacidia-type, 8-spored, clavate, surrounded by a gelatinous K/I+ blue sheath, with a well-developed K/I+ blue tholus containing a deeper-staining tube and pronounced ocular chamber. Ascospores (1-) 3- to 7-septate, colourless, acicular, fusiform, cylindrical or ellipsoidal, without a distinct perispore. Conidiomata rarely seen; when present immersed pycnidia. Conidia filiform, curved. Chemistry: lichen products not detected by TLC. Ecology: often initially associated with cyanolichens and possibly parasitic, later free-living, mainly on \pm base-rich rock and soil in exposed habitats, also on bark.

A segregate from *Toninia* with strong molecular support. It is distinguished in morphological terms more particularly by the reddish brown pigmentation of the hypothecium and inner part of the exciple, and in the green pigments ("Bagliettoana-green"; Meyer & Printzen 2000) of the epithecium that are found in most species.




Literature

Hitch et al. (2009), Kistenich et al. (2018), Meyer & Printzen (2000), Timdal (1991).

1	Ascospores mostly 3- to 7-septate, length/breadth ratio > 8:1, acicular or narrowly cylindrical
2 (1)	Ascospores $11-19 \times 1.9-2.3 \mu m$, (0-) 3 (-5) septate at maturity (the septa developing at a late stage); on acid rock
3 (2)	On trunks of mature trees in ancient woodlands; thallus granular
4 (3)	Hymenium 40–55 µm tall; ascospores 2–2.5 (–3) µm broad; widespread <i>Toniniopsis bagliettoana</i> Hymenium 70–80 µm tall; ascospores 3–4 µm broad; montane, very rare <i>Toniniopsis coelestina</i>
5 (1)	Epithecium brown, N–
6 (5)	Thallus crustose, areolate to rimose; areoles without maculae
7 (6)	Thallus finely warted to ± granular; on limestone, montane
8 (6)	Ascospores narrowly ellipsoidal to cylindrical with blunt rounded ends; lowland habitats
	Ascospores persistently cylindrical with pointed ends: montane habitats <i>Toninionsis fusispora</i>

Toniniopsis aromatica (Sm.) Kistenich, Timdal, Bendiksby & S. Ekman (2018) *Toninia aromatica* (Sm.) A. Massal. (1855)

Squamules to 4 mm diam., widely scattered or contiguous, rounded or irregular; upper surface flat or irregularly convex, pale grey to dark brown, often tinged green, pruinose or not, dull, usually with faint, paler spots and short lines along more convex areas and ridges, without regular fissures and pseudocyphellae, margin concolorous, not pruinose; upper cortex $60-90 \mu m$ thick, lacking a well-defined epineeral layer, without calcium oxalate crystals; lower cortex poorly developed or absent; photobiont zone continuous; medulla lacking crystals. Apothecia to 1.5 mm diam., ± persistently flat and marginate, not or sometimes faintly white-pruinose; true exciple confluent with the hypothecium, uniformly dark reddish brown, K–, N–; epithecium of $12-32 \times 3-64$ µm tall, colourless to pale brown; hypothecium dark reddish brown.



LC

colourless to pale brown; hypothecium dark reddish brown. Ascospores $12-23 \times 3-6 \mu m$, (1-) 3-septate, narrowly ellipsoidal with rounded ends. Lichen products not detected by TLC. **BLS 1415**.

In coastal and lowland inland sites on \pm base-rich soft rock, old mortar, cemented walls, especially in fissures or seepage tracks, also on consolidated soil, shell-sand dunes, very rarely on bark. Usually in close association with or on cyanolichens; sometimes parasitizing *Verrucaria nigrescens*; common, widespread. Throughout Great Britain and Ireland.

Very variable, but distinguished by the pale, irregular-white flecks on the upper surface of the squamules. Differs from *T. verrucarioides* mainly in the pigment in the epithecium and shape and colour of the squamules. The exclusively coastal *T. mesoidea* has a more crustose thallus and is not white-flecked. The spores of *T. coelestina* are mostly 7-septate.

Toniniopsis bagliettoana (A. Massal. & De Not.) Kistenich & Timdal (2021)

Bacidia bagliettoana (A. Massal. & De Not.) Jatta (1900)

Thallus white or green-white, \pm granular or warted; photobiont cells 7–15 µm diam. Apothecia 0.3–1 (–1.2) mm diam., flat and marginate, eventually \pm convex, usually distinctly constricted below, black; true exciple red-brown in upper and outer parts, pale red-brown within but becoming colourless below, hyphae radiating, 3–5 µm diam. (in K) with thick, gelatinized walls and lumina to less than 1.5 µm; epithecium olive-to blue-green, K–, N+ violet with blue granules; hymenium 40–55 µm high; hypothecium red-brown and K+ intensifying red in upper 25–35 µm, pale red to colourless below; paraphyses 1.5–2 µm diam., unbranched or a few forked above, the apices swollen to 4 (–5) µm. Ascospores 25–45 × 2–2.5 (–3) µm, 3- to 7-septate, acicular or \pm bacilliform. **BLS 0158**.

Over mosses or plant debris on calcareous rocks (including old walls) or on the ground in chalk or limestone grassland or calcareous dunes; local. Throughout Britain, a few scattered Irish records.

Considered by Kistenich *et al.* (2018) to belong within *Toniniopsis* based on both molecular and morphological criteria. The necessary combination was not made at that time due to the possibility that an earlier name might exist for the species, but further investigation has identified typification complexities for one candidate and confusion between the other and a species of *Bacidina* that also occurs in our area. We prefer to maintain usage of the well-known epithet *bagliettoana*, and the necessary new combination is made below.

Sometimes confused in the field with *Bilimbia sabuletorum*, but easily separated by the ascospore shape and width, and black, not piebald apothecia. *Bacidia herbarum* grows in similar habitats, but has red-brown apothecia and *Bacidina indigens* has a colourless hypothecium.

Toniniopsis coelestina (Anzi) Kistenich, Timdal, Bendiksby & S. Ekman (2018) *Toninia coelestina* (Anzi) Vězda (1961)

Thallus crustose to subsquamulose, of small proliferating granules forming a thick, \pm continuous crust; upper surface greyish brown, not pruinose, dull, lacking fissures and pseudocyphellae; upper cortex varying from almost absent to 20 µm thick, irregular, lacking crystals; lower cortex absent; photobiont layer filling the inner part of granules or restricted to the upper part; medulla, when present, lacking crystals. Apothecia to 1.5 mm diam., flat but later becoming weakly convex, not pruinose; true exciple distinct when young, later becoming excluded, dark brown in the inner part, with a green edge visible in section, K–, N+ violet; epithecium green, lacking crystals, K–, N+ violet; hymenium 70–80 µm tall, colourless; hypothecium dark brown. Ascospores 25–38 × 3–4 µm, (3-) 7-septate, acicular. Lichen products not detected by TLC. **BLS 1424**.

On mosses and soil on calcareous schist, apparently associated with cyanolichens; not seen since the 1960s; very rare. Central Highlands (Mid-Perth and S. Aberdeenshire).

Resembles *T. aromatica* in apothecial anatomy, but the ascospores are acicular and mainly 7-septate. The widespread *T. bagliettoana* is very similar but has slightly narrower ascospores and a shorter hymenium.

Toniniopsis coprodes (Körb.) S. Ekman & Coppins (2021)

Bacidia coprodes (Körb.) Lettau (1912)

Thallus crustose, thin, pale green to grey-green or brownish green, finely warted to \pm granular (particularly when overgrowing bryophytes), the granules when present 60–250 µm diam. Prothallus lacking or thin and arachnoid, white. Apothecia 0.3–1.2 mm diam., rounded or irregularly lobed, at first flat, becoming \pm convex with age, rarely with a thin whitish pruina; disc dark purplish brown to black; margin concolorous with the disc, often shiny, distinct, slightly raised in young apothecia, becoming excluded; true exciple composed of radiating hyphae with thick gelatinous walls and cell lumina 7–12 × 1.5–3 µm in size, gradually wider towards the edge, laterally redbrown to greenish black, containing a mixture of a red-brown (K+ purplish, N+

orange-red) and a sordid green pigment (K+ intensifying green, N+ purple with the deposition of blue crystals), rim sometimes paler than the inner exciple; hypothecium in upper part dark red-brown to greenish black (with a red-brown, K+ purplish and N+ orange-red, and sometimes also a green, K+ intensifying green and N+ purple



VU(D1, D2)



LC



pigment), concolorous with upper part of exciple, lower part of hymenium gradually merging into a paler medulla; hymenium 50–64 μ m tall, colourless below, upper part with varying amounts of green pigment, as a distinct epihymenial layer or diffusely and unevenly dispersed in upper part. Paraphyses 1.5–2.8 μ m diam., unbranched or sparingly branched in the upper part, the apices \pm clavate, 2.5–5 μ m diam., sometimes with a gelatinous cap with green pigment. Asci clavate, 8-spored. Ascospores $10-20 \times 2.5-4.5 \,\mu$ m, colourless, straight or slightly curved, cylindrical or narrowly ellipsoidal, sometimes slightly tapering towards one end, 3- (to 5)-septate. Pycnidia often present, semi-immersed in the thallus except for a dark brown to blackish ostiolar region, 50–100 μ m diam., with a brown (K+ purplish, N+ orange-red) pigment (but no green pigment) in the upper part; Conidia 3–10 \times 1.5–2.8 μ m, bacilliform, narrowly ellipsoidal, or tear-shaped, or 6–20 \times 0.8–1.0 μ m, filiform, curved. No lichen substances detected by TLC. **BLS 2635**.

On limestone or other base-rich types of rock, usually in shade, such as crevices or overhangs. Scotland (Angus), with only a single confirmed record from the Britain; two further collections from the Ben Lawers massif have longer (19–26 μ m), 5- to 7-septate ascospores and may represent a different species according to Ekman (2014).

Toniniopsis coprodes may be compared with *T. inornata* which has \pm tuberculate apothecia with a thinner hymenial layer and occurs on acid rocks; it also has narrower ascospores.

Toniniopsis fusispora (Hepp ex Körb.) Cl. Roux (2020)

Toninia fusispora (Hepp ex Körb.) Th. Fr. (1867)

Squamules to 1.5 mm diam., flat to slightly convex, with flexuose margins, whitish or pale grey, tinged green in places, maculate when wet; widely scattered to contiguous on a black mat of cyanobacterial tissue; *ca* 0.2 mm thick, upper cortex 50 μ m thick with no definite epinecral layer and no crystals; photobiont layer 100 μ m thick, discontinuous, with individual photobiont cells from 2.5–10 μ m diam.; medulla to 50 μ m thick with no clear-cut lower cortex, lacking crystals. Apothecia to 1 mm diam., remaining marginate when mature, not pruinose, true exciple tumid, brown-black, shining, paler than the disc which remains flat, red-brown internally, K– N–, confluent with the hypothecium; epithecium brown-green to green, lacking crystals, K–, N+

violet, hymenium 60–65 μ m tall, colourless to straw-coloured, K–; hypothecium dark red-brown. Ascospores (14–) 16–29 (–35) × 3.5–5 μ m, cylindrical with pointed ends. Pycnidia black, to 50 μ m diam., sessile, on the thallus areoles; conidia filiform, sickle-shaped, 10–12.5 × *ca* 1 μ m. Lichen products not detected by TLC. **BLS 1577**.

On vertical montane limestones and calcareous schist from 300–1150 m; rare. Central Highlands (Ben Alder, Ben Lawers, Caenlochan), N. Wales (Snowdonia), N.W. Ireland (Slieve League).

Distinguished from *Toniniopsis aromatica* by the cylindrical spores with pointed (not rounded) apices, and the montane habitat.

Formally transferred into *Toniniopsis* below. There are several names previously placed into synonymy with *T. aromatica* that might possibly provide an earlier name for this lichen, but we prefer to maintain usage of Körber's name for the present.

Toniniopsis inornata (Nyl.) S. Ekman & Coppins (2021)

Bacidia inornata (Nyl.) Blomb. & Forssell (1880)

Thallus thin, pale green to grey-green, almost granular or finely areolate, with a \pm smooth, warted or scurfy surface. Prothallus thin, white, arachnoid. Apothecia 0.2–0.7 mm diam., rounded or irregularly lobed, flat, somewhat convex with age, without pruina, often becoming tuberculate by regeneration of several young apothecia from aging apothecia; disc yellow-brown to red-brown or black, sometimes piebald; margin darker than or concolorous with disc, slightly raised in young apothecia, soon level, persistent; true exciple composed of radiating, mainly dichotomously branched hyphae with thick gelatinous walls and cell lumina 7–12 × 2–2.5 µm in inner part, gradually wider towards the edge, terminal cells up to 8 µm diam., blackish purplebrown or blackish green with a mixture of a red-brown (K+ purplish, N+ orange-red)

and, in the upper lateral parts, a sordid green pigment (K+ intensifying green, N+ purple with the deposition of blue crystals); hypothecium in upper part dark red-brown, with a red-brown, K+ purplish and N+ orange-red pigment); hymenium 32–46 μ m tall, colourless or dilute red-brown, upper part also with unevenly distributed



LC



Nb

spots of red-brown and sordid green pigment. Paraphyses 1.2-1.6 µm diam., unbranched or sparingly branched in the upper part, apices clavate, 2-4 µm diam., sometimes with a gelatinous cap with red-brown or green pigment. Asci clavate, 8-spored. Ascospores $11-19 \times 1.9-2.3 \mu m$, colourless, straight, cylindrical or shortacicular with blunt ends, (0-) 3 (-5) septate at maturity, the septa apparently forming late during ascospore development. Pycnidia often present, sessile to stipitate, 60-90 µm diam., unilocular; wall with a red-brown (K+ purplish, N+ orange-red) pigment. Conidia $4-7 \times 1.2-1.5 \,\mu$ m, bacilliform to narrowly ellipsoidal. No lichen substances detected by TLC. BLS 2636.

On acid, easily weathering rocks and boulders in humid and shady situations, often near water. Wales (Carmarthen) and Scotland (Mid-Perthshire).

Similar to T. coprodes but with apothecia that tend to become \pm tuberculate and clustered, and with a thinner hymenium. That species occurs on base-rich rocks.

Toniniopsis mesoidea (Nyl.) Timdal (2018)

Toninia mesoidea (Nyl.) Zahlbr. (1926)

Thallus crustose, not on cyanolichens when young, rimose-cracked to areolate; areoles to 0.5 mm diam., flat, thin, rounded or irregular, sometimes crenulate, brown, olivebrown or somewhat green-grey, not pruinose, not white-flecked; upper cortex ± absent, to 40 µm thick, poorly developed, lacking crystals; lower cortex absent; photobiont layer filling the entire inner part of the areoles or \pm restricted to the upper part; medulla (when present) without crystals. Apothecia to 0.8 mm diam., flat, later becoming weakly to moderately convex, not pruinose; true exciple distinct when young, later becoming excluded, dark red-brown towards the rim, somewhat paler in the inner part; epithecium green, lacking crystals, K-, N+ violet; hymenium 60-70 µm tall,

colourless; hypothecium dark reddish brown throughout or faintly greenish in the upper part, K-, N- or N± violet (green pigment). Ascospores $14.5-17 \times 5.5-6 \,\mu m$, 3-septate, narrowly ellipsoidal to cylindrical. Lichen products not detected by TLC. BLS 1423.

On ± base-rich coastal rocks and serpentine (but not limestone); local. S.W. England, Wales, W. Scotland, Ireland, Isles of Scilly, Channel Islands.

Resembles T. aromatica, which may also occur on coastal rocks, but differs mainly in the rimose-cracked to scattered-areolate, never squamulose, thallus and the absence of white surface flecking. The ascospores tend to be shorter, but those of *T. aromatica* can be very variable in size.

Toniniopsis separabilis (Nyl.) Gerasimova & A. Beck (2021)

Bacidia subincompta auct. br., non (Nyl.) Arnold (1870)

Thallus of white scattered to confluent granules, not forming a thick granular crust, the granules $40-100 \,\mu\text{m}$ diam.; photobiont cells $7-14 \,\mu\text{m}$ diam. Apothecia $0.3-0.6 \,(-100 \,\mu\text{m})$ 0.9) mm diam., flat, later convex, sometimes tuberculate and to 1.2 mm diam., black or rarely pale (albino morph); true exciple weakly developed, dark red-brown within, the outer edge \pm colourless; epithecium pale to dark green, K-, N+ purple-violet; hymenium 50-65 µm high, colourless; hypothecium dark red-brown, K± purple in upper part, pale red-brown below; paraphyses 1–1.5 µm diam., unbranched or rarely forked above; apices only slightly wider, to 3 μ m diam. Ascospores 20–36 (–40) × 2.3–3.5 (–4) μ m, 3- to 7-septate, \pm cylindrical. Pycnidia inconspicuous, blackish; conidia $10-20 \times ca \ 0.8 \ \mu\text{m}$, filiform, curved. **BLS 0168**.

On trunks of mature trees (Fraxinus, Quercus, Populus tremula, Betula pubescens and Ulmus) in wound tracks, in ancient woodlands; rare. N. England (Cumbria, Durham), C. Wales, S.E. Scotland (Selkirkshire), N. Scotland (C. & E. Highlands).

Characterized by the thinly granular thallus, black apothecia, green epithecium and red-brown upper hypothecium (except the rare albino morph), and cylindrical ascospores. Bellicidia incompta has a granularverrucose thallus, a colourless or pale red epithecium, shorter ascospores, a completely dark red-brown hypothecium and cylindric-ellipsoidal conidia.

This species was treated as Bacidia subincompta by Coppins & Aptroot (2009) and Toniniopsis subincompta by Kistenich et al. (2018), but Gerasimova et al. (2021) demonstrated that the type of that species belongs to Bellicidia incompta. British material studied to date belongs to T. separabilis, but the look-alike species T. dissimilis Gerasimova & Beck (2021) could also occur in our region.



Nb

74



VU(C, D1)

Toniniopsis verrucarioides (Nyl.) Kistenich, Timdal, Bendiksby & S.Ekman (2018) LC NS Toninia verrucarioides (Nyl.) Timdal (1991)

Squamules to 2 mm diam., scattered to imbricate, flat to weakly convex, irregularly crenulate; upper surface dark grey-brown, partly faintly pruinose or not, dull or somewhat shiny, often with shallow fissures, lacking maculae and pseudocyphellae, the edge concolorous with the upper side; upper cortex 50–120 μ m thick, with a well-developed epinecral layer, often containing crystals of calcium oxalate; lower cortex poorly developed or absent; photobiont layer continuous; medulla without crystals. Apothecia to 1 mm diam., \pm persistently plane, faintly white-pruinose or not; true exciple persistent, confluent with the hypothecium below, uniformly dark reddish brown, K–, N–; epithecium brownish black, sometimes with a faint green tinge,



without crystals, K–, N– or faintly violet (green pigment); hymenium 70–80 μ m tall, colourless to pale brown; hypothecium dark red brown. Ascospores 10–18 × 4–6 μ m, (1-) 3-septate, cylindrical. Lichen products not detected by TLC. **BLS 1418**.

Overgrowing cyanolichens, especially *Placynthium*, on calcareous rock; locally common. Scattered throughout Britain and Ireland.

Differs from *T. aromatica* in the brown epithecium, sometimes with a green tinge and brown, often somewhat imbricate, squamules without white flecks.

TYLOTHALLIA P. James & H. Kilias (1981)

Thallus thick, of convex and warty-verrucose areoles, often mosaic-forming, white to green-grey, purple-grey or dull green-white. **Prothallus** black, often well-developed. **Photobiont** chlorococcoid, cells 6–12 µm diam. **Ascomata** apothecia, to 1.5 mm diam., at first flat, becoming convex and at times tuberculate, irregularly thickened with a warty surface, dark blue-grey to black. **Disc** sometimes thinly pruinose, especially when young. **True exciple** 1–1.5 mm wide, distinct at first but becoming excluded, of richly branched, coherent hyphae, each surounded by a gel coat that swells to 10 µm wide in K, K+ yellowish to orange, Pd+ pale yellow. **Hamathecium** of paraphyses, 1.5–2 µm diam., numerous, slender, richly branched above and sometimes anastomosed, the apices mostly slightly irregularly swollen, not regularly capitate, K/I+ blue. **Asci** *Biatora*-type. **Ascospores** (0-) 1-septate, ellipsoidal, without a distinct perispore, colourless. **Conidiomata** pycnidia, immersed, often with a residual thalline rim. **Conidiogenous cells** ± cylindrical, enteroblastic, acrogenous. **Conidia** ellipsoidal or shortly cylindrical, aseptate, colourless. **Chemistry**: orcinol depsides, β-orcinol depsides and depsidones. **Ecology**: on siliceous rocks.

Similar to *Cliostomum*, but with more coherent and more branched and anastomosed paraphyses and with immersed pycnidia with colourless walls, except for a green, not purple, pigment around the ostioles. There is only one species from our region.

Literature:

James (2009), Kantvilas (2014), Kistenich et al. (2018).

Tylothallia biformigera (Leight.) P. James & H. Kilias (1981) LC

Thallus thin to thick, irregularly warted, conspicuously rimose-cracked, \pm dull green-grey. Apothecia 0.4–0.8 mm diam., to 1.5 mm diam. when tuberculate with a thick, often flexuose proper margin, scattered or sometimes \pm clustered; true exciple colourless to pale red-brown within, K \pm intensified or orange-brown, the outer edge pale to dark brown, K \pm olivaceous-black, N+ red, Pd+ yellow-orange; epithecium black-blue-green or in part dark olive- to fuscous-brown, minutely granular, K \pm green or black, K+ intensifying, N+ red, this and the outer edge of the exciple \pm with scattered minute interspersed crystals; hymenium 50–70 µm tall, usually tinged blue; hypothecium massive, downwardly extended, pale. Ascospores 10–15 × (2.5–) 3–5 µm, elongate-ellipsoidal with

abruptly rounded ends. Conidia 3.5-4 × 1-1.5 µm. Cortex and medulla C-, K± yellow to orange, $Pd\pm$ orange, UV- or faint blue-white (atranorin, 2'-O-methylperlatolic acid. \pm 2 unidentified depsides, norstictic and fumarprotocetraric acids). BLS 1440.

On shaded, dry sides of \pm vertical siliceous coastal rocks and walls, more rarely on dry sheltered vertical rock faces or below overhangs in inland montane areas (to 640 m), often on boulders and walls along woodland margins; rather local. N. & W. Britain and W. Ireland.

A very variable species often forming extensive mosaics.

Ramalinaceae species of uncertain placement

Three species of Ramalinaceae do not currently have appropriate generic placements, or have problems of nomenclature such that they cannot formally be included in their likely generic positions. They are listed here on a temporary basis pending further taxonomic research.

Catillaria aphana (Nyl.) Coppins (1989)

Thallus effuse, cream-white to pale grey, thin to verrucose or rimose, rarely immersed, often following lines in rock; areoles 0.1-1.0 mm diam.; photobiont cells 7-13 µm diam. Apothecia sessile, 0.2-0.5 mm diam., scattered or a few confluent, dark brown to black, often with piebald areas; disc concave to flat, later convex and roughened; true exciple shallow, becoming excluded, the outer and upper parts mostly dark redbrown, K+ tinged purple or violaceous, but upper part can be dark grey-brown, K+ green-grey, hyphae coherent in K, with 1-2 µm diam. lumina and thick gelatinized walls, overall 5-8 µm diam. in K; inner parts colourless to pale straw-yellow; epithecium dark red-brown, K+ tinged purple or violaceous, with some grey, K+ green-grey pigment; hymenium 43–55 μ m tall, \pm colourless below, pale red-brown

above; hypothecium colourless or pale straw-yellow; paraphyses 1.5-2 µm diam., coherent in K, occasionally branched; apices clavate, to 4.5 µm diam., most surrounded by dense dark brown or grey pigment. Asci Bacidiatype. Ascospores (8–) 9–11 (–13) × 3.5–4.5 µm, 0- to 1 (-3)-septate, ellipsoidal to cylindric-ellipsoidal. Pycnidia not found. Lichen products not detected by TLC. BLS 0696.

On calcareous rocks, often weakly so (schists, calcite, chalk), on vertical dry ± well-lit coastal and inland cliff faces below 300 m; rare. S.W. England, Mid Wales, W. Scotland, W. &. N. Ireland.

Similar to C. scotinodes, which has longer ascospores. Morphs with a well-developed thallus can resemble Diplotomma species and endolithic forms of Catillaria lenticularis; the latter has paraphyses which are lax in K, with discrete, dark brown apical caps.

The relationship between C. aphana and C. scotinodes was confirmed by Reese Naesborg et al. (2007), with sequences occupying a clade sister to Cliostomum tenerum and Lecania naegelii. The two species were transferred to Coppinsidea by Kondratyuk et al. (2019), but they did not present convincing evidence of a close relationship with the type of that genus, and they admitted that the genus was polyphyletic in their circumscription.

Catillaria modesta (Müll. Arg.) Coppins (1989)

Thallus effuse, pale fawn to ochraceous, thin, rimose or slightly warted; photobiont cells 5-14 µm diam. Apothecia 0.2-0.4 mm diam., flat to convex; true exciple becoming excluded, with the outer edge pale brown or colourless, the hyphae coherent in K, 2-4 (-6) µm diam., the inner part dark red-brown; epithecium indistinct; hymenium 45-55 mm tall, colourless, or pale red-brown below (or in vertical streaks); hypothecium dark red-brown, K+ purple; paraphyses 1.3-2 µm diam., unbranched or branched above, apices swollen to 3(-4) µm diam., colourless. Asci Bacidia-type. Ascospores (8–) 9–12 (–15) \times 3.5–4.5 µm, 0- to 1-septate, ellipsoidal or ovoid-

VU (D2)







NT



ellipsoidal to cylindrical. Pycnidia not found. Lichen products not detected by TLC. BLS 0750.

On limestone; rare. Only a few British and Irish records, N. England (Durham), Scotland (Mid Perths., West Ross, Skye), N. Ireland.

Similar to *C. aphana* and *C. scotinodes* but with a dark hypothecium and inner true exciple as also seen in *C. picila*. The *Bacidia*-type ascus structure distinguishes this and *C. picila* from the common *Clauzadea monticola* which has *Porpidia*-type asci. Reese Naesborg *et al.* (2007) found that a sequence of *C. modesta* clustered with *Toninia cinereovirens*, but the branch lengths were long and more data are required to fix its application. There are no sequences available for *C. picila* so its affinities are unknown.

Catillaria scotinodes (Nyl.) Coppins (1989)

Like *C. aphana*, but the thallus always epilithic, dark brown-grey, continuous, rimose, not following lines in rock, thinly vertucose. Outer part of true exciple, upper hymenium and epithecium mostly dark green, a brown K+ purple pigment sometimes additionally present, Paraphyses $1.5-1.8 \mu m$, apices to $5 \mu m$ diam., dark green-pigmented. Ascospores (10-) 12–17 $(-19) \times 4.5-5 \mu m$. Pycnidia rare, immersed, black, 50–60 μm diam.; wall green; conidia strongly curved, $18-20 \times ca 0.5 \mu m$. **BLS 0770**.

On calcareous mica-schist and calcareous sandstone on \pm vertical, overhung clifffaces; scarce. N.E. England (N.E. Yorkshire), N. Wales, S.E. Scotland, scattered throughout the Scottish Highlands.

Similar and apparently related to *C. modesta*, which has a dark hypothecium and inner true exciple. See under that species for more information.



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