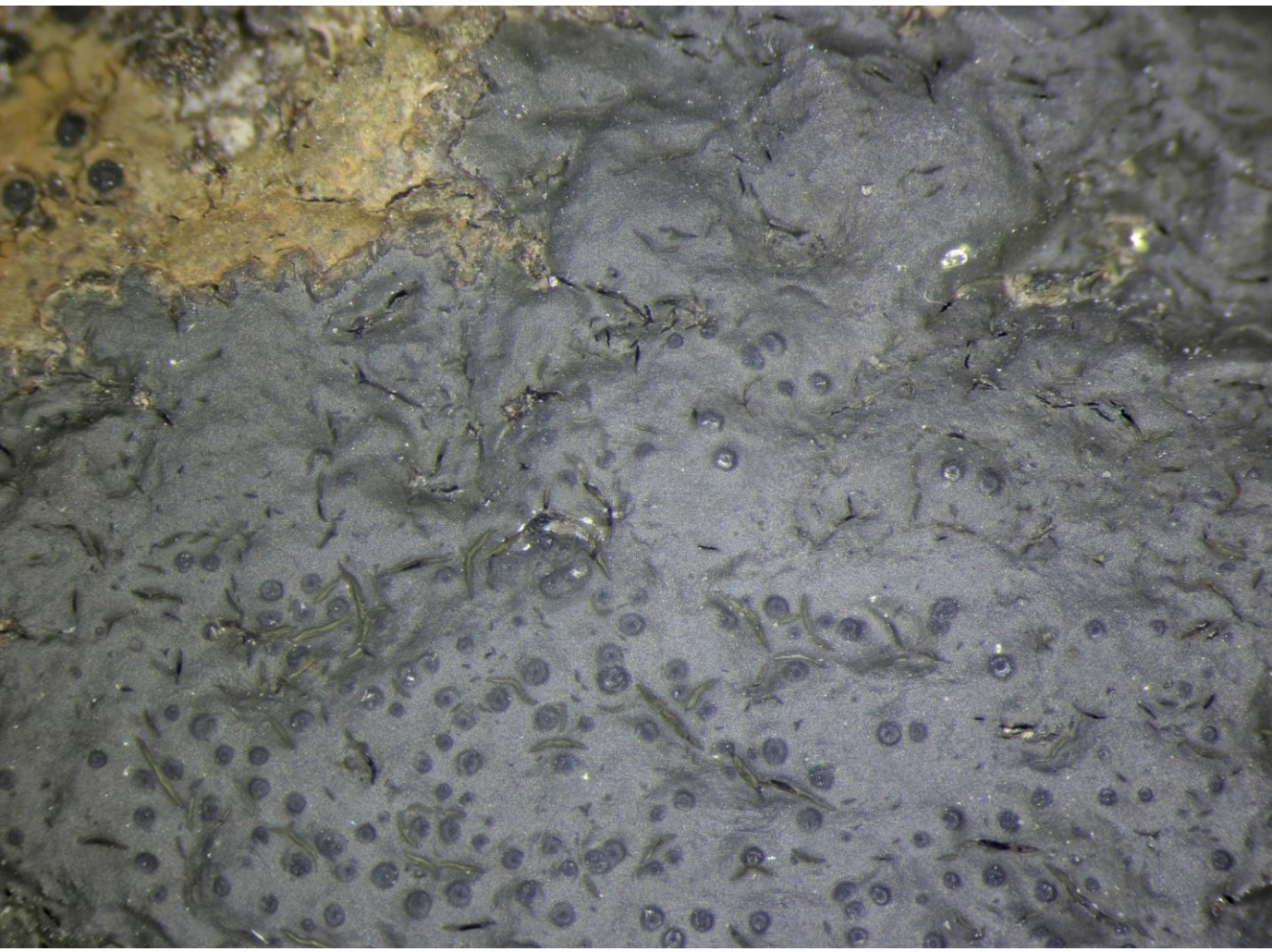
Revisions of British and Irish Lichens

British Lichen Society

Volume 31 **February 2023**



Verrucariales: Verrucariaceae

Cover image: *Verrucaria pachyderma*, on siliceous rock in a stream, Invermark, Glen Esk, Angus, Scotland.

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to compile new printed editions of the entire lichen biota of Britain and Ireland is extensive, and many parts are out-of-date even as they are published.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*.

Downloads can be obtained from the British Lichen Society website at
https://www.britishlichensociety.org.uk/content/lgbi3

ISSN 2634-7768

Revisions of British and Irish Lichens **vol. 31**

Verrucariales: Verrucariaceae

including the genera *Agonimia*, *Atla*, *Bagliettoa*, *Catapyrenium*, *Dermatocarpon*, *Endocarpon*, *Henrica*, *Heteroplacidium*, *Hydropunctaria*, *Involucropyrenium*, *Merismatium*, *Nesothele*, *Normandina*, *Parabagliettoa*, *Placidopsis*, *Placidium*, *Placopyrenium*, *Polyblastia*, *Psoroglaena*, *Sporodictyon*, *Staurothele*, *Thelidium*, *Trimmatothele*, *Verrucaria*, *Verrucula*, *Verruculopsis* and *Wahlenbergiella*.

by

Alan Orange†
52 Insole Grove East, Llandaff, Cardiff CF5 2HP, UK

Paul Cannon
Royal Botanic Gardens, Kew, Surrey TW9 3AB, UK; email p.cannon@kew.org

Maria Prieto
Department of Biology and Geology, Physics and Inorganic Chemistry, Rey Juan Carlos University, C/Tulipán s/n, 28933, Móstoles, Madrid, Spain

Brian Coppins
Royal Botanic Garden Edinburgh, 20A Inverleith Row, Edinburgh EH3 5LR, UK

Neil Sanderson
3 Green Close, Woodlands, Southampton, Hampshire, SO40 7HU, UK

Janet Simkin
School of Natural and Environmental Science, Newcastle University, Newcastle upon Tyne NE1 7RU, UK

This publication can be cited as:

Orange, A., Cannon, P., Prieto, M., Coppins, B., Sanderson, N. & Simkin, J. (2023). Verrucariales: Verrucariaceae, including the genera *Agonimia*, *Atla*, *Bagliettoa*, *Catapyrenium*, *Dermatocarpon*, *Endocarpon*, *Henrica*, *Heteroplacidium*, *Hydropunctaria*, *Involucropyrenium*, *Merismatium*, *Nesothele*, *Normandina*, *Parabagliettoa*, *Placidopsis*, *Placidium*, *Placopyrenium*, *Polyblastia*, *Psoroglaena*, *Sporodictyon*, *Staurothele*, *Thelidium*, *Trimmatothele*, *Verrucaria*, *Verrucula*, *Verruculopsis* and *Wahlenbergiella*.. *Revisions of British and Irish Lichens* **31**: 1-104.

Alan Orange (1955 – 2023)

Most regrettably, Alan Orange died shortly before publication of this work, and was not able to oversee its final stages. Alan was a greatly respected lichenologist, equally at home in the field and in the laboratory, naturally modest but highly dedicated to his studies and a valued teacher. He was a prolific author and a world-renowned specialist in the Verrucariaceae, combining expertise in molecular phylogenetics with meticulous morphological observation. Any imperfections in this volume must of course be the responsibility of his co-authors.

VERRUCARIACEAE Zenker (1827)

Thallus crustose, squamulose, minutely fruticose or foliose, sometimes composed of goniocysts, very rarely the form determined by a blade-like photobiont. **Upper cortex** a pseudocortex or a paraplectenchyma; epinecral layer sometimes present. **Photobionts** include members of Trebouxiophyceae (*Asterochloris*, *Diplosphaera*, *Elliptochloris*, *Myrmecia*, *Prasiola*, *Trebouxia*), Xanthophyceae (*Heterococcus*), and very rarely Ulvophyceae (*Blidingia*) or Phaeophyceae (*Petroderma maculiforme*); photobiont absent in some lichenicolous taxa that may not belong in this family. **Soralia** very rare, **isidia** rare, but sometimes propagating via blastidia. **Ascomata** perithecial, often clypeate with a well-developed involucrellum. **Hamathecium** of periphyses and/or periphysoids in the upper part of the acomatal cavity; interascal filaments absent. **Asci** clavate, rarely cylindrical, mostly fissitunicate and dehiscence rostrate, sometimes obscure and/or evanescent, ocular chamber usually present, not blueing in iodine, (1–)2–8(–many)-spored. **Hymenial gel** I+ red (+ blue at very low concentrations of iodine), K/I+ blue. **Ascospores** aseptate, septate or muriform, colourless to brown. **Conidiomata** pycnidia, immersed in the thallus or on the margins of squamules. **Conidiogenous cells** short, proliferating percurrently. **Conidia** aseptate, rod-shaped to curved.

One of the largest families of lichens, containing 43 genera and around 950 species as enumerated by Lücking *et al*. (2016). It is the type family of the Verrucariales, which also includes the Adelococcaceae and perhaps also the Sarcopyreniaceae, as well as some genera of uncertain disposition.

The perithecial ascomata that lack interascal filaments but usually have periphysoids (apical paraphyses), and the fissitunicate asci with rostrate dehiscence are key diagnostic features. Ascospore measurements and length/breadth ratios are important for identification in many genera.

There is a number of non-lichenised, mostly lichenicolous taxa that resemble Verrucariaceae in the nature of the hamathecium and in the hemiamyloid hymenial gel; species from 16 genera fall into this category and are placed in the family by Diederich *et al*. (2018). Except where there is good molecular data it is difficult to be certain of the phylogenetic position of these, but it is possible that no non-lichenised taxa belong in Verrucariaceae. With this in mind, the following lichenicolous genera are excluded from this account and will be dealt with in a separate volume: *Endococcus*, *Halospora* (questionably distinct from *Merismatium*), *Phaeospora* and *Telogalla*. The lichen genus *Phylloblastia* was included in the Verrucariaceae by Lücking *et al*. (2016), but at least the British and Irish species belong in the Chaetothyriales.

Literature

Breuss (2010), Diederich *et al*. (2018), Gueidan *et al*. (2007, 2009), Krzewicka (2012), Lücking *et al*. (2016), Moberg *et al*. (2017), Muggia *et al*. (2010), Orange (2013a), Pérez-Ortega *et al*. (2018), Thüs *et al*. (2011), Thüs & Schultz (2009).

The key below includes some sterile material, but in many cases it will not be evident that sterile material belongs in Verrucariaceae, so it will be necessary to use in conjunction with the keys to sterile lichens in *Lichens of Great Britain and Ireland*. Characters sometimes apply only to British and Irish species of the respective genera.

1 Thallus squamulose (sometimes minutely) or foliose 2
Thallus crustose (smooth, granular, areolate or subsquamulose) or minutely fruticose (terete branches <50 µm wide), or no lichenised thallus present 10

Squamulose and foliose taxa

2(1) Thallus foliose (usually distinctly so, but rarely of crowded thalli only 2-7 mm diam.), attached by one or more hapters; rhizines and rhizoidal hyphae absent, lower cortex pseudoparenchymatous, ascospores aseptate ..... ***Dermatocarpon***
Thallus squamulose, sometimes attached by rhizoidal hyphae or thin rhizines, lower cortex various or absent 3

3(2) Ascospores aseptate or 1-septate 4
Ascospores 5-septate to muriform 8

4(3) Perithecia situated between the squamules, surrounded by an involucrellum; exciple dark, rhizoidal hyphae brown; ascospores aseptate, 17–21 µm long ..... ***Involucropyrenium waltheri***
Perithecia immersed in the squamules, without an involucrellum 5

5(4) Thallus subsquamulose, underside black, without rhizoidal hyphae, ascospores 0–1-septate ..... ***Placopyrenium trachyticum***
Thallus squamulose, rhizoidal hyphae often present 6

6(5) Ascospores 1-septate; upper cortex a pseudocortex; pycnidia absent ..... ***Placidiopsis***
Ascospores aseptate, rarely with a septum in overmature spores 7

7(6) Rhizoidal hyphae strongly pigmented, forming a dark layer below the squamules, upper cortex a poorly defined pseudocortex; asci clavate; pycnidia absent ..... ***Catapyrenium***
Rhizoidal hyphae colourless, upper cortex distinct; asci mostly cylindrical; pycnidia usually present ..... ***Placidium***

8(3) Photobiont present in hymenium; asci 2-spored ..... ***Endocarpon***
Photobiont absent from hymenium 9

9(8) Squamules bluish grey, up to 1.7mm diam., with a raised margin; medulla of filamentous hyphae; spores (5–)7-septate ..... ***Normandina pulchella***
Squamules dull green to green-brown, usually smaller but often confluent and hard to measure, without a raised margin; thallus with isodiametric cells throughout; spores muriform ..... ***Agonimia***

10(1) Asci with >8 spores 11
Asci with (1-)2-8 spores 13

11(10) Ascospores brown, 1-septate; non-lichenised ..... ***Muellerella*** (probably not Verrucariaceae)
Ascospores colourless 12

12(11) Exciple with dark pigments, involucrellum present, vulpinic acid derivatives absent; lichenised ..... ***Trimmatothele***
Exciple without dark pigments, involucrellum absent, yellow-green vulpinic acid derivatives sometimes present; lichenised or not ..... ***Thelocarpon*** (Thelocarpales)

13(10) Thallus thin, superficial on living leaves, composed of a weft of brown, branched hyphae with cells mostly 8–22 × 3–6.5 µm, often constricted at the septa; ascopores 3–8-septate or submuriform; non-lichenised but a few algae may be present ..... ***Phylloblastia*** (Chaetothyriales)
Thallus various; if the hyphal nature is clearly apparent, then hyphae immersed in the substratum, colourless, or narrower 14

14(13) Ascospores septate or muriform 15
Ascospores aseptate 39

Crustose species with septate to muriform ascospores

15(14) Ascomata pale, exciple at most pale brown, without dark pigments; involucrellum absent; ascospores septate or muriform; thallus crustose to minutely fruticose, cells sometimes with minute papillae;on bark, wood, soil, or on thin soil or bryophytes over rock ..... ***Psoroglaena***
Ascomata dark, exciple and/or involucrellum with dark pigments (apart from rare albino morphs, which typically occur with the normal form) 16

16(15) Ascospores transversely septate, occasionally with a proportion of spores submuriform; colourless ... 17
Ascospores consistently submuriform or muriform, colourless or brown 18

17(16) Ascospores predominantly 5–7-septate, narrowly ellipsoidal, 3.5–6.5 times as long as broad; involucrellum absent, exciple dark more or less throughout ..... ***Normandina***
Ascospores predominantly 1–3(–5)-septate, mostly 2–3 times as long as broad; involucrellum present or absent ..... ***Thelidium***

18(16) Hymenium containing photobiont cells..... ***Staurothele***
Hymenium not containing photobiont cells 19

19(18) Involucrellum absent; exciple more or less three layered, the outer layer pigmented; ascospores colourless; cortical cells of thallus sometimes with minute papillae; on bark, soil and bryophytes (these sometimes over rock)..... ***Agonimia***
Involucrellum present or absent; if involucrellum absent then exciple only one- to two-layered; cortical cells without papillae; on soil, bryophytes over rock, or directly on rock 20

20(19) Ascospores brown, with a distinct perispore ..... ***Merismatium*** *p.p.*
Ascospores colourless or brown, but if brown then without a distinct perispore 21

21(20) Soralia present; perithecia 0.30–0.95 mm diam., ascospores colourless, 36–50 µm long ..... ***Polyblastia efflorescens***
Soralia absent 22

22(21) Perithecia at least two-thirds immersed in well-defined pits in limestone, involucrellum absent 23
Perithecia not in pits, superficial or partly immersed in thallus or in soil, involucrellum present 24

23(22) Ascospores muriform, with *ca* 10–36 cells visible in optical section ..... ***Polyblastia albida***
Ascospores submuriform, with 3–4 transverse and 1–2 longitudinal septa, with *ca* 6–14 cells visible in optical section ..... ***Polyblastia dermatodes***

24(22) Ascospores brown when mature, with brown pigment visible in cell walls (immature spores may be colourless) 25
Ascospores colourless or faintly yellow-brownish when mature, brown pigment visible in cell walls only in withered or over-mature spores..... 32

25(24) Ascospores small, in the range 14–38.5 µm long 26
Ascospores large, in the range 48–150 µm long 27

26(25) Perithecia large, 0.5–0.8 mm diam., involucrellum present; lichenised, thallus whitish ..... ***Henrica melaspora***
Perithecia small, 0.1–0.3 mm diam., involucrellum absent; lichenised thallus absent, lichenicolous ..... ***Merismatium*** *p.p.*

27(25) Involucrellum absent, ascospores large, 70–160 µm long 28
Involucrellum present, ascospores smaller, 48–98 µm long 29

28(27) Asci (1–)2-spored, spores cylindrical-ellipsoidal ..... ***Polyblastia helvetica***
Asci (3-)4-8-spored, spores ellipsoidal or cylindric-ellipsoidal ..... ***Atla wheldonii***

29(27) Thallus of strongly convex areoles; perithecia half-immersed amongst areoles, but without a covering of thalline material; exposed surface more or less smooth; ascospores (51–) 53.5–63.5 (–70) µm long; cephalodia absent ..... ***Henrica theleodes***
Thallus smooth to verrucose; perithecia prominent or partly covered by a thalline layer, exposed surface often becoming rough 30

30(29) Ascospores (47.5–) 55–65.5 (–75) µm long, medium brown when mature but rarely opaque; thallus more or less smooth to somewhat verrucose; perithecia forming projections 0.5–0.7 mm diam.; cephalodia absent ..... ***Sporodictyon cruentum***
Ascospores 50–98 µm long, dark brown and often opaque when mature, with cell outlines obscured; thallus usually verrucose; perithecia forming projections (0.44–) 0.6–1.2 mm diam. 31

31(30) Perithecia partly covered by irregular patches of thalline material, ascospores (50–) 63–73 (–76) µm long; cephalodia present ..... ***Sporodictyon schaererianum***
Perithecia partly immersed or prominent, but without a covering of thalline material, ascospores (63–) 72–87 (–98) µm long; cephalodia absent ..... ***Atla alpina***

32(24) Ascospores submuriform, with up to 3–5 transverse and 1–2 longitudinal septa 33
Ascospores muriform 35

33(34) Involucrellum absent (ascospores 12.5–15 µm long) ..... ***Polyblastia plicata***
Involucrellum present 34

34(35) Ascospores 12–20 µm long ..... ***Polyblastia quartzina***
Ascospores 30–45 (–68) µm long ..... ***Polyblastia verrucosa***

35(33) Ascospores relatively small, 17–45 µm long 36
Ascospores larger, 38–81 µm long 37

36(35) Thallus slightly cartilaginous in appearance, with a colourless hyphal cortex; ascospores (17–) 21.5–25.5 (–28) µm long; on mossy soil ..... ***Polyblastia sendtneri***
Thallus not cartilaginous, without a hyphal cortex; ascospores (21.5–) 26–38.5 (–45) µm long; on rock, rarely on soil ..... ***Polyblastia cupularis***

37(35) Asci 2-spored; involucrellum absent ..... ***Polyblastia agraria***
Asci 8-spored 38

38(37) Perithecia two-thirds to almost completely immersed in soil, projecting part with no thalline covering ..... ***Polyblastia philaea***
Perithecia forming projections which are usually partly covered by a layer of thallus ..... ***Sporodictyon terrestre***

Crustose species with aseptate ascospores

39(14) Thallus nearly all immersed in calcareous rock, at most the very upper part appearing at the surface as minute flecks or as a very thin and inconspicuous covering, usually uncracked; perithecia sometimes in well-defined pits eroded in the substrate 40
Thallus mostly superficial (although sometimes thin), at most the lower part immersed, or thallus absent (lichenicolous species) 48

40(39) Involucrellum absent; exciple more or less pigmented throughout (usually thickened above, but without a distinct involucrellum) 41
Involucrellum present; in section clearly distinct from exciple (but sometimes small and developed only around the apex of the exciple) 42

41(40) Ascospores (25–) 29–34.5 (–41.5) µm long, exciple 375–700 µm diam.; thallus usually without cracks ..... ***Verrucaria hochstetteri***
Ascospores (21–) 23–27 (–29) µm long, exciple 240–420 µm diam.; thallus often with cracks radiating from the perithecium ..... ***Bagliettoa calciseda***

42(40) Involucrellum in the form of a small disc, attached only to the apex of the exciple, in surface view usually with minute cracks radiating from the ostiole (× 20 lens) ..... ***Bagliettoa***
Involucrellum not disc-shaped, in surface view without cracks 43

43(42) Ascospores 7.5–11 µm long ..... ***Verrucaria knowlesiae***
Ascospores larger 44

44(43) Ascospores (24–) 27–33 (–41) µm long ..... ***Verrucaria viridula***
Ascospores at most (17–) 19.5–24 (–26) µm long, and often much shorter 45

45(44) Perithecia forming small projections 120–300 µm diam. 46
Perithecia forming larger projections 240–500 µm diam. 47

46(45) Thalli occurring in mosaics of conspecific thalli separated by dark lines; ascospores 13.5–18.5 µm long; perithecia forming very low to moderate projections, base of perithecium sometimes ± immersed in the substratum ..... ***Parabagliettoa cyanea***
Thalli not forming mosaics; ascospores (14.5–) 18–24 (–28.5) µm long; perithecia forming moderate to prominent projections, the base not immersed in the substratum ..... ***Verrucaria*** spp. (specimens needing further study)

47(45) Apex of perithecium flat to depressed; ascospores (15.5–) 16.5–20 (–23.5) µm long, cylindrical to ellipsoidal, length/width ratio (1.9–) 2.0–2.7 (–3.4); pycnidia frequent ..... ***Parabagliettoa dufourii***
Apex of perithecium rounded to slightly flattened, rarely shallowly depressed; ascospores (17–) 20–24 (–27) µm long, ellipsoidal, length/width ratio (1.4–) 1.7–2.3 (–3.1); pycnidia apparently rare or absent ..... ***Verrucaria muralis***

48(39) Thallus in section with more or less discrete densely pigmented areas, these either free or extending upwards from a dark basal layer; in surface view dark dots or ridges visible on the thallus.. 49
Thallus in section without such areas; a blackish basal layer may be present, but without distinct upward projections; in surface view without dots or ridges (except dark pycnidia in some species); ascospores various; habitats various, sometimes lichenicolous 58

49(48) Species of freshwater habitats; thallus often with dots but no ridges in surface view 50
Species of maritime habitats; thallus often with dots, or ridges, or both 51

50(49) Thallus with green pigment in the cortex (or pigment absent); ascospores (11–) 14–17.5 (–21.5) µm long; exciple *ca* 275–290 µm diam.; medulla dilute to densely pigmented ..... ***Hydropunctaria scabra***
Thallus with brown pigment in the cortex (or pigment absent); ascospores (8.5–) 11–14.5 (–16) µm long; exciple *ca* 110–210 µm diam.; medulla colourless or with dilute pigment ..... ***Hydropunctaria rheitrophila***

51(49) Ascospores 13–19.5 µm long 52
Ascospores 7–10 µm long 56

52(51) Actively growing thallus with dark ridges 40–400 × 40–50 µm perpendicular to thallus margin; length/width ratio of ascospores (2.1–) 2.4–3.1 (–3.5) ..... ***Hydropunctaria amphibia***
Actively growing thallus margin with dark dots or very short ridges; length/width ratio of ascospores (1.5–) 1.7–2.1 (–2.3) 53

53(52) Thallus relatively thick, 60–300 µm, mostly cracked into discrete areoles; cortical pigment brown (rarely in part greenish brown); marine..... ***Hydropunctaria maura***
Thallus relatively thin, to 200 µm thick, cracks sparse to numerous, thallus always thinner and less cracked than *H. maura* when the species are growing contiguously; cortical pigment brown or green; marine or freshwater 54

54(53) Cortical pigment brown; marine..... ***Hydropunctaria oceanica***
Cortical pigment dull green to green-brown..... 55

55(54) Thallus typically uncracked when fresh (fine cracks may appear on storage); freshwater ..... ***Hydropunctaria scabra***
Thallus usually with cracks when fresh; marine ..... ***Hydropunctaria aractina*** and ***H. orae***

56(51) Thallus cracked into areoles, these bordered by dark ridges ..... ***Verrucaria degelii***
Thallus not cracked (but new cracks can appear in dried collections)..... 57

57(56) Thallus with black ridges to 100–200 µm wide ..... ***Wahlenbergiella striatula***
Thallus with small dark dots or short irregular ridges 10–100 × 10–60 µm ..... ***Verrucaria ditmarsica***

58(48) On maritime rocks; thallus cracked, the cracks with dark sides; in section with the cells in columns; perithecia immersed, ascospores 8.5–10.5 µm long ..... ***Verrucaria ceuthocarpa***
Not this combination of characters 59

59(58) Thallus well-developed, often pruinose, non-gelatinous, cracked, the cracks with blackish sides; perithecia immersed in the thallus, involucrellum absent 60
Thallus various, if with dark-sided cracks then involucrellum present 64

60(59) Perispore present, ascospores (14–) 17.5–26.5 (–30.5) µm long; young thallus initially parasitic on *Aspicilia* or *Circinaria* species, later independent 61
Perispore absent or present but indistinct, ascospores (10.5–) 12.5–21 (–25.5) µm long; young thallus independent, or sometimes on *Staurothele* or *Verrucaria* species 62

61(60) Ascospores (14–) 17.5–22.5 (–27) µm long, thallus initially parasitic on *Aspicilia aquatica* ..... ***Placopyrenium formosum***
Ascospores (18.5–) 21.5–26.5 (–30.5) µm long, thallus initially parasitic on *Circinaria* (*Aspicilia*) *calcarea* ..... ***Placopyrenium canellum***

62(60) Thallus margin thin, prothallus often visible; perithecia arising between photosynthetic units on the thallus surface, in surface view often appearing as if connected by dark lines... ***Verrucaria polysticta***
Thallus margin abrupt and often thick, prothallus absent or very thin and inconspicuous; perithecia arising within photosynthetic units on the thallus surface, in surface view not connected by dark lines 63

63(62) Ascospores (13–) 16–21 (–25.5) × (5.5–) 6.5–8 (–9.5) µm, length/width ratio (1.9–) 2.2–2.9 (–4.0); upper surface of areoles typically undivided or occasionally divided by a few dark lines; on regularly inundated siliceous rocks by water, sometimes parasitic on *Staurothele fissa* ..... ***Placopyrenium cinereoatratum***
Ascospores (11.5–) 13–17 (–20.5) × (4.5–) 5–6 (–7.5) µm, length/width ratio (1.9–) 2.3–3 (–3.7); upper surface of areoles typically divided by dark lines; on calcareous rocks in terrestrial habitats, sometimes parasitic on *Verrucaria* spp..... ***Placopyrenium fuscellum***
(See also *Placopyrenium trachyticum* with larger areoles tapering below into stipes, and often a proportion of 1-septate ascospores)

64(59) Parasitic on lichens, a lichenized thallus present or not 65
Not parasitic on lichens 67

65(64) Lichenized thallus absent; growing on *Ionaspis* ..... ***Verrucaria conturmatula***
Lichenized thallus present; growing on other lichens 66

66(65) Growing on *Caloplaca* s.l., *Diplotomma* and *Lecanora* ..... ***Verrucula*** and ***Verruculopsis***
Growing on *Circinaria* (*Aspicilia*) *calcarea* ..... ***Heteroplacidium fusculum***

67(64) Average ascospore length in the range 8–10 µm, extreme lengths in range 7–12 µm 68
Average ascospore length higher, at least 12 µm, extreme lengths as low as 9 µm 75

68(67) Maritime species, thallus subgelatinous 69
Freshwater or terrestrial species 70

69(68) Perithecia completely immersed in the thallus ..... ***Wahlenbergiella mucosa***
Perithecia forming projections (compare also smooth morphs of *Verrucaria ditmarsica* and *Wahlenbergiella striatula*) ..... ***Verrucaria halizoa***

70(68) Involucrellum absent 71
Involucrellum present (but may be appressed to exciple) 72

71(70) Thallus very thin, perithecia 80–130 µm, ascospores 6–10.5 × 3.5–5.5 µm ..... ***Verrucaria simplex***
Thallus well-developed, lumpy, perithecia 200–300 µm, ascospores 9–12 × 7.5–10 µm ..... ***Verrucaria sphaerospora***

72(70) Perithecia 100–150 µm diam; involucrellum appressed except at the base, scarcely spreading; on stones in terrestrial habitats ..... ***Verrucaria bulgarica***
Perithecia 120–300 µm diam. 73

73(72) Thallus semi-immersed and inconspicuous, or superficial, thin, and brownish grey; perithecia without a thalline covering ..... ***Verrucaria knowlesiae***
Thallus superficial, brown to blackish; perithecia sometimes with a thin, partial thalline covering 74

74(73) In freshwater habitats; thallus uncracked or cracks few; perithecia forming projections 120–240 µm diam. ..... ***Verrucaria aquatilis***
In terrestrial habitats; thallus cracked; perithecia forming projections 200–300 µm diam. ..... ***Verrucaria aranensis***

75(67) Involucrellum absent; on rock, soil or mosses 76
Involucrellum present, at least as a small dark structure at the apex of the exciple; or if involucrellum absent then growing on rock 80

76(75) Ascospores narrowly ellipsoidal, (15–) 19–25 (–29) × (5–) 6–7 (–8) µm, often truncate at the ends and with small gelatinous appendages; thallus without pigment ..... ***Verrucaria bryoctona***
Ascospores ellipsoidal, (13.5–) 16.5–22 (–27) × (5.5–) 6.5–8 (–10) µm, without appendages 77

77(76) On soil ..... ***Verrucaria xyloxena***
On rock 78

78(77) Thallus with epinecral layer, ascospores narrowly cylindric-ellipsoidal, 16–22 × 7–8 µm ..... ***Verrucaria obfuscans***
Thallus without epinecral layer, ascospores usually slightly broader 79

79(78) Thallus composed of goniocyst-like units; on stones in streams ..... ***Verrucaria consociata***
Thallus continuous, areoles not well-developed; on limestone in woodland..... ***Verrucaria policensis***

80(75) Ascospores narrowly ellipsoidal, 12–14 × 2–3 µm; maritime ..... ***Verrucaria sandstedei***
Ascospores more than 3 µm diam. (often much more) 81

81(80) Thallus subgelatinous, uncracked (fine cracks may appear in old dried material); growing in freshwater habitats 82
Thallus non-gelatinous; habitats various 89

82(81) Ascospores 9–14 µm long; asci (3–)4(–5)-spored ..... ***Verrucaria madida***
Ascospores 15–27 µm long; asci 8-spored 83

83(82) Perithecia often completely immersed in the thallus, rarely some projecting; thallus with dull green or brown pigment in the cortex when well-lit; ascospores (15–) 16–22 (–23.5) µm long ..... ***Verrucaria pachyderma***
Perithecia forming at least low projections; pigment if present brown; ascospores usually larger 84

84(83) Perithecia forming projections 200–360 µm diam., without a thalline covering ..... ***Verrucaria humida***
Perithecia with a thin layer of thallus covering at least the lower part 85

85(84) Ascospores broadly ellipsoidal, (17–) 20–24 (–27.5) × (11–) 12–13.5 (–15.5) µm, length/width ratio (1.2–) 1.5–1.9 (–2.3); on limestone in calcareous streams ..... ***Verrucaria elaeomelaena*** *s.l.*
Ascospores narrower in shape 86

86(85) Perithecial projections shallow and poorly defined; thallus variable but usually rather thick, (20–) 80–160 (–240) µm, the involucrella often wide-spreading and partly joined to form a black basal layer to the thallus; ascospores (19–) 22.5–26 (–30) × (8–) 9–11 (–13) µm ..... ***Verrucaria funckii***
Perithecial projections usually distinct; thallus thin, 20–50 µm thick; involucrella rarely joined 87

87(86) Ascospores relatively small, (15–) 19.5–23 (–26) × (6.5–) 8–9.5 (–11) µm, perithecia relatively small, forming projections 240–400 µm diam., exciple 240-400 µm diam.; perithecia rather dense, 29–64 in an area of 25 mm^2 ..... ***Verrucaria hydrophila***
Ascospores and perithecia larger; perithecia 13–26 in an area of 25 mm^2 88

88(87) *Three options:
Ascospores (19–) 21.5–26.5 (–30.5) × (8–) 9–10.5 (–12) µm ..... ***Verrucaria placida***
Ascospores (19–) 23–27 (–32) × (9.5–) 11.5–13.5 (–16.5) µm..... ***Verrucaria elaeomelaena*** *s.l. p.p.*
Ascospores (19–) 24.5–32.5 (–43.5) × (9.5–) 12.5–16 (–19) µm ..... ***Verrucaria alpicola***
(These species are easily confused; if possible confirm material by ITS sequencing).

89(81) Thallus in section composed of more or less distinct goniocyst-like units (thallus varying from minute flecks to a cracked crust; ascospores in the range (13–) 15–26.5 (–28.5) µm long, average length in individual specimens less than 27 µm) 90
Thallus in section not composed of goniocysts 92

90(89) Ascospores (17–) 20.5–27 (–32) µm long, average length 22–25 µm; thallus well-developed, often lumpy or with areas of new growth..... 91
Ascospores (17–) 18–21.5 (–23) µm long, average length 19–20 µm; thallus thin and not obviously lumpy or with areas of new growth ..... ***Verrucaria lapidicola***

91(90) Thallus of relatively coarse units, in section divided into units 30–325 µm wide..... ***Verrucaria nodosa***
Thallus of somewhat finer and more crenulate units, in section divided into units 30–50 µm wide ..... ***Verrucaria rosula***
(Typical *V. rosula* is distinctive in appearance, but *V. nodosa* is variable and should usually be sequenced)

92(89) Ascopores in the range (20–) 24–33 (–40) µm long, average length 26–30 µm, average length in individual specimens in the range 25–33 µm; thallus well-developed, thin to thick, but covering the substratum, pale to dark brown 93
Ascospores smaller, average length no more than 25 µm, **OR** thallus scanty, discontinuous, or developed only in small, sheltered depressions in the substratum..... 98
(The spores in *Verrucaria latebrosa* are usually large, but rarely less than an average length of 23 µm in individual specimens; it occurs in freshwater habitats and a distinct perispore is often visible)

93(92) On calcareous or base-rich siliceous rocks in terrestrial habitats (epinecral layer or blastidia occasionally present) 94
On calcareous or siliceous rocks in freshwater habitats (epinecral layer and blastidia always absent) .. 96

94(93) Perithecia partly immersed in the substratum, often produced into a beak at apex; involucrellum weakly developed, to well-developed around the upper half of the exciple (thallus variable, ± immersed to well-developed and cracked, never blastidiate; pycnidia rather frequent) ..... ***Verrucaria viridula***
Perithecia not immersed in the substratum, not much produced; involucrellum well-developed, often reaching to the base-level of the exciple (thallus well-developed, occasionally blastidiate)..... 95

95(94) Initial areoles discrete, with a rather smooth outline, later overlapping; epinecral layer absent or thin ..... ***Verrucaria romeana***
Initial areoles less discrete, soon crenulate, losing their identity in a cracked-areolate crust; epinecral layer well-developed ..... ***Verrucaria macrostoma***

96(93) Involucrellum conical ..... ***Verrucaria margacea***
Involucrellum not distinctly conical, mainly developed around the apex or in the upper half of the exciple, or absent..... 97

97(96) Involucrellum absent or weakly developed around the apex of the exciple, perithecia immersed to somewhat projecting; thallus often relatively thick and cracked (up to 480 µm thick)..... ***Verrucaria anziana***
Involucrellum well-developed, flanking 0.33 to 0.5 of the height of the exciple; perithecia usually projecting; thallus variable but usually only up to 200 µm thick ..... ***Verrucaria latebrosa*** and ***V. tephromela***

98(92) Perithecia immersed in the thallus, involucrellum absent; ascospores 16–26 µm long ..... ***Verrucaria ochrostoma***
Perithecia not immersed, or an involucrellum is present..... 99

99(98) Thallus usually very thin, often with a waxy appearance under the dissecting microscope; perithecia large, up to 800 µm diam., prominent, with thick involucrellum; ascospores (10.5–) 11.5–14 (–16) µm, usually distinctly oblong; on maritime rocks ..... ***Verrucaria prominula***
Thallus various; perithecia smaller; terrestrial or freshwater habitats 100

100(99) Ascospores (12–) 12–20 (–24.5) µm long..... 101
Ascospores (15–) 17.5–25 (–30) µm long..... 104

101(100) Thallus pale grey to dull grey-brown, closely and finely cracked, with an epinecral layer; perithecia three-quarters to completely immersed ..... ***Verrucaria caerulea***
Thallus various, but epinecral layer absent 102

102(101) Involucrellum well-developed, thick in the upper part and often appressed to the exciple below; ascospores often cylindrical or cylindric-ellipsoidal ..... ***Parabagliettoa pinguicula***
Involucrellum not conspicuously thick in the upper part, sometimes conical, or poorly developed; ascospores more or less ellipsoidal or tapering towards the base..... 103

103(102) Perithecia immersed in the thallus, involucrellum rather poorly developed, often confined to the apex of the exciple; by streams or rivers ..... ***Verrucaria sublobulata***
Perithecia prominent, involucrellum well-developed, often conical; in terrestrial habitats ..... ***Verrucaria dolosa***

104(100) Perithecia immersed in thallus, at most forming very ill-defined projections; involucrellum ± conical, becoming joined with others to form a dark basal layer; freshwater habitats 105
Perithecia often forming projections; involucrellum various 106

105(104) Thallus relatively thin, 40–70 µm thick away from perithecia, grey-green to mid brown (well-pigmented in unshaded habitats), continuous to cracked ..... ***Verrucaria devensis***
Thallus well-developed, (40–) 100–240 µm thick, grey-green to pale brown (typically weakly pigmented even in unshaded habitats), typically cracked ..... ***Verrucaria praetermissa***
(Differences are obvious when the two grow together, but single specimens may be difficult to identify)

106(104) Perithecia forming low to moderate projections covered by a layer of thallus; thallus usually continuous; on rocks and stones by streams or in shady woodland; ascospores (15–) 19–23 (26) µm long ..... ***Verrucaria hydrophila***
Perithecial projections, if present, with at most a slight and irregular covering of thallus 107

107(106) In freshwater habitats or on seeping rocks, thallus grey-brown to dark brown, regularly cracked; ascospores rather short and broad, (15–) 18–22 (–27) × (7.5–) 9.5–11.5 (–14) µm; pycnidia often present, scattered on the thallus surface ..... ***Verrucaria cernaensis***
In terrestrial habitats; thallus various; ascospores often slightly larger or more narrowly ellipsoidal 108

108(107) Thallus well-developed and regularly cracked into discrete areoles, mid to dark brown, the sides of the areoles often pigmented 109
Thallus various, sparse to well-developed; whitish, grey-green or brown 110

109(108) Perithecial projections low to rather prominent, prothallus often conspicuous, dark brown; on siliceous rocks, often near the coast ..... ***Verrucaria fusconigrescens***
Perithecial projections very low to moderate, prothallus less conspicuous; on calcareous rocks or siliceous rocks subject to calcareous influence (such as on mortared walls) ..... ***Verrucaria nigrescens***

110(108) Ascospores rather narrowly ellipsoidal, (15–) 17.5–21 (–24) × (6–) 7.5–8.5 (–9.5) µm wide, length/width ratio (1.7–) 2.2–2.7 (–3.5); thallus grey-green to pale brownish-green, rarely pale brown; apex of perithecium sometimes slightly irregular, with whitish areas and dark dots in surface view ..... ***Verrucaria elaeina***
Ascospores longer, or more broadly ellipsoidal 111

111(110) Perithecial projections 240–780 µm diam., exciple 200–380 µm diam.; thallus endolithic or well-developed and whitish 112
Perithecial projections 180–300 (–400) µm diam., exciple 160–280 (–320) µm diam., thallus usually thin and discontinuous, unpigmented or distinctly brown 113

112(111) Thallus superficial, whitish or brownish white, usually well-developed; on siliceous rocks in the supralittoral zone of sea shores ..... ***Verrucaria internigrescens***
Thallus immersed to superficial, but rarely well-developed; on limestone, rarely siliceous rocks, not maritime ..... ***Verrucaria muralis*** and ***V. submersella***

113(111) Thallus weakly pigmented even in good light, cortex with at most dilute brown pigment (thallus surface can be discoloured brown by cyanobacteria) ..... ***Verrucaria pallidomurina***
Thallus brown in good light, cortex brown ..... ***Verrucaria ahtii*** and ***V. vitikainenii***
(It is doubtful whether these three species can be reliably distinguished without sequencing).

Crustose Verrucariaceae with aseptate ascospores, arranged in descending order of spore size														
species	**length**					**width**					**habitat**			
	min	-1 SD	**mean**	+1 SD	*max*	*min*	-1 SD	**mean**	+1 SD	*max*	**F**	**M**	**T**	**L**
Verrucaria hochstetteri	*24.6*	29.1	**31.8**	34.4	*41.4*	*13.1*	15.2	**17.6**	20.0	*24.6*			T	
Verrucaria viridula	*24.2*	27.4	**30.3**	33.2	*41.0*	*12.0*	14.8	**17.1**	19.4	*23.4*			T	
Verrucaria margacea	*20.1*	26.6	**29.8**	32.9	*40.5*	*9.0*	11.4	**12.8**	14.2	*17.5*	F			
Verrucaria alpicola	*22.6*	26.3	**29.5**	32.8	*36.1*	*11.9*	14.1	**15.3**	16.5	*18.9*	F			
Verrucaria macrostoma	*21.3*	25.2	**28.5**	31.8	*36.1*	*9.4*	11.6	**13.2**	14.9	*17.2*			T	
Verrucaria anziana	*23.0*	25.5	**28.4**	31.2	*36.5*	*10.3*	11.4	**12.2**	13.1	*14.5*	F			
Verrucaria latebrosa	*21.3*	23.8	**26.4**	28.9	*35.0*	*8.2*	10.4	**11.4**	12.5	*14.5*	F			
Verrucaria romeana	*23.0*	24.0	-	27.0	*28.0*	*8.0*	9.0	-	13.0	*15.0*			T	
Bagliettoa parmigera	*18.5*	21.0	**25.1**	29.3	*32.0*	*9.8*	10.4	**11.7**	13.1	*14.5*			T	
Verrucaria rosula	*20.5*	22.8	**24.8**	26.8	*32.0*	*7.5*	9.0	**10.0**	10.9	*13.9*	F			
Bagliettoa calciseda	*20.9*	22.7	**24.7**	26.7	*29.1*	*8.6*	10.0	**11.3**	12.7	*14.8*			T	
Verrucaria elaeomelaena	*17.0*	22.6	**24.6**	26.6	*32.0*	*9.5*	11.4	**12.5**	13.5	*16.4*	F			
Verrucaria funckii	*19.3*	22.3	**24.0**	25.8	*30.0*	*8.0*	9.2	**10.1**	11.0	*13.0*	F			
Verrucaria vitikainenii	*19.5*	22.0	-	25.5	*28.5*	*10.0*	11.0	-	13.0	*14.5*			T	
Verrucaria placida	*19.0*	21.4	**24.0**	26.5	*30.3*	*8.2*	9.2	**9.9**	10.7	*12.0*	F			
Placopyrenium canellum	*18.5*	21.3	**23.9**	26.5	*30.3*	*6.6*	7.7	**8.5**	9.4	*10.3*			T	L
Verrucaria ahtii	*17.0*	20.5	-	27.5	*28.5*	*9.0*	10.0	-	13.5	*14.5*			T	
Verrucaria pallidomurina	*19.6*	18.7	**23.1**	27.6	*28.4*	*8.8*	9.3	**11.3**	13.2	*13.7*			T	
Verrucaria internigrescens	*15.0*	19.8	**22.4**	25.0	*30.0*	*7.5*	9.2	**10.5**	11.8	*13.1*			T	
Verrucaria nodosa	*17.2*	20.5	**22.2**	23.9	*27.9*	*7.8*	9.0	**9.7**	10.4	*11.5*	F			
Verrucaria muralis	*16.8*	19.9	**22.0**	24.0	*27.1*	*7.4*	9.9	**11.2**	12.5	*14.4*			T	

Crustose Verrucariaceae with aseptate ascospores, arranged in descending order of spore size														
species	**length**					**width**					**habitat**			
	min	-1 SD	**mean**	+1 SD	*max*	*min*	-1 SD	**mean**	+1 SD	*max*	**F**	**M**	**T**	**L**
Verrucaria bryoctona	*15.0*	19.3	**22.0**	24.7	*29.0*	*5.0*	5.8	**6.4**	7.0	*8.0*			T	
Verrucaria submersella	*18.0*	-	-	25.0	*30.0*	-	8.5	-	14.0	-			T	
Bagliettoa marmorea	*13.0*	-	-	-	*30.0*	*9.0*	-	-	-	*15.0*			T	
Verrucaria consociata	*16.8*	19.5	**21.8**	24.1	*26.7*	*8.2*	8.9	**10.0**	11.2	*11.9*				L
Verrucaria praetermissa	*16.0*	19.3	**21.1**	22.8	*28.0*	*6.5*	7.8	**8.7**	9.6	*10.5*	F			
Verrucaria policensis		18.0	21**.0**	24.0			7.5	**10**	11				T	
Verrucaria hydrophila	*14.8*	19.3	**21.1**	22.9	*25.8*	*6.5*	8.1	**8.9**	9.7	*11.5*	F			
Verrucaria ochrostoma	*15.6*	18.4	**20.9**	23.5	*27.1*	*8.6*	10.2	**11.5**	12.9	*13.9*			T	
Verrucaria nigrescens	*15.2*	15.6	**20.6**	25.5	*24.6*	*7.8*	7.3	**9.5**	11.7	*12.3*			T	
Verrucaria devensis	*16.0*	18.7	**20.3**	22.0	*23.0*	*7.4*	8.3	**8.9**	9.5	*10.3*	F			
Placopyrenium formosum	*14.0*	17.8	**20.3**	22.8	*27.9*	*7.0*	8.2	**9.0**	9.8	*11.1*	F			L
Bagliettoa parmigerella	*14.0*	-	-	-	*21.0*	*6.0*	-	-	-	*8.0*			T	
Verrucaria fusconigrescens	*16.8*	18.8	**20.1**	21.5	*23.4*	*7.4*	7.8	**8.6**	9.3	*10.3*			T	
Verrucaria cernaensis	*15.0*	18.0	**20.0**	22.0	*27.0*	*7.5*	9.5	**10.6**	11.7	*14.0*	F			
Verrucaria lapidicola	*16.8*	17.9	**19.6**	21.4	*23.0*	*6.6*	6.7	**7.4**	8.2	*10.3*			T	
Verrucaria obfuscans	*16.0*	-	-	-	*22.0*	*7.0*	-	-	-	*8.0*			T	
Verrucaria elaeina	*15.0*	17.7	**19.4**	21.0	*24.0*	*6.0*	7.4	**8.0**	8.7	*10.0*			T	
Verrucaria pachyderma	*15.0*	16.1	**19.1**	22.0	*23.5*	*6.0*	6.5	**7.7**	8.8	*9.4*	F			
Verrucaria xyloxena	*13.5*	16.6	**18.8**	21.0	*27.0*	*5.5*	6.3	**7.3**	8.2	*10.0*			T	
Placopyrenium cinereoatratum	*12.7*	16.2	**18.5**	20.8	*25.4*	*5.3*	6.5	**7.2**	8.0	*9.4*	F			L
Parabagliettoa dufourii	*15.6*	16.4	**18.1**	19.8	*23.4*	*6.6*	7.1	**7.8**	8.4	*9.0*			T	

Crustose Verrucariaceae with aseptate ascospores, arranged in descending order of spore size														
species	**length**					**width**					**habitat**			
	min	-1 SD	**mean**	+1 SD	*max*	*min*	-1 SD	**mean**	+1 SD	*max*	**F**	**M**	**T**	**L**
Verrucaria sublobulata	*13.5*	15.3	**16.9**	18.4	*21.5*	*5.5*	6.8	**7.6**	8.4	*9.8*	F			
Parabagliettoa pinguicula	*11.9*	13.9	**16.7**	19.5	*24.6*	*4.9*	5.7	**7.0**	8.4	*11.0*			T	
Verruculopsis flavescentaria	*15.5*	-	**-**	-	*19.5*	*5.5*	-	**-**	-	*7.0*			T	L
Verrucula helvetica	*14.0*	-	**-**	-	*19.5*	*7.5*	-	**-**	8.0	*8.5*			T	L
Hydropunctaria amphibia	*13.1*	15.0	**16.6**	18.1	*19.7*	*4.9*	5.6	**6.2**	6.8	*7.4*		M		
Hydropunctaria maura	*13.9*	15.0	**16.3**	17.6	*18.9*	*7.0*	7.5	**8.3**	9.0	*10.3*		M		
Hydropunctaria orae	*13.1*	14.7	**16.1**	17.6	*19.7*	*6.2*	6.9	**7.4**	7.9	*8.6*		M		
Verrucaria dolosa	*14.4*	14.9	**15.9**	17.0	*18.0*	*5.7*	6.4	**7.0**	7.5	*7.8*			T	
Hydropunctaria scabra	*11.0*	13.9	**15.7**	17.5	*21.3*	*7.0*	7.6	**8.3**	9.0	*10.5*	F			
Parabagliettoa cyanea	*13.5*	14.1	**15.5**	16.9	*18.5*	*5.7*	6.1	**7.0**	7.8	*9.0*			T	
Placopyrenium fuscellum	*11.5*	13.2	**15.1**	17.0	*20.5*	*4.5*	5.2	**5.7**	6.2	*7.4*			T	L
Verrucaria caerulea	*11.9*	12.8	**15.0**	17.3	*23.5*	*5.0*	5.3	**6.2**	7.0	*9.5*			T	
Hydropunctaria oceanica	*12.3*	13.5	**15.0**	16.5	*18.0*	*5.7*	6.8	**7.3**	7.8	*8.6*		M		
Hydropunctaria aractina	*11.9*	13.3	**14.6**	15.8	*17.2*	*6.6*	7.0	**7.5**	8.0	*8.2*		M		
Verrucula sp.	*12.5*	-	**-**	-	*16.0*	*5.5*	-	**-**	-	*6.5*			T	L
Verrucaria sandstedei	*12.0*	-	**-**	-	*16.0*	*2.0*	-	**-**	-	*3.5*		M		
Verrucaria polysticta	*10.3*	12.6	**14.1**	15.7	*16.4*	*5.3*	5.6	**6.2**	6.9	*7.8*			T	
Verrucaria conturmatula	*11.5*	12.6	**14.1**	15.6	*18.0*	*3.3*	4.9	**5.4**	6.0	*6.5*				
Verrucula maritimaria	*11.0*	12.0	**-**	15.0	*16.0*	*4.0*	4.5	**-**	5.5	*6.0*			T	L
Verrucaria prominula	*10.3*	11.7	**12.9**	14.2	*16.0*	*4.5*	6.7	**7.4**	8.2	*9.0*		M		
Hydropunctaria rheitrophila	*8.5*	11.2	**12.8**	14.4	*16.0*	*6.0*	6.6	**7.4**	8.2	*9.5*	F			

Crustose Verrucariaceae with aseptate ascospores, arranged in descending order of spore size

species	length					width					habitat			
	min	-1 SD	**mean**	+1 SD	*max*	*min*	-1 SD	**mean**	+1 SD	*max*	**F**	**M**	**T**	**L**
Verrucaria madida	*9.0*	10.6	**12.1**	13.6	*14.8*	*5.3*	6.1	**6.6**	7.1	*7.4*	F			
Heteroplacidium fusculum	*7.0*	10.0	**-**	13.0	*15.0*	*6.0*	-	**-**	-	*10.0*			T	L
Verrucaria humida	*9.8*	10.0	**10.6**	11.3	*12.3*	*1.9*	2.1	**2.2**	2.4	*2.5*	F			
Verrucaria sphaerospora	*9.0*	-	**-**	-	*12.0*	*7.5*	-	**-**	-	*10.0*			T	
Verrucaria ceuthocarpa	*8.5*	-	**-**	-	*10.0*	*6.0*	-	**-**	-	*7.5*		M		
Verrucaria aranensis	*7.0*	-	**9.8**	-	*11.0*	*5.5*	-	**6.3**	-	*7.0*			T	
Verrucaria degelii	*7.0*	-	**-**	-	*10.0*	*4.0*	-	**-**	-	*7.0*		M		
Wahlenbergiella mucosa	*7.0*	-	**-**	-	*10.0*	*4.0*	-	**-**	-	*7.0*		M		
Verrucaria ditmarsica	*7.4*	8.6	**9.6**	10.6	*12.0*	*5.0*	5.9	**6.6**	7.3	*8.0*		M		
Wahlenbergiella striatula	*7.8*	8.2	**9.1**	10.1	*11.9*	*4.9*	5.3	**5.6**	5.9	*6.2*		M		
Verrucaria halizoa	*7.0*	7.8	**9.1**	10.5	*11.9*	*3.3*	3.6	**4.1**	4.7	*5.3*		M		
Verrucaria knowlesiae	*7.5*	-	**8.9**	-	*11.0*	*5.5*	-	**5.9**	-	*7.0*			T	
Verrucaria bulgarica	*7.0*	7.9	**8.6**	9.4	*10.0*	*4.5*	4.4	**4.8**	5.1	*5.5*			T	
Verrucaria simplex	*6.0*	7.0	**8.2**	9.4	*9.5*	*3.5*	3.8	**4.4**	4.9	*5.0*			T	
Verrucaria aquatilis	*6.5*	7.4	**8.2**	8.9	*10.0*	*4.5*	7.4	**6.1**	6.7	*8.0*	F			

Measurements given as: minimum, mean − standard deviation, mean, mean + standard deviation, maximum, except where there are gaps in the measurements.
Major habitats: F = freshwater, M = marine, T = terrestrial, L = (sometimes) lichenicolous

AGONIMIA Zahlbr. (1909)

Thallus crustose, composed of aggregations of goniocyst-like units, or minutely squamulose to coralloid, in one species more or less foliose with fragile lobes up to 5 mm broad; in squamulose species surface cells forming a pseudocortex, sometimes with brown pigment, cells often with one or more small papillae per cell; in one species papillae greatly elongated and adhering to form stiff hairs; epinecral layer absent, or present in one species as isodiametric cell remains with refractive contents; squamules often fragile and disentegrating into granules or irregular fragments, sometimes producing blastidia, or isidium-like or soredium-like propagules. **Prothallus** absent or inconspicuous. **Photobiont** chlorococcoid, cells 4–13 × 3.5–7.5 µm. **Ascomata** perithecia, black, sometimes grey-brown due to a very thin unpigmented surface layer, subglobose to barrel-shaped, often situated between squamules or granules, surface smooth to strongly roughened. **Involucrellum** absent (or at least not distinguishable from the exciple). **Exciple** thick, ± layered, outer part of ± rounded cells which are densely pigmented, middle layer of similarly shaped but unpigmented cells, innermost layer of compressed, colourless cells; pigments dark brown, K+ grey-brown or reddish-brown or greenish. **Hymenial gel** hemiamyloid: I+ red (I+ blue at low concentrations of iodine), K/I+ blue. **Hamathecium** of periphyses and periphysoids; interascal filaments absent. **Asci** fissitunicate, 2- or 8-spored, I−, K/I−. **Ascospores** colourless (sometimes slightly browned when over-mature), muriform. **Conidiomata** pycnidia, absent in most species. **Conidia** colourless, bacilliform. **Chemistry**: no lichen substances detected. **Ecology**: on neutral or slightly basic soil, bark and rock, often associated with mosses.

The genus as currently defined is apparently non-monophyletic. Muggia *et al*. (2010) found that *Agonimia repleta* occurred in a different clade to *A. allobata* and *A. tristicula*, contradicting research by Schmitt *et al*. (2009) which placed *A. repleta* and *A. tristicula* together in a clade close to *Verrucaria bryoctona*, but *A. gelatinosa* in a distantly related clade. More analysis is needed. *Psoroglaena* (q.v.) has been compared with *Agonimia* (Lücking 2008); it also has the unusual feature of papillate thalline hyphae but has ± colourless to pale brown ascomata. That genus also appears to be polyphyletic (Muggia *et al*. 2010).

Sérusiaux *et al*. (1999) suggested that British material of *Polyblastia agraria* Th. Fr. was close to *Agonimia vouauxii* (de Lesd.) M. Brand & Diederich (1999), but Tibell & Tibell (2017) suggested an affinity with *P. helvetica*. It will be retained in *Polyblastia* pending further analysis.

Other genera of *Verrucariaceae* with muriform ascospores differ in characters including an involucrellum present as a separate structure from the exciple, ascospores brown when mature, exciple colourless, or perithecia forming pits in rock. The 'layered' exciple of *Agonimia* is a less distinctive character if it is interpreted as an entire involucrellum surrounding an exciple. *Protothelenella* and *Thelenella* differ in the presence of abundant interascal filaments.

In the squamulose species, 'squamule size' is not a very useful character, as squamules are of indeterminate growth and soon lose their individuality; measuring the width of the ultimate lobes is more useful.

Literature

Czarnota & Coppins (2000), Dymytrova *et al*. (2011), Guzow-Krzemińska *et al.* (2012), Hafellner (2014), Lücking & Moncada (2017), Muggia *et al*. (2010), Orange (2013a), Orange & Purvis (2009), Schmitt *et al.* (2009).

1 Thallus with a distinct epinecral layer of dead ± isodiametric cells, resulting in a pale to dull mid-grey colour and a faint pruina to the lobes; lobes often with minute stiff projecting hairs to 40 µm long (visible with a 10× handlens) ..... ***opuntiella***

Thallus crustose or squamulose, but without a distinct epinecral layer, and never with stiff projecting hairs 2

2(1) Ascospores (25–) 29–55 µm long; thallus crustose and finely verrucose, or squamulose-coralloid with narrow lobes to 40 µm broad; asci 8-spored 3
Ascospores (42–) 57–120 µm long; thallus squamulose, with lobes 30–160 µm broad; asci (1-) 2- or 8-spored 8

3(2) Perithecia rough-walled, the upper part with vertical cracks or furrows ..... ***repleta***
Perithecia smooth, uncracked 4

4(3) Perithecia small, 120–220 µm diam.; ascospores (25–) 29–35 (–44) µm long; usually on bark 5
Perithecia small or large, 140–600 µm diam.; ascospores 31–55 µm long; on soil or on mosses over soil and rock 6

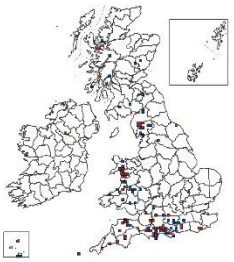
5(4) Thallus a thin, slightly uneven and faintly roughened crust ..... ***allobata***
Thallus with narrow branched lobes in one plane or in coralloid clusters ..... ***flabelliformis***

6(4) Perithecia 140–230 µm diam., asci 2-spored ..... See ***Polyblastia agraria***
Perithecia 250–600 µ diam., asci 8-spored 7

7(6) Glossy sterile black globules 70–240 µm usually present on thallus; thallus grey-green; cortical cells without pigment ..... ***globulifera***
Sterile black globules absent; thallus brown; cortical cells brown-pigmented ..... ***gelatinosa***

8(2) Asci (1-) 2-spored; squamules with the lobes usually distinctly flattened, 30–160 µm broad, brownish green to brown ..... ***tristicula***
Asci 8-spored; squamules with the lobes terete (or rarely slightly flattened when poorly developed), 40–100 µm broad, grey-green ..... ***octospora***

Agonimia allobata (Stizenb.) P. James (1992) **Nb**

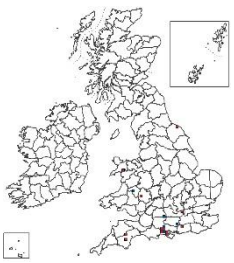


Thallus crustose, thin, uneven and minutely roughened, grey-green to brown, sometimes with minute granules *ca* 20 µm diam.; thallus composed of goniocysts 14–30 µm diam., surface cells isodiametric, without papillae. Perithecia 120–220 µm diam., ± globose or taller than broad, occasionally collapsed when dry, two-thirds immersed in the thallus to almost superficial; grey-brown when young, later often black, surface smooth, matt. Asci 8-spored. Ascospores (25–) 29–35 (–44) × 10–15 (–16.5) µm, ellipsoidal, muriform. **BLS 1149**.

On bark, often amongst mosses, on trunks of old trees, particularly *Quercus*, *Ulmus* and *Fraxinus*, in long-established woodlands, sheltered gullies, rarely on wayside trees; local. S., S.W. and N. England, throughout Wales, scattered in Scotland, rarely recorded from Ireland. Some records in the south and south west at least are of *A. flabelliformis*.

The species needs further attention; it was recovered as polyphyletic by Guzow-Krzemińska *et al*. (2012). *Agonimia flabelliformis* differs in the coralloid thallus. *A. vouauxii* differs in the 2-spored asci, larger ascospores, and it usually grows on soil. *A. borysthenica* Dymytrova, Breuss & S.Y. Kondr. (2011) differs in the more coarsely granular thallus and the larger ascospores (33–) 40–55 (–75) × (15–) 18–24 µm; it has not been reported from Great Britain and Ireland.

Agonimia flabelliformis Halda, Czarnota & Guzow-Krzemińska (2012) **NE**

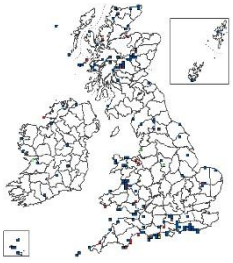


Thallus pale green-grey to brown-green, of repeatedly-branched, very narrow terete lobes 20–40 µm broad, branched either in one plane (thallus flabelliform-squamulose) or in more than one plane (thallus coralloid), squamules or coralloid clusters to 300 µm wide or tall, comprising photobiont cells completely enclosed by ± isodiametric fungal cells 4–7.5 µm diam., surface cells without papillae; older parts of lobes composed of goniocyst-like units, pale brown-green. Perithecia globose, rarely ovoid to pyriform, 150–250 µm diam., smooth, superficial or partly immersed in the thallus. Asci 8-spored. Ascospores cylindrical to ellipsoidal, (23–) 28–36 × 11−15 µm, hyaline, muriform, fewer than 20 cells visible in optical section. **BLS 2588**.

On bark. Scattered in S. England (especially the New Forest) and Wales (and at least as frequent as *A. allobata* in the south), single records from Cumbria and N. Yorkshire and one from Ireland (Co. Down). Apparently absent from Scotland.

Differs from *A. allobata* in the distinctive coralloid, sometimes fan-shaped dissected thallus lobes.

Agonimia gelatinosa (Ach.) M. Brand & Diederich (1999) **Nb**

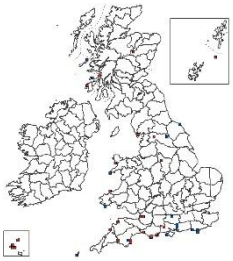


Thallus dark brown, composed of rounded goniocysts 20–40 µm diam., or lobed goniocysts 70–120 µm long; surface cells brown, papillae absent; sterile globules absent; prothallus sometimes visible, of dark hyphae. Perithecia almost superficial, 300–500 µm diam., surface smooth, black, matt; exciple 40–70 µm thick, of ± rounded cells. Asci 8-spored. Ascospores ellipsoidal, 31–55 × 15–20 µm, muriform, with 16–30 cells visible in optical section. Pycnidia rare, small, ovoid, *ca* 70 × 40 µm, black; conidia bacilliform, 2.3–3 × 0.7–0.8 µm. **BLS 1155**.

Over mosses or on soil in calcareous habitats, limestone, mortar, mica-schist and on dunes, from sea-level to at least 700 m altitude. Most lowland and southern records are probably of *Agonimia globulifera*, there are some correct records from the southern chalk. Frequently recorded in S. England (although many of these records may refer to *A. globulifera*), Wales and the Scottish Highlands, scattered in N. England and Ireland.

Data on pycnidia are from Sérusiaux *et al*. (1999). This species has been confused with *Agonimia globulifera*, which differs in the unpigmented thallus, the presence of distinctive black sterile globules, and the more strongly muriform ascospores. *Polyblastia philaea* differs in the perithecia two-thirds to almost completely immersed in soil (not merely in the thallus), the densely pigmented, unlayered exciple, and the thallus not composed of goniocysts.

Agonimia globulifera M. Brand & Diederich (1999) **Nb**

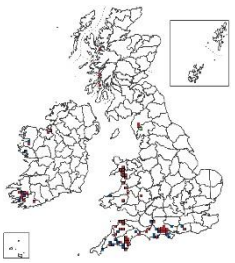


Thallus grey-green to greenish, of minute granules or short finger-like lobes 20–50 µm long, surface cells without pigment, often with papillae 1–2.5 µm high; prothallus indistinct; sterile globules frequent, subspherical to cylindrical, 70–240 µm long, black, glossy, superficial or with the lower third immersed in the thallus, composed of thin-walled colourless to pigmented cells each containing a large oil drop. Perithecia rare, superficial or partly immersed, 250–600 µm diam., black, matt. Asci 8-spored. Ascospores ellipsoidal, muriform, (32–) 37–50 × (15–) 16–26 µm, with (22–) 35–60 cells visible in optical section. Pycnidia unknown. **BLS 0026**.

Overgrowing mosses, lichens, sand, or rarely rocks, in calcareous habitats; possibly locally frequent but overlooked. Scattered records in England, Wales & Scotland.

Distinguished by the conspicuous glossy black sterile globules scattered over the thallus. See also *A. gelatinosa*.

Agonimia octospora Coppins & P. James (1978) **NT IR**



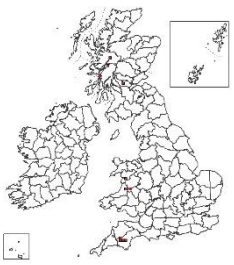
Thallus minutely squamulose; young thalli can have a basal crustose thallus from which the squamules grow, but this disappears as the squamules develop, squamules ± elongate, to 250 µm in length, of narrow lobes 40–100 µm broad, lobes sparingly to repeatedly branched, fragile, terete or slightly flattened (especially when the thallus is poorly developed), irregularly and slightly constricted, matt, pale grey-green, blue-green when wet, scattered and dispersed or in more or less contiguous groups and becoming imbricate; surface cells with papillae which are easily seen under a 40× objective. Photobiont cells 6–10 × 5–8 µm. Perithecia occasional, scattered amongst squamules, 460–800 µm, one-quarter- to half-immersed, globose or ± pyriform, black, matt or ± glossy, the surface smooth or slightly roughened or shallowly fissured above; exciple 120–160 µm thick, ostiole somewhat papillate, pale pink-grey to black, often eccentric. Asci 8-spored. Ascospores ellipsoidal, muriform, 60–75 (–85) × 20–26 (–30) µm. **BLS 0037**.

On base-rich bark of trunks of aged *Quercus* and *Fagus*, often amongst mosses, in somewhat sheltered situations in old woodlands; rare. Frequently recorded in S.W. England, the New Forest and Wales, scattered records from the Lake District, W. Scotland (Kintyre, Argyll, Skye), also S. and W. Ireland.

The perithecia sometimes occur near to, but not contiguous with, the squamules. Sterile specimens can be

confused with *Agonimia tristicula*, which has distinctly wider flattened lobes. The isidiate lobes of *Rinodina isidioides* can look very similar in size and shape: they are paler, grey rather than grey-green, and are visibly K+ yellow and K/UV (dry)+ bright yellow (though testing these rare species in the field is scarcely recommended). Confusingly, *A. octospora* squamules frequently diffuse a yellow pigment when irrigated with K viewed under a microscope, but this is not field visible, or is K/UV (dry)+ bright). The surface of the lobes in *Rinodina isidioides* is of isodiametric to shortly oblong cells, but is distinctly hyphal in squashes, unlike the apparently non-hyphal surface of *Agonimia*; some of the surface cells project, giving a knobbly outline under the microscope, but they are smooth, without papillae; the photobiont cells are 7–14.5 µm long.

Agonimia opuntiella (Buschardt & Poelt) Vězda (1997) **Nb**

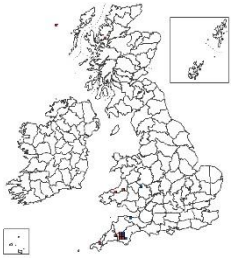


Thallus of squamules, these subglobular at first, rapidly becoming flattened and lobed, lobes convex, 100–260 µm broad, sometimes concave below when well-developed, pale grey in shade to dull greenish grey when well-illuminated, minutely roughened and ± pruinose, blastidia often produced on the underside or also the upper side of the lobes, visible as granules 30–40 µm diam. at first. Thallus anatomy of isodiametric cells throughout, with intercellular spaces; a brown pseudocortex is present, overlain by a very distinct epinecral layer of isodiametric cells 6–10.5 µm diam., each bearing several conspicuous papillae mostly 1.5–3.3 × *ca* 1.5 µm, and sometimes very long hairs to *ca* 40 µm, comprising very long papillae adhering in bundles; the cells of the epinecral layer are colourless, with refractive contents; in K the epinecral layer becomes indistinct, with broken remains of cells without refractive contents. Photobiont distributed throughout the squamules, cells isodiametric to irregularly cylindrical, 4–13 × 3.5–7.5 µm. Perithecia (unknown in the region) pyriform, 200–250 µm diam., rough around the ostiole. Asci (1–) 2-spored. Ascospores muriform, 60–80 × 25–30 µm. **BLS 2449**.

Among mosses on *Quercus* and in crevices in siliceous rocks in open or lightly shaded habitats, sometimes beside streams on mosses including *Andreaea rothii*. Scotland (Argyll, Stirlingshire, Outer Hebrides), Wales (rare), Cornwall and Devon.

In many collections the lobes have very distinctive stiff hairs which are visible with a 10× handlens, but these are sometimes rare or absent. In well-lit habitats the dull grey colour and (under the dissecting microscope) faintly pruinose surface are distinctive, and are due to the presence of a remarkable layer of dead refractive cells overlying the brown pseudocortex. *Agonimia tristicula* has lobes of a similar size, and the two species can grow together; it differs in the green to brown, non-pruinose thallus surface, and slightly less convex lobes without a distinct epinecral layer.

Agonimia repleta Czarnota & Coppins (2000) **Nb**



Thallus dull green, rarely brownish, granular, granular-verrucose or minutely squamulose; granules (30–) 40–120 µm diam., often coalescing; squamules sometimes present, elongate, to 240 × 100 µm; cortex often with papillae to 1.7 µm high on a few cells. Perithecia mostly half to three-quarters immersed in the thallus, 140–200 µm diam., globose when young, later pyriform, the upper part roughened with vertical cracks or grooves. Asci 8-spored. Ascospores muriform, 20–46 × 12–20 µm, mainly ellipsoidal, sometimes subglobose. **BLS 0023**.

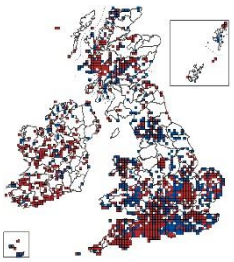
On bark, often where mossy, soil on mine sites, and on mossy riverine rocks; local. S.W. England, Wales (Ceredigion, Radnorshire), Scotland (Wester Ross, St Kilda).

Distinguished from *A. allobata* by the roughened surface of the perithecia that often become pyriform rather than remaining globose. *A. tristicula* has similarly ornamented perithecia, but (1-) 2-spored asci with much larger ascospores.

Agonimia tristicula (Nyl.) Zahlbr. (1909) **LC**

Thallus minutely squamulose, squamules to 100–1600 × 100–300 (–500) µm, but soon becoming confluent or losing their identity and then impossible to measure, scattered or crowded and overlapping, with mostly short lobes 30–160 µm broad, shallowly convex, smooth to very faintly pruinose-roughened, grey-green to brown; the larger lobes slightly concave below; lower surface pale, uneven; some narrow-lobed squamules readily disintegrating into granules. Upper surface with a pseudocortex, unpigmented to brown, with or without papillae to 2.5 µm high, epinecral layer absent; remainder of the thallus with photobiont throughout, with intercellular

spaces; lower surface rather lax, sometimes producing blastidia. Perithecia 240–500 µm diam., sparse to frequent, often in between or overgrown by squamules, barrel-shaped, the surface black, matt, roughened and furrowed; exciple thick. Asci (1-) 2-spored. Ascospores (42–) 57–120 (–150) × 26–50 µm, elongate-ellipsoidal, densely muriform, in some cases becoming brown when over-mature. **BLS 0038**.



On calcareous soil and dunes, or on mosses and lichens in crevices of ± calcareous rocks and walls, including limestone, mortar, basalts and serpentine, more rarely on bark of base-rich trees, especially *Acer, Ulmus* and *Fraxinus*, also amongst bryophytes on periodically inundated siliceous rocks by rivers and lakes; frequent. Throughout Britain and Ireland.

Sterile corticolous specimens are distinguished from *A. octospora* by their larger, more distinctly flattened lobes which are brown when well-illuminated. There is evidence that material on siliceous rocks is not conspecific with material on calcareous rocks, but no firm morphological differences have been found.

ATLA S. Savić & Tibell (2008)

Thallus crustose, immersed, or superficial, granular to areolate. **Photobiont** a green alga; sometimes cyanobacteria including *Nostoc* and *Stigonema* are also associated with the thallus, and may be symbiotic; hymenial algae absent. **Ascomata** perithecia, projecting, in thalline warts, or immersed in the substratum, 0.3–1 mm diam. **Involucrellum** absent or well-developed. **Hamathecium** of periphyses and periphysoids, interascal filaments absent; gel hemiamyloid, I+ red (+ blue at very low concentrations of I), K/I+ blue. **Asci** clavate, K/I–, fissitunicate, wall thickened above when young. **Ascospores** (3-)8 per ascus, often very large, ellipsoidal, muriform, colourless to dark brown. **Conidiomata** unknown. **Chemistry**: lichen products absent. **Ecology**: on calcareous rocks and soil.

A monophyletic genus of seven species in Europe, Novaya Zemlya and Alaska. The genus cannot be distinguished by morphology from *Sporodictyon* or *Polyblastia s. str*.

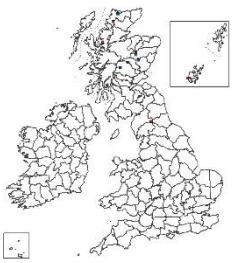
Literature

Hafellner (2010), Moberg *et* al. (2017), Orange (2009a), Pykälä & Myllys (2016), Savić & Tibell (2008a), Tibell & Tibell (2015).

1 Perithecia immersed in the substratum, on soil; involucrellum absent ..... ***wheldonii***
Perithecia prominent, on rock; involucrellum present ..... ***alpina***

Atla alpina S. Savić & Tibell (2008) **Nb**

Thallus superficial, thin and inconspicuous, or well-developed and uneven, continuous or cracked, grey-green to pale brown. Perithecia forming hemispherical projections or strongly projecting, 0.6–1.0 mm diam., black, the surface rough, without a thalline covering or with at most a very low thalline collar at the base. Involucrellum present, more or less clasping the exciple, or somewhat diverging below. Ascospores dark brown when mature, the cell outlines mostly obscured; (63–) 72–87 (–98) × (30–) 35–47.5 (–52) µm, length/width ratio (1.5–) 1.7–2.3 (–2.7). **BLS 2494**.

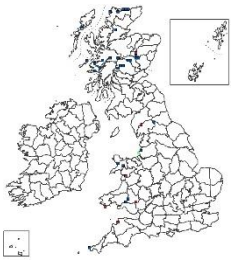


On damp limestone and calcareous sandstone on cliff ledges and below overhangs, upland, 150–900 m; true distribution unknown due to previous taxonomic misunderstanding. S. Wales, N. Pennines, C. and W. Scotland.

This species has been confused with *Sporodictyon schaererianum*, which differs in the presence of at least a partial thalline covering to the perithecia, and slightly smaller ascospores. Colonies of *Nostoc* have been reported in association with the thallus of *A. alpina*, but true cephalodia are unknown.

Atla wheldonii (Travis) S. Savić & Tibell (2008 **NT IR**

Thallus superficial, granular, brown to dark brown, granules 20-100 µm diam., composed of distinct goniocysts, but cyanobacteria also often associated with the thallus. Perithecia immersed in the substratum with only the apex projecting, occasionally partly exposed, 0.64–0.8 mm diam. Involucrellum absent. Exciple pigmented throughout, somewhat extended above into a short neck. Asci (3-)4- to 8-spored when mature. Ascospores muriform, brown to dark brown, opaque when mature, 80–160 × 40–92 µm (the larger spores are probably derived from asci with fewer than 8 spores). **BLS 1164**.



On base-rich soil and on dying mosses, over limestone, basic metamorphic rocks and calcareous sandstone; also on dunes and mine spoil-heaps; rare. Wales, S.W. & N. England, Scotland.

BAGLIETTOA A. Massal. (1753)

Thallus endolithic, the surface comprising a lithocortex (densely conglutinated hyphae mixed with calcite crystals) or a micrite layer (a redeposited layer of fine-grained calcite, with sparse hyphae); medulla often with swollen oil cells in the lower part. **Photobiont** *Asterochloris* or *Trebouxia* (Trebouxiophyceae). Algal layer discontinuous, 50–120 µm high, photobiont cells in clusters 25–40 µm diam., rounded, scattered, cells 6–12 µm diam. **Prothallus** absent or brown-black to black, in contiguous conspecific thalli visible as thin dark lines. **Medulla** often with oil cells in the lower part, laterally or terminally branching and often with a basal swelling. **Ascomata** perithecial, completely immersed, forming pits in rock. **Involucrellum** either present, more or less flat and confined to the apex of the exciple (appearing lid-like) and often with fine radial cracks, or absent. **Exciple** dark or pale. **Hymenium** colourless, K/I+ blue. **Hamathecium** of periphysoids located in the ostiolar canal and the upper half of the perithecial cavity, sometimes with detachable tips. **Asci** 8-spored, *Verrucaria*-type. **Ascospores** aseptate, colourless, often absent or deformed. **Conidiomata** absent or very rare (not seen in British or Irish material). Periphysoid tips may act as propagules.

The genus is monophyletic (Gueidan *et al*. 2007, 2009), characterised by the endolithic thallus, presence of oil cells, and the lid-like radially-cracked involucrellum (when present). In some species (*Bagliettoa baldensis*, *B. parmigera s.l.* in part and *B. parmigerella*) ascospores are either absent or deformed, and it seems likely that the detachable tips of the periphysoids may act as propagules (Gueidan *et al.* 2007). Thallus anatomy was investigated by Pinna *et al*. (1998) and Bungartz *et al*. (2004). Yuzon *et al*. (2014) investigated the species-level taxonomy, but some taxa are still unresolved and more studies are needed.

The relationship between the diameter of the involucrellum and the exciple has been used as a character at species level, but this is difficult to observe because of the immersed perithecia and the fragile involucrellum. The radial cracks in the involucrellum are a well-known character for some species, but may be difficult to see in the field, and in some specimens they are scarcely developed.

In addition to the key to species below, *Bagliettoa* species are included in the main key to Verrucariaceae (above). *V. hochstetteri* Fr. (1831) is morphologically similar to species of *Bagliettoa*, especially *B. calciseda*, but has larger perithecia and ascospores; it should perhaps be included in *Thelidium* (Gueidan *et al*. 2009).

Literature

Bungartz *et* al. (2004), Gueidan *et al*. (2007, 2009), Halda (2003), Krzewicka (2012), Orange *et al*. (2009b), Pinna *et al*. (1998), Yuzon *et al*. (2014).

1 Involucrellum absent; thallus smooth or with a few long radiating cracks.....2
Involucrellum present, lid-shaped, often with cracks radiating from the perithecium.....4

2(1) Ascospores 13–30 µm long; perithecia 240–420 µm diam. 3
Ascospores (25–) 29–34.5 (–41.5) µm long, exciple 380–700 µm diam.....***Verrucaria hochstetteri***

2(1) Thallus without pigment .....***calciseda***
Thallus with at least localized purple-red pigment.....***marmorea***

4(1) Cortex containing blue-green pigment .....***parmigerella***
Cortex without pigment..... (***baldensis*** *sensu lato*) 5

5(4) Thallus with a translucent, porcelain-like appearance.....***baldensis***
Thallus dull .....***parmigera***
(These two should be confirmed by sequencing)

Bagliettoa baldensis (A. Massal.) Vězda (1981) **NE**

Verrucaria baldensis A. Massal. (1852)

Thallus immersed, white to pale blue-grey, not cracked, matt with a somewhat translucent appearance, without blue-green or purple pigment. Involucrellum 160–240 µm diam., flat to slightly convex, in surface view black, rough or with cracks radiating from the ostiole. Perithecia 260–360 µm diam. when detached from the thallus and moist, almost completely immersed in well-defined pits in the substratum, broader than the involucrellum, the wall black when viewed in a perithecium cut in half. Ascospores not observed. **BLS 2840** (**BLS 1479** *sensu lato*; see text below).

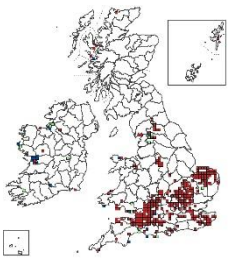
On limestone, where there is slight moisture or seasonal seepage, but few records have been confirmed. Wales, but probably widespread.

Until recently this name has been used for one of the commonest and most easily recognizable lichens on hard limestone, but it is used here in a much narrower sense. Most material previously referred here belongs in *B. parmigera s.l.*, which is said to differ in the perithecium equal to or broader than the involucrellum, although it is unlikely that this is a reliable distinction. The very limited confirmed material from Britain has a thallus with a porcelain-like appearance when compared to *B. parmigera*, suggesting the presence of a micrite layer, but more studies are needed.

Potentially host to *Opegrapha rupestris*, though probably most colonies occur on *B. parmigera s. lat*. That species also occurs on *B. calciseda* (Coppins *et al*. 2021).

Bagliettoa calciseda (DC.) Gueidan & Cl. Roux (2007) **LC**

Verrucaria calciseda DC. (1805)



Thallus endolithic, white or pale grey, the surface smooth or with a few long cracks radiating from some of the perithecia, apparently composed of redeposited calcite; without pigment. Perithecia immersed in well-defined pits in the rock, 240–420 µm diam.; the wall pigmented throughout; involucrellum absent. Ascospores ellipsoidal, (21–) 23–27 (–29) × (8.5–) 10–13 (–15) µm, length/width ratio (1.7–) 2.0–2.5 (–2.8), perispore absent; ascospores sometimes with dull grey-brown contents. Conidiomata not seen. **BLS 1480**.

On limestone rocks; frequent but much under-recorded until recently. Common in S. England, scattered in N. England, Wales, W. Scotland and W. Ireland.

In the field, the often white thallus and the radiating cracks running from the perithecial pits are distinctive, but the cracks are not always present; these probably result from fracture of the brittle surface layer by an expanding perithecium. Ascospores and asci often (when over-mature or unhealthy?) have dark contents, which are distinctive for this species.

Bagliettoa marmorea (Scop.) Gueidan & Cl. Roux (2007) **NE**

Thallus endolithic, smooth, purple-pink, or grey with purple-pink pigment associated with the perithecia; pigment K+ dull green. Perithecia 200–300 µm diam., colourless below; involucrellum absent. Ascospores 13–30 × 9–15 µm.

On limestone. One unconfirmed record of immature material from stonework, S. England.

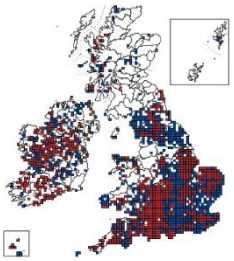
B. cazzae (Zahlbr.) Vězda & Poelt from southern Europe also has a purple-pink thallus, but a lid-like involucrellum is present.

Bagliettoa parmigera (J. Steiner) Vězda & Poelt (1981) *sensu lato* **LC**

Bagliettoa steineri (Kušan) Vězda (1981)

Bagliettoa suzaeana (Servít) Gueidan & Cl. Roux (2014)

Verrucaria baldensis auct. p.p.



Thallus endolithic, white, matt, uncracked. Involucrellum in surface view black, flat to slightly convex, 140–320 µm diam., rough or with radial grooves or cracks. Perithecia 200–350 µm diam. when detached from the thallus and moist, as broad as or broader than the involucrellum, the wall colourless to rarely black when viewed in a perithecium cut in half, colourless to translucent brown in a squash. Ascospores 18.5–22.5 × 9–10 µm (only a few measured), often absent (hymenia in poor condition). **BLS 1479**.

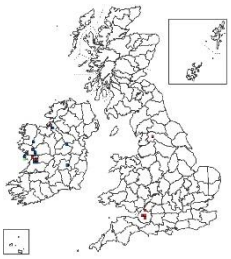
On limestone, frequent on sunny rocks but tolerant of some shade, widespread and frequent. The map is an approximation of distribution; it includes records for *B. baldensis* and *B. parmigera* s. lat. and some misidentified records of *B. calciseda*.

Molecular studies indicate three main clades in this complex, corresponding to *B. parmigera sensu stricto*, *B. steineri* and a variable clade named provisionally as *B. suzaeana*. The morphological differences between these, if any, are currently obscure. Only *B. steineri* [**BLS 2841**] and *B. suzaeana* [**BLS 2842**] have so far been detected in Britain, and both are probably widespread.

Bagliettoa species are host to *Opegrapha rupestris*, *Toninia verrucariae* and *Polycoccum dzieduszyckii* (Boberski) D. Hawksw. (1980), the last only from a 19th century specimen from Gloucestershire. Also, may be associated with *Lichenothelia renobalesiana* D. Hawksw. & V. Atienza (2008).

Bagliettoa parmigerella (Zahlbr.) Vězda & Poelt (1981) **Nb**

Verrucaria parmigerella Zahlbr. (1919)



Thallus immersed, grey, dark grey- or blue-green, often glossy, uncracked; upper thallus containing blue-green pigment. Involucrellum disc-like, flat to slightly convex, 150–220 µm diam., spreading sideways but scarcely downwards; in surface view usually with 3–6 fine cracks radiating from the ostiole. Perithecia almost completely immersed in pits in the rock, numerous but often sterile, globose to slightly pyriform, 180–260 µm diam. and 220–300 µm high, the wall colourless to pale brown below. Ascospores 14–21 × 6–8 µm, but usually absent. **BLS 1621**.

On hard, exposed limestone; rare. England (Cotswolds and Pennines), scattered in Ireland, mainly in the west.

Differs from *B. baldensis* in thallus colour and the smaller involucrellum.

CATAPYRENIUM Flot. (1850)

Thallus squamulose, attached to the substratum by intertwined colourless or brownish rhizoidal hyphae. **Upper cortex** rather thin (10–30 µm), uneven in thickness and poorly differentiated from the algal layer, composed of small (5–8 µm diam.) roundish-angular cells; **lower cortex** composed of roundish-angular cells, or absent. **Photobiont** *Diplosphaera* (Trebouxiophyceae). **Ascomata** perithecia, immersed in the thallus. **Involucrellum** absent. **True exciple** composed of tangentially arranged ± elongated cells, pigmented around the ostiole, lower part pale or ± darkened. **Hamathecium** of periphyses; paraphyses absent. **Asci** 8-spored, clavate, thin-walled, non-amyloid

and without an ocular chamber. **Ascospores** biseriate, colourless, aseptate, ellipsoidal or ± ovoid-clavate. **Conidiomata** absent. **Chemistry**: no lichen products detected by TLC. **Ecology**: mostly on soil or over decaying bryophytes and plant debris, preferring calcareous substrata, one species on bark.

The genus *Catapyrenium* has been used in a broad sense to include all squamulose Verrucariaceae without hymenial algae, but it is now applied to a small monophyletic group of about eight species in the *Staurothele* group of genera (Gueidan *et al*. 2009). *Placidiopsis* is a closely related genus, differing in the consistently one-septate ascospores (a few 'pseudoseptate' spores may be observed in *Catapyrenium*). Both genera are monophyletic, and occupy sister clades (Prieto *et al*. 2010b). Several species formerly assigned to *Catapyrenium* (none from our area) were excluded from the genus by Prieto *et al*. (2012) and placed in the genera *Clavascidium* and *Placidium.*

Literature

Breuss (1990, 1996, 2009a, 2010), Breuss & Hansen (1988), Gueidan *et* al. (2009), Prieto *et al*. (2010a,b, 2012).

Key to species of the genera *Catapyrenium, Involucropyrenium* and *Placidium*

1 Perithecia between the squamules, globose, black; involucrellum entirely surrounding the perithecia; thallus minutely squamulose and crust-like ..... ***Involucropyrenium waltheri***
Perithecia immersed in the squamules; involucrellum absent; thallus more distinctly squamulose 2

2(1) Rhizoidal hyphae brown, forming a dense, dark prothallus; upper cortex thin and poorly delimited from the algal layer; asci clavate 3
Rhizoidal hyphae colourless; upper cortex clearly delimited from the algal layer; asci cylindrical 5

3(2) Squamules rarely >2 mm diam., totally appressed, finely notched to deeply incised, usually ± whitish pruinose; lower cortex present ..... ***Catapyrenium cinereum***
Squamules <4 mm across, irregularly rounded or ± elongated, especially the peripheral ones; lower cortex absent 4

4(3) Usually on bark; distal parts of squamules often with grey or violet-grey pruina in defined patches ..... ***Catapyrenium psoromoides***
Usually on soil; pruina, if present, not in defined patches ..... ***Catapyrenium daedaleum***

5(2) Squamules usually loosely appressed or partly ascending, crowded to overlapping; pycnidia marginal 6
Squamules ± firmly appressed, not ascending, dispersed to contiguous; pycnidia laminal 8

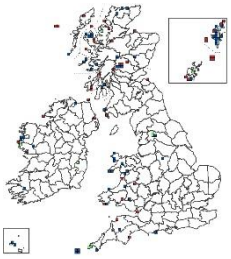
6(5) Pycnidia usually very conspicuous, globose, black and friable; lower cortex of vertically arranged angular cells; conidia 5–7 µm long, bacilliform ..... ***Placidium lachneum***
Pycnidia less conspicuous; lower cortex of globose cells, not distinctly vertically arranged; conidia 3–5 µm long, cylindric-ellipsoidal 7

7(6) Ascospores 15–20 × 7.5–9.5 µm; squamules to 10 mm across, thick and leathery, ± wavy, with thick medullary tissue of elongate hyphae ..... ***Placidium rufescens***
Ascospores 12–17 (–19) × 5.5–7.5 µm; squamules to 6 mm across, thin; medullary tissue less well-developed, formed of a mix of globose and elongate cells ..... ***Placidium pilosellum***

8(5) True exciple brownish to black throughout when mature ..... ***Placidium michelii***
True exciple persistently pale, only the uppermost part around the ostiole pigmented 9

9(8) On mortar or calcareous rocks; squamules 2–4 mm across, often with dark margins; lower side black ..... ***Placidium boccanum***
On soil; squamules 2–7 mm across, not dark-margined; lower side pale to brown, rarely blackish ..... ***Placidium squamulosum***

Catapyrenium cinereum (Pers.) Körb. (1855) **Nb**

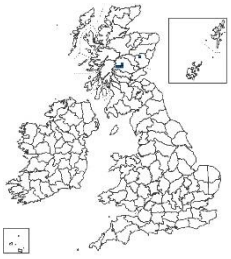


Thallus of small, ± densely aggregated squamules, to 0.3 mm thick, rarely more than 2 mm across, closely appressed, finely incised especially at the periphery, sometimes subgranular in central parts of the thallus, usually whitish-pruinose, rarely glabrous and brown, often with a darker margin; lower cortex paraplectenchymatous, blackish; hypothallus blackish, spongy, of intricately interwoven brown to black rhizoidal hyphae *ca* 4 µm diam. Perithecia numerous, immersed in the squamules, the ostioles sometimes slightly elevated; exciple pale when young, soon becoming brown or blackish throughout. Asci clavate. Ascospores 17–23 × 6–9 µm, usually ± clavate, biseriately arranged. **BLS 0300**.

On soil, humus or mosses, especially on calcareous ground; frequent in upland areas, also on consolidated soil on or near the coast. Mainly in N. & W. British Isles.

The small, rather regular squamules with an often densely white-pruinose upper surface and a distinct lower cortex with black, matted rhizoidal hyphae are distinctive. *Placidiopsis pseudocinerea* is similar but has uniseptate ascospores, and larger and less deeply incised squamules (Breuss & Hansen 1988).

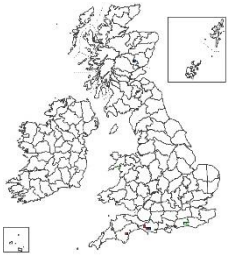
Catapyrenium daedaleum (Kremp.) B. Stein (1879) **VU (D1)**



Squamules to 4 mm across, dispersed to crowded and then thalli often almost rosette-like, thickish, rounded or slightly elongated at the periphery, firmly appressed or with slightly raised margins; upper surface matt, not pruinose and brown, or weakly pruinose and then with a greyish tinge; lower surface non-corticate; medullary tissue merging into the hypothallus of dark rhizoidal hyphae. Perithecia usually numerous, immersed; exciple, except for the ostiole, pale when young, later brownish throughout. Asci clavate. Ascospores 17–22 × 6–9 µm, cylindric-ellipsoidal to slightly clavate, biseriately arranged. **BLS 1560**.

On soil or humus or moribund bryophytes, confined to upland areas; rare. E.C. Scotland (Mid-Perth, Breadalbane Mts.).

Catapyrenium psoromoides (Borrer) R. Sant. (1980) **CR (D)**



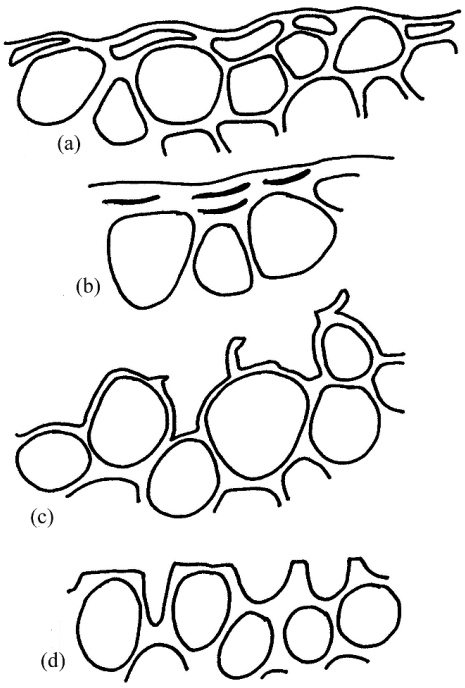
Squamules to 4 mm across, dispersed to contiguous or partly imbricate, ± divided, often somewhat elongate (especially at the periphery), loosely attached or slightly ascending at the apices; upper surface dull greyish or greenish brown to fawn; distal parts of squamules often with grey-violet pruina in defined patches; lower surface non-corticate; medullary layer gradually merging into the dark hypothalline tissue of interwoven rhizoidal hyphae. Perithecia moderately frequent, fully immersed; exciple pale or slightly brownish. Asci clavate. Ascospores 14–18 × 5–7 µm, ellipsoidal or ± attenuated at the apices, sometimes pseudoseptate, biseriately arranged. **BLS 0303**.

Mostly on bark or bryophytes thereon; very rare and local. E.C. Scotland (E. Perth), England (Devon, Dorset, Sussex) & Wales (Gwynedd, Harlech).

The only bark-inhabiting species of *Catapyrenium* in Europe, closely related to *C. daedaleum*. The ± patchy pruina is a diagnostic feature.

DERMATOCARPON Eschw. (1824)

Thallus squamulose to foliose, grey to brown, attached by one or more central or scattered holdfasts; true rhizines and rhizoidal hyphae absent; both surfaces corticate, specialized vegetative propagules absent; some species with nodular or rhizine-like structures on the lower surface. **Upper cortex** of pseudo-parenchymatous cells, often with brown pigment near the surface. **Epinecral layer** thin, comprising cells that are either compressed (the thallus surface usually not pruinose) or broken and air-filled (then often visible as a pale pruina). **Medulla** of filamentous hyphae. **Lower cortex** pseudo-parenchymatous, of anticlinal rows of thick-walled cells, the inner cells larger than the outer, with brown pigment at the surface. **Photobiont** *Diplosphaera* (Trebouxiophyceae) (*D. chodatii* fide Fontaine *et al*. 2012); *Myrmecia biatorellae* and *Protococcus dermatocarponis* have also been reported. **Ascomata** perithecioid, immersed in the thallus. **Involucrellum** absent. **Exciple** unpigmented except at the apex. **Hamathecium** of periphyses and periphysoids, interascal filaments absent. **Hymenial gel** hemiamyloid, I+ red (I+ blue at very low concentrations of iodine), K/I+ blue. **Asci** clavate, rarely cylindrical, the wall thickened above, I–, K/I–, 8-spored. **Ascospores** aseptate, colourless, ellipsoidal, smooth, without a perispore, usually irregularly arranged in the ascus. **Conidiomata** pycnidia, laminal, immersed in the thallus. **Conidia** aseptate, rod-shaped. **Chemistry**: acetone-soluble secondary products absent, some species with an I+ red polysaccharide in hyphal walls. **Ecology**: on siliceous or calcareous rock, often in damp habitats.



Cross-section of cortex types in *Dermatocarpon.* (a, b) Compressed type (surface cells crushed); (c, d) air-filled type (surface cells broken).

A monophyletic genus. There are rather few taxonomically useful characters to differentiate the species; these include ascospore size, the colour of the lower surface, and the nature of the epinecral layer (viewed in thin section). The presence of pruina usually indicates an air-filled epinecral layer, but an absence of pruina is not conclusive. Care should be taken not to mistake a pale upper surface for pruina, nor the pale incrustations seen on some dried specimens. The iodine reaction of some species should be observed on thin sections viewed under a stereomicroscope. The reaction with 1.5% IKI is weak and is obscured by the reaction of the cell contents, so the test is best carried out with Melzer's reagent, or using the 20%>0.15% IKI test on sections previously bleached in sodium hypochlorite solution (Orange 1998). The cellulose cell walls of the photobiont also react with I and should not be confused with the reaction of the hyphae. Despite the imprecise characters used in the key, each species has a habitus which makes it easily recognised once known.

Species of *Catapyrenium* are distinguished by the absence of holdfasts, and by the presence of rhizoidal hyphae on the lower surface. The presence of one or more of the following characteristics distinguishes sterile specimens of *Lasallia* or *Umbilicaria* species from *Dermatocarpon*: lower surface of rhizines or black thalloconidia; upper surface or margin with isidia, erose sorediate areas or cilia; photobiont trebouxioid; detectable lichen products in the medulla (by spot tests or TLC). *Endocarpon* differs in the multiseptate to muriform ascospores and the presence of hymenial algae.

The lichenicolous *Opegrapha pulvinata* has been reported on the thallus of *D. intestiniforme*, *D. luridum*, *D. miniatum* and *D. meiophyllizum*.

Literature

Amtoft *et al*. (2008), Fontaine *et al*. (2012), Heiðmarsson (1998, 2000), Orange (1998), Orange & Coppins (2009).

1 Medulla I+ red or violet; thallus not pruinose, repeatedly lobed, with scattered holdfasts; beside streams ..... ***luridum***
Medulla I– 2

2(1) Thallus repeatedly lobed, holdfasts several, scattered; ascospores (8–) 8.5–15 (–16) µm long ..... ***intestiniforme***
Thallus various, but attached by a single holdfast (colonies of small, crowded thalli may be confused with a single multi-lobed thallus) 3

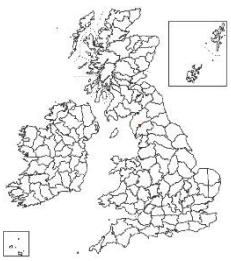
3(2) Ascospores (8–) 9–14 (–15) µm long ..... ***miniatum***
Ascospores (12–) 14–22 (–25) µm long 4

4(3) Epinecral layer of 'compressed' type (see figure above), upper surface of thallus not pruinose 5
Epinecral layer of 'air-filled' type, upper surface of thallus pruinose or not 6

5(4) Thallus underside wrinkled (but variable in a single colony); thallus 0.10–0.38 mm thick when moist (measured between wrinkles and perithecia) ..... ***rivulorum***
Thallus underside smooth, rarely with a few wrinkles or folds; thallus 0.24–0.5 (–0.8) mm thick when moist (measured between perithecia) ..... ***meiophyllizum***

6(4) Thalli 2–7 mm diam., typically forming dense colonies in which the limits of the individual thalli may be difficult to discern; thallus pruinose or not ..... ***leptophyllodes***
Thalli to 22 mm diam., often crowded but not forming dense colonies in which the limits of the individual thalli are difficult to discern; thallus usually pruinose ..... ***deminuens***

Dermatocarpon deminuens Vain. (1921) **DD Nb**



Thallus to 22 mm diam., attached by a single central holdfast, ± unlobed or slightly lobed; 0.25–0.4 mm thick when moist, measured in fertile parts of the thallus between the perithecia and veins; upper surface light to dark grey or grey-brown, pruinose, pruina often conspicuous and easily seen with the unaided eye, sometimes sparse but only very rarely absent, epinecral layer of air-filled type; lower surface mid- to dark brown, usually slightly glossy, smooth to wrinkled or with a reticulum of raised veins; medulla I–. Ascospores (14–) 16–22 (–25) × (5.5–) 6.5–8.5 (–9) µm. **BLS 0524**.

On intermittently inundated rocks on the shore of a small base-rich lake; very rare, only known from a single site at 615 m altitude (Brown Cove Tarn, English Lake District), but possibly overlooked.

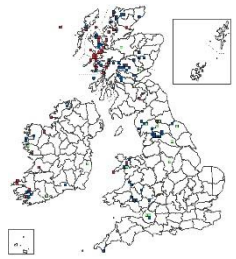
Distinguished by the pruinose upper surface, brown lower surface, and large ascospores; specimens with a veined underside are striking, but many specimens are smooth; *D. meiophyllizum* and *D. rivulorum* are brown and not pruinose above; *D. meiophyllizum* is slightly thicker and is never veined below and its lower surface is often darker but the colour range overlaps in the two species. *D. miniatum* differs in the shorter ascospores.

Dermatocarpon intestiniforme (Körb.) Hasse (1912) **LC**

Thallus repeatedly lobed, to 70 mm diam., attached by numerous scattered holdfasts; lobes 3–20 mm wide, often crowded and overlapping; upper surface pale grey to dark brown, pruina thin to well-developed, at least on young lobes, very rarely absent, epinecral layer of air-filled type; lower surface smooth, rarely wrinkled, light to dark brown; medulla I–. Ascospores broadly ellipsoidal to ellipsoidal, (8–) 8.5–15 (–16) × (5.0–) 5.5–7.5 (–8) µm. **BLS 0480**.

On damp siliceous, often slightly basic rocks on flushed (but often seasonally dry) rock-faces, on lake shores

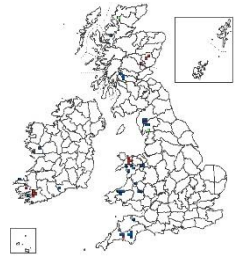
and in the upper part of the inundated zone of rivers; widespread but local. N. & W. Britain and S. & W. Ireland.



This is a member of the *D. miniatum* group; it differs from that species only in the strongly divided thallus with numerous scattered holdfasts; lobed specimens of *D. miniatum* still have only a central holdfast. *D. luridum* differs in the non-pruinose upper surface and I+ red medulla. The species as currently defined is a species complex; British and Irish material is uniform in ITS sequence, but differ from material from Austria.

There are a few records of *Opegrapha pulvinata* on this host.

Dermatocarpon leptophyllodes (Nyl.) Zahlbr. (1921) **Nb**

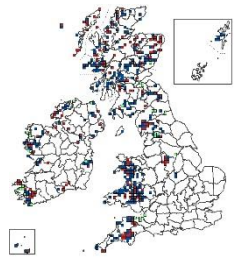


Thallus 2–7 mm diam., attached by a central holdfast, secondary holdfasts absent or rare; thalli usually crowded, often difficult to distinguish from each other, forming colonies to 30 mm or more diam.; a common dark brown prothallus can often be seen below the thalli; upper surface pale grey to dark brown, pruina absent or thinly present; lower surface pale to dark brown; medulla I–. Ascospores (12–) 15–22 × 5–7.5 (–8) µm. **BLS 0481**.

On siliceous rocks that are intermittently inundated, by unpolluted and unacidified rivers and lakes, often on the tops of boulders and on well-drained rock crests, occasional. W. Britain and W. Ireland.

Distinguished by the small, tightly crowded thalli, which sometimes give a superficial appearance of a cracked crustose thallus. Small colonies of *D. intestiniforme* may be superficially similar, but in that species the lobes are part of a single thallus.

Dermatocarpon luridum (With.) J.R. Laundon (1984) **LC**

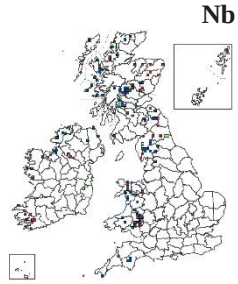


Thallus repeatedly lobed, mat-forming, ± flaccid when moist; lobes 5–15 mm wide, 0.15–0.4 mm thick, often convex especially in the centre of the mat, attached by scattered holdfasts; upper surface not pruinose, but often developing clusters of white crystals in dried collections, grey to pale brown, rarely dark brown in exposed places but bright green when wet; lower surface smooth, pale brown; medulla I+ red or violet (in section, best seen using Melzer's reagent). Ascospores (10–) 12–19 (–23) × 5–8 µm. **BLS 0487**.

On intermittently inundated siliceous rocks and limestone by rivers and lakes, in the lower part of the inundated zone, occasionally on dripping rocks, avoiding acid water, tolerant of some shade; locally frequent, but intolerant of water pollution and acidification. Widespread in N. & W. Britain, very rare in C. & S.E. England, near the coasts in Ireland.

Distinguished by the large lobed non-pruinose thallus which is bright green when wet, and the scattered holdfasts. *D. intestiniforme* differs in the usually pruinose upper surface. Very young or difficult specimens are distinguished from all other British and Irish species by the I+ red medulla. *D. polyphyllizum* (Nyl.) Vainio from Fennoscandia and Russia has a similar I reaction, but differs in the much smaller thallus (to 14 mm diam.), monophyllous but lobed, with secondary holdfasts rare or absent, lobes 0.4–3 (–6) mm wide, ascospores 9.5–14 × (5–) 5.5–7.5 µm. *Opegrapha pulvinata* has been found on specimens from St Kilda.

Dermatocarpon meiophyllizum Vain. (1921) **Nb**



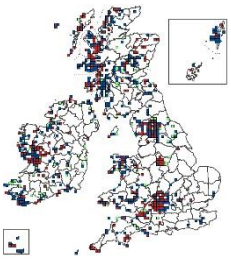
Thallus 8–18 (–30) mm diam., attached by a central holdfast; 0.25–0.5 (–0.8) mm thick when moist (measured between perithecia); upper surface light to dark brown or greyish brown, pruina absent or rarely thin and inconspicuous, epinecral layer of compressed hyphae; lower surface dark brown to blackish brown, matt, sometimes slightly roughened, smooth or rarely with a few wrinkles or folds; medulla I–. Ascospores (13–) 14–20 (–23) × (6–) 6.5–9 (–10) µm. **BLS 0483**.

On intermittently inundated siliceous rocks by rivers and lakes, in the lower part of the inundated zone. Widespread but local in N. & W. Britain and mainly in the W. in Ireland, possibly a little under-recorded.

Distinguished by the dark lower surface and the large ascospores. Easily overlooked when submerged, as it may grow appressed to the rock and covered by a thin layer of silt. See also *D. diminuens* and *D. rivulorum*.

There are two records of *Opegrapha pulvinata* (from Skye) on this host.

Dermatocarpon miniatum (L.) W. Mann (1825) **LC**



Thallus to 20–50 mm diam., entire or lobed, attached by a central holdfast; upper surface pale grey to greyish brown to dark brown (mainly in exposed upland habitats), pruina absent to conspicuous; lower surface smooth to rugose, occasionally with reticulate veins, light brown or occasionally dark brown; medulla I–. Ascospores 10–15 × (4.5–) 5–6.5 (–7) µm. **BLS 0484**.

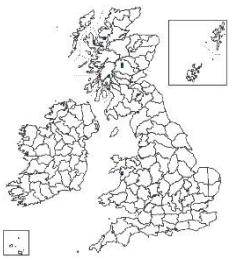
On limestone or other calcareous rocks, often where seasonally flushed; inland or on sea cliffs; widespread in Britain and Ireland.

Variable in colour and in development of pruina; distinguished from most other species with a single holdfast by the short ascospores. *D. intestiniforme* is multi-lobed and has numerous scattered holdfasts. *D. leptophyllum* (Ach.) K.G.W. Lang is not correctly recorded from the region; it has a thin thallus (130–300 µm thick), a single holdfast, pruina, and small, broadly ellipsoidal ascospores 6–12 × 4–8 µm in size.

There is a probably widely overlooked species on periodically inundated siliceous rocks in base-rich upland streams above 330 m. that is morphologically difficult to distinguish from *D. miniatum* but differs in a somewhat thinner thallus, lack of pruina, ecology and ITS sequence. It has been referred to as *D. arnoldianum* Degel. (1936) but appears not to be conspecific with that taxon. Material from N. Wales has been confirmed using molecular techniques, and more sequencing is required.

The most common host of *Opegrapha pulvinata*. Also host to unidentified species of *Zwackhiomyces* (from Somerset; spores 16–22 × 8–9 µm) and *Stigmidium* (spores 12–15 × 3–3.5 µm; from Islay).

Dermatocarpon rivulorum (Arnold) Dalla Torre & Sarnth. (1902) **DD Nb**



Thallus 15–35 mm diam., attached by a single holdfast; 0.1–0.38 mm thick (between perithecia and wrinkles); upper surface light to dark brown, pruina absent or very thin and inconspicuous, epinecral layer of compressed type; lower surface light to dark brown, often darker than the upper surface, almost smooth to strongly wrinkled; medulla I–. Ascospores 16.5–23 (–24) × (6–) 6.5–9 µm. **BLS 0486**.

On rocks beside montane streams and on flushed rock faces; very rare. Known from half a dozen localities in the Scottish Highlands (Perth, Ben Lawers, Liathach); a record from N. Wales needs to be confirmed.

D. meiophyllizum has a thicker thallus which is usually smooth below (at most a few folds or wrinkles in some specimens in a colony). See also *D. deminuens*.

ENDOCARPON Hedw. (1789)

Thallus squamulose, rarely subfoliose, appressed to ascending. **Upper cortex** composed of cells with isodiametric lumina; medulla similar or partly composed of elongate cells; lower cortex absent or of angular to globose cells; rhizines often present. **Photobiont** *Diplosphaera* (Trebouxiophyceae), present in both the thallus and the hymenium, often arranged as columns in the thallus. **Ascomata** perithecia, immersed in the thallus, usually with a slightly projecting ostiole. **Exciple** dark throughout. **Involucrellum** absent. **Hymenium** I+ reddish or bluish, K/I+ blue. **Hamathecium** without paraphyses; periphyses numerous; with hymenial algae. **Asci** (1-) 2 (-4) spored, clavate or saccate, fissitunicate, thick-walled, the apex with a chitinoid plug staining red in Congo Red. **Ascospores** muriform, colourless, yellowish brown to brown. **Conidiomata** pycnidia, immersed. **Conidiogenous cells** elongate ampulliform. **Conidia** rod-shaped, aseptate, colourless. **Chemistry**: lichen products not detected by TLC. **Ecology**: on soil, or sometimes directly attached to rock.

The genus is well-defined in morphological terms, and appears to be monophyletic. However, several well-known species assigned to *Verrucaria* by Orange *et al*. (2009b) are close

phylogenetically, and the combined clade was referred to as the *Endocarpon* group by Gueidan *et al*. (2009). The species concerned include *V. macrostoma*, *V. nigrescens* and *V. viridula*. It is likely that these will be excluded from *Verrucaria* following more detailed studies, but not placed in *Endocarpon* itself (Prieto *et al*. 2012).

Endocarpon differs from *Catapyrenium*, *Dermatocarpon* and *Placidiopsis* in having algal cells within the perithecial cavity and muriform spores. The British species need more study, but this is hampered by their rarity.

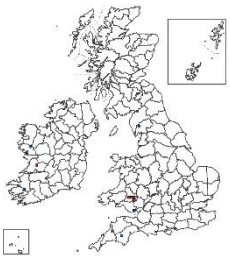
Literature

Giavarini & Fox (2009), Gueidan *et al*. (2009), McCarthy (1991), Prieto *et al.* (2010b, 2012), Pykälä *et al*. (2017b).

1 Mature squamules to 3.5 mm wide, anchored by blackish rhizines 0.05–0.3 mm thick; on soil ..... ***pusillum***
Mature squamules <2 mm wide, anchored by rhizoidal hyphae 2.5–7 µm thick; usually on rock, rarely on soft substrata such as soils 2

2(1) Asci 90–120 × 20–27 µm; ascospores 28–51 × 16–24 µm; on semi-aquatic and aquatic rocks by rivers, sometimes among mosses ..... ***adscendens***
Asci 60–74 × 14–18 µm; ascospores 22–36 × 9–16 µm; directly on damp limestone or greensand ..... ***pallidulum***

Endocarpon adscendens (Anzi) Müll. Arg. (1881) **EN (D)**

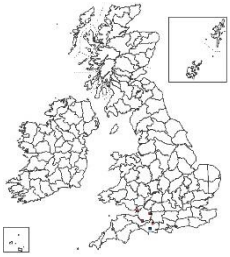


Thallus nodulose-squamulose, the squamules 0.35–1.5 mm diam., 0.1–0.26 mm thick when wet, overlapping, divided into ± radiating lobes 0.4–0.8 mm wide, margins appressed, or free and somewhat raised; upper surface grey-green to pale brown, bright green when fresh and wet; lower surface pale brownish; rhizines not seen. Epinecral layer sometimes present, *ca* 3 µm thick. Perithecia 0.2–0.4 mm diam., 1-2 per squamule; upper part brown-black, conspicuous, ± elevated around the ostiole; ostiole depressed, globose; wall brown-black above, pale below; discrete crystal clusters few to frequent within the perithecium; hymenial algae 3.5–4.5 µm diam., spherical or shortly ellipsoidal. Asci 90–120 × 20–27 µm, 2-spored. Ascospores (29–) 31.5–40 (–51) × (10.5–) 12.5–16 (–24) µm, muriform, elongate-ellipsoidal. Pycnidia *ca* 0.1 mm diam., frequent; conidia 4–6 × *ca* 0.8 µm. **BLS 0502**.

On calcareous siliceous rocks or limestone, on well-drained but periodically inundated surfaces beside streams and lakes, directly on rock or rarely also growing over mosses, rarely on damp limestone; rare. In favoured sites this species appears to be a fairly rapid coloniser, but a poor competitor, often occupying small bare patches amongst mosses (often *Cinclidotus fontinaloides*); it is tolerant of some shade. S. Wales (Glamorgan; Breconshire: River Usk), S. and W. England (River Dart; Steep Holm; Herefordshire: Downton Gorge), N.W. England (Windermere), W. Ireland (N. Kerry, Clare, Connemara).

Distinguished from *E. pallidulum* by the larger asci and ascospores and quite different habitat. British material is likely to be *Endocarpon psorodeum* (Nyl.) Th. Fr., and there appear to be two cryptic species (Orange, *in litt.*). Material examined recently does not have a black lower surface as previously reported.

Endocarpon pallidulum (Nyl.) Nyl. (1892) **CR**



Thallus minutely squamulose, the squamules finely lobed, loosely aggregated to imbricate, 0.5–1.5 mm diam., 0.1–0.2 mm thick; upper surface grey-green to pale brown, smooth, matt; lower surface with a weakly differentiated cortex, dirty white to blackish except at the margins; rhizines absent. Perithecia to 0.3 mm diam., causing swellings on the lower surface of the squamules; hymenial algal cells globose, 2.5–3.5 µm diam. Asci 60–74 × 14–18 µm, 2-spored. Ascospores muriform, colourless to pale yellowish-brown, 22–36 × 9–16 µm. Pycnidia not seen. **BLS 2481**.

On the shaded greensand wall of a churchyard and damp limestone by an outside

drain of a manor house, and on coastal limestone; very rare. S.W. England (Dorset, Somerset).

The smaller asci and ascospores, and different habitat, separate this species from *E. adscendens*. *Endococcus propinquus* (Körb.) D. Hawksw. (1979) has been reported on this host from Dorset.

Endocarpon pusillum Hedw. (1789) **LC NR**

Thallus of scattered or contiguous squamules 0.5–3 (–4) mm diam, 0.15–0.25 (–0.35) mm thick, closely appressed to the substratum, the margins crenate, only slightly raised; upper surface pale to dark reddish brown, matt; undersurface pale or dark brown to black, with rhizines; rhizines usually conspicuous, moderately to richly branched, dark brown to black. Perithecia 0.15–0.25 (–0.3) mm diam., globose; hymenial algae 3–7 × 2–4 µm. Asci 2-spored. Ascospores muriform, pale to dark brown, (29.5–) 45–55 (–58) × 14–19 (–28) µm. **BLS 0503**.

On soil overlying chalk and limestone and over old walls; rare. S. England (S. Devon, Dorset, Norfolk, Sussex), S. Wales (Glamorgan).

The presence of rhizines distinguishes *E. pusillum* from other British species of *Endocarpon*. Morphs with a pale lower surface have been referred to *E. pusillum* var. *pallidum* (Ach.) Körb. (1855); the taxonomic significance of this variation is not known.

HENRICA B. de Lesd. (1921)

Thallus crustose, white or pale grey to fawn, almost immersed to superficial, thin to thick, smooth to verrucose and strongly areolate, or almost peltate and with ± crenulate margins, non-pruinose to strongly white-pruinose. **Photobiont** chlorococcoid, cephalodia not known, hymenial algae not present. **Perithecia** medium-sized to rather large, hemispherical, sessile or partly immersed. **Involucrellum** well-developed, in the upper part fused with the exciple. **Exciple** black to dark brown. **Hamathecium** composed of short periphysoids. **Asci** *Verrucaria*-type, ellipsoidal to clavate, 8-spored. **Ascospores** ellipsoidal, when mature medium to dark brown, muriform, with 5-16 transverse and 1-5 longitudinal walls. **Conidiomata** unknown. **Chemistry**: lichen products absent. **Ecology**: on calcareous and siliceous rocks.

Species of *Henrica* were included in *Polyblastia* by Orange *et al*. (2009a); that genus differs most simply in morphological terms by its colourless or pale yellow, rather than mid to dark brown ascospores. The genus was monographed by Savić & Tibell (2008b), with phylogenetic data indicating that *Henrica* is not closely related to other genera of the Verrucariaceae with dark muriform ascospores, such as *Atla* and *Sporodictyon*. The species found here can also be identified using the key to *Polyblastia* (q.v.) and similar genera.

Literature

Orange *et al*. (2009a), Savić & Tibell (2008b), Savić *et al*. (2008).

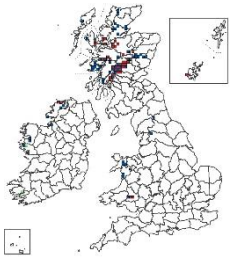
1 Ascospores (20.5–) 28.5–36 (–38.5) µm long; thallus uneven to verrucose but not divided into discrete areoles ..... ***melaspora***

Ascospores (51–) 53.5–63.5 (–70) µm long; thallus of discrete convex, sometimes almost stalked areoles ..... ***theleodes***

Henrica melaspora (Taylor) Savić & Tibell (2008) **Nb**

Polyblastia melaspora (Taylor) Zahlbr. (1921)

Thallus superficial, whitish, uneven to verrucose, thin to well-developed, to 200 µm thick, sometimes cracked. Perithecia forming moderately projecting to rather prominent mounds 0.5–0.8 mm diam., without a thalline covering, rarely partly covered by a lumpy thalline layer in specimens with a thick thallus; involucrellum well-developed. Asci 8-spored. Ascospores muriform, dark brown, (20.5–) 28.5–36 (–38.5) × (12–) 15–20.5 (–23.8) µm, length/width ratio (1.3–) 1.6–2.2 (–3.1). **BLS 1158**.



On damp calcareous sandstone, mica-schist and limestone, on damp cliffs, below moist overhangs and near streams, mainly upland; occasional. Widespread in Highland Scotland, also Wales, N. England and W. Ireland.

Henrica theleodes (Sommerf.) Savić, Tibell & Nav.-Ros. (2008) **Nb**

Polyblastia theleodes (Sommerf.) Th. Fr. (1867)

Thallus superficial, areolate, the areoles strongly convex, sometimes almost stalked and peltate, discrete to contiguous and forming lobed aggregations, 0.4–1 mm diam., grey to light grey-brown. Perithecia 0.44–0.76 mm diam., adjacent to groups of areoles or half-immersed amongst them, black, surface ± smooth. Ascospores dark brown, cell outlines often obscured when mature, (51–) 53.5–63.5 (–70) × (26–) 29.5–37 (–40) µm, length/width ratio (1.5–) 1.6–1.9 (–2.1). **BLS 2495**.

On damp calcareous rock, apparently rare. C. Scotland (Caenlochan and Craig Leek).

The name *P. theleodes* has been widely misapplied: most British and Irish records under this name refer to *Sporodictyon schaererianum*, which differs in the rough perithecia with an irregular thalline covering and the presence of cephalodia. The name has also been applied incorrectly to *Atla alpina*.

HETEROPLACIDIUM Breuss (1996)

Thallus crustose-areolate to small-squamulose, composed throughout of compacted ± globose cells, often with a conspicuous epinecral layer, with rhizoidal hyphae below. **Photobiont** *Myrmecia* (Trebouxiophyceae). **Ascomata** perithecia, immersed in the thallus. **Involucrellum** absent. **Exciple** dark brown, at least at maturity. **Hamathecium** composed of periphyses, interascal filaments not present. **Asci** *Verrucaria*-type, clavate, the ascospores arranged biseriately. **Ascospores** colourless, aseptate, thin-walled. **Conidiomata** pycnidia, laminal, *Dermatocarpon*-type. Conidia cylindric-ellipsoidal to cylindric-bacilliform, aseptate, colourless. **Ecology**: on rock or soil; some are facultative parasites on other lichens.

A genus of about 10 species; most species were keyed out by Breuss (1996). The genus was demonstrated to be monophyletic and a sister group to *Placidium* and *Clavascidium* by Gueidan *et al*. (2009) and Prieto *et al.* (2012). *Placidium* differs in the medulla of filamentous or mixed filamentous and rounded cells, and in some species the marginal position of the pycnidia.

Only one species has been reported from Great Britain and Ireland.

Literature

Breuss (1994, 1996), Gueidan *et al*. (2007, 2009), Prieto *et al*. (2010a, 2012), Prieto & Westberg (2017).

Heteroplacidium fusculum (Nyl.) Gueidan & Cl. Roux (2007) **NE**

Thallus epilithic, crustose, areolate to subsquamulose, areoles to 2 mm diam. and 0.6 mm thick, angular to rounded, flat to slightly convex; upper surface medium to dark brown, dull to somewhat glossy; upper cortex 10–25 µm thick with cells 5–8 µm diam., with an epinecral layer to 20 µm thick; medulla composed of globose cells 7–10 µm diam. with some intertwined hyphae; lower cortex not well delimited; rhizoidal hyphae 4–6 µm. Perithecia ± immersed, 250–400 µm diam., ± globose, the wall initially pale but darkening with age. Asci clavate. Ascospores (7–) 10–13 (–15) × 6–10 µm, colourless, aseptate, thick-walled, ellipsoidal. Pycnidia laminal; conidia rod-shaped, 3–5 µm long. **BLS 2614**.

On thallus of *Circinaria calcarea* on maritime limestone, Somerset and N. Wales; probably initially parasitic but forming an independent thallus.

Heteroplacidium compactum (A. Massal.) Gueidan & Cl. Roux from southern Europe is very similar, and is said to be distinguished by larger ascospores (11–18 µm) and conidia (5–7 µm) (Breuss 1994, Prieto *et al*. 2010a).

HYDROPUNCTARIA Keller, Gueidan & Thüs (2009)

Thallus crustose, superficial, continuous to rimose or areolate, green (in shade), yellowish-brown, dark greyish olive to black, subgelatinous; vegetative propagules unknown.. **Photobiont** *Dilabifilum* (Ulvophyceae) or *Heterococcus* (Xanthophyceae). **Cortex** weakly differentiated, the uppermost layer, when present, often with yellowish to brown or olive-blackish pigments; black dot-like patches sometimes visible at the surface of the thallus, at least in wet thalli. **Algal layer** not clearly delimited from the upper cortex, with algal cells usually arranged in vertical columns, sometimes interrupted by black patches or columns. **Medulla** often replaced by a black carbonaceous layer, interrupted by isolated black patches or columns, but never forming black ridges. **Perithecia** immersed to half-immersed. **Involucrellum** black, apical to dimidiate or encircling the perithecia, the upper surface often roughened. **Exciple** either pale with a brown ostiole or entirely pigmented. **Hymenium** colourless, K/I+ blue in Lugol's solution. **Hamathecium** of periphyses and short periphysoids. **Asci** clavate, 8-spored, *Verrucaria*-type. **Ascospores** aseptate, colourless, ellipsoidal or cylindric-ellipsoidal, smooth, wall thin or only slightly thickened, rather small. **Conidiomata** pycnidia, sometimes present, immersed in the thallus. **Conidia** aseptate, rod-shaped, colourless. **Ecology**: on rocks; some species riverine but most maritime.

A monophyletic and morphologically reasonably distinctive segregate from *Verrucaria* in its traditional circumscription, containing some of the most iconic maritime lichens. The genus is characterized in morphological terms by the formation of columns and punctiform clumps of carbonaceous material in the thallus (sections needed), which can also develop from the involucrellum, giving it an uneven surface. Similar structures in other segregates of *Verrucaria*, e.g. *Wahlenbergiella* (q.v.) tend to fuse and form elongated ridges and branched structures, giving a fingerprint-like appearance if viewed from above.

Literature

Gueidan *et al*. (2009), Orange (2012, 2013a), Orange *et al*. (2009b).

The following key is provisional; the marine species are morphologically similar and *H. maura* is very variable. The rarer marine species are best detected in the field, when differences from the overwhelmingly abundant *H. maura* can be seen, but they are best confirmed by molecular methods.

1 Ascospores small, (8.5–) 11–12 × 7–14 (–16) µm long; thallus thin, 60–95 mm, typically uncracked, cortical pigment brown; perithecia immersed or forming only very low projections; freshwater habitats ..... ***rheitrophila***
Ascospores larger, average length 14.5 µm or more 2

2(1) Dark tissue in thallus reaching the surface as distinctly elongated bars 40–400 × 40–60 µm, at least near the thallus margin, where they are perpendicular to the margin; apex of perithecium flat or crenulate; cortical pigment brown; marine ..... ***amphibia***
Dark tissue in thallus in the form of small isodiametric punctae or occasionally minute ridges 20–90 × 20–40 µm in size, visible or not at the thallus surface 3

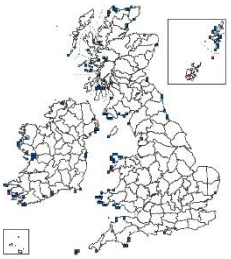
3(2) Thallus relatively thick, 60–300 mm, mostly cracked into discrete areoles; cortical pigment brown (rarely in part greenish brown); marine ..... ***maura***
Thallus relatively thin, to 200 mm thick, cracks sparse to numerous, thallus always thinner and less cracked than *H. maura* when the species are growing contiguously; cortical pigment brown or green; marine or freshwater 4

4(3) Cortical pigment brown; marine ..... ***oceanica***
Cortical pigment dull green to green-brown 5

5(4) Thallus typically uncracked when fresh (fine cracks may appear on storage); freshwater ..... ***scabra***
Thallus usually with cracks when fresh; marine ..... ***aractina*** *and* ***orae***

Hydropunctaria amphibia (Clemente) Cl. Roux (2011) **Nb**

Verrucaria amphibia Clemente (1807)

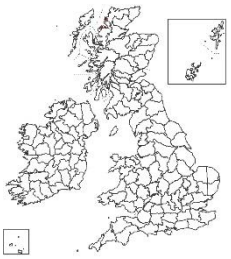


Prothallus inconspicuous, or rarely whitish and very locally developed. Thallus superficial, dark greenish brown to blackish brown (black to the unaided eye), abundantly cracked, often into discrete areoles, the surface uneven with abundant blackish ridges; actively growing thallus margin well-delimited, the ridges 40–400 × 40–50 µm and orientated more or less perpendicular to the margin; interior of thallus with ridges short, often branched, not orientated in one direction. Pseudocortex with brown pigment. Perithecia forming projections 220–360 µm diam., often distinctly flat-topped, the sides often uneven or with bosses; ostiole often visible as a minute pit. Involucrellum well-developed. Ascospores narrowly cylindric-ellipsoidal, (13–) 15–18 (–19.5) × (5–) 5.5–7 (–7.5) µm, length/width ratio (2.1–) 2.4–3.1 (–3.5). **BLS 1474**.

On rocks on the sea shore, on siliceous rocks and limestone, frequent. Widespread, but absent from most of E. England.

This species differs from the other *Hydropunctaria* species by the apex of the perithecium being flat-topped or crenulate, rather than more or less rounded (or immersed). Additionally, there is greater development of densely pigmented tissue. The thallus contains densely pigmented areas reaching to the surface, in the form of elongated bars to 60 µm broad. These are particularly conspicuous near the thallus margin, where they are perpendicular to the margin, and parallel to elongated cracks. *Wahlenbergiella striatula* may have ridges on the thallus, but it has smaller ascospores.

Hydropunctaria aractina (Wahlenb.) Orange (2012) **NE**



Prothallus not seen. Thallus brownish black to dark grey, or greenish black or green in moist shade, thin to moderately thick, 20–200 µm thick, cracks usually numerous, but in some specimens only rarely forming discrete islands; sterile areoles flat, mostly 120–400 µm diameter, fertile 200–860 µm diameter, surface matt, smooth, or rough with ill-defined punctae. Thallus in section with a basal layer which varies from mostly colourless to densely pigmented above, and with densely pigmented columns rising into the photobiont layer, sometimes reaching the surface; the columns either appearing isolated or joined below, depending on degree of pigmentation of basal layer. Thallus with a pseudocortex, surface cells with dilute to dense, dull green to green-brown, K– pigment, often overlain by a thin decolourised epinecral layer. Perithecia forming low to moderate projections 400–600 µm diam., but often too indistinct to measure accurately; surface smooth to roughened. Ascospores cylindric-ellipsoidal, (12–) 13.5–16 (–17) × (6.5–) 7–8 µm, 1.7–2.2 (–2.5) times as long as wide. **BLS 2610**.

In the littoral zone of the sea shore, in conjunction with *H. maura*. N.W. Scotland.

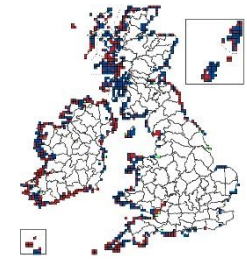
Differs from contiguous thalli of *H. maura* in the thinner thallus, and the presence of dull green to green-brown pigment in the pseudocortex (brown in *H. maura*). Thalli in the field are sometimes strikingly green compared to *H. maura* nearby. Although the distinction between the two species is easily seen when they are growing together, the differences are small, and the range of thickness overlaps, so that isolated thalli may be difficult to identify with certainty. The apparently slightly smaller spore size in *H. aractina* needs to be confirmed when more specimens are collected, as mature ascospores were often difficult to find in the sequenced material.

H. aractina and *H. orae* cannot be reliably distinguished using morphological methods; sequencing is preferred.

Hydropunctaria maura (Wahlenb.) Keller, Gueidan & Thüs (2009) **LC**

Verrucaria maura Wahlenb. (1803)

Prothallus narrow, sometimes scarcely visible, whitish to pale brown, not or scarcely fimbriate. Thallus moderately thick, 60–300 µm thick, greenish black to brownish black, sometimes brown near the margin, or green-brown in shade, but typically very dark and appearing almost black to the unaided eye; young margin thin, continuous, soon cracked into separate areoles 100–600 µm diam. (sterile) or 300–600 µm diam. (fertile), areoles flat or slightly concave to slightly convex, matt or rarely slightly glossy, surface frequently roughened by slightly raised punctae or short ridges 20–60 (–90) × 20–30 µm in size, these black and contrasting with the surrounding thalli in shaded specimens, but often concolorous and with the outline indistinct; older areoles sometimes with



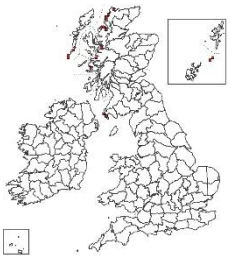
the surface partly subdivided by dark lines; sides of areoles black. Thallus in section with a basal layer which is often colourless below in part, but with the upper part densely pigmented, with pillars of densely pigmented tissue projecting upwards into the algal layer and often reaching the thallus surface, pigment dark brown to dark reddish brown, K+ dulling or K+ dark grey-brown. Thallus surface with a pseudocortex, scarcely differentiated from tissue below except for the presence of brown K– pigment (rarely in part greenish brown); sometimes with a decolourised epinecral layer above. Perithecia varying from largely immersed in the thallus to moderately projecting, projections 160–440 µm diam. when measurable, conical-hemispherical and sometimes slightly irregular in shape, but not distinctly angular nor with projections. Perithecia 70–190 µm diam. when viewed in section (few measured), darkly pigmented. Involucrellum well-developed, merging with parts of the dark basal layer. Ascospores cylindric-ellipsoidal, (14.5–) 15.5–18 (–19) × (7.0–) 7.5–8.5 (–9) µm, (1.6–) 1.9–2.3 (–2.5) times as long as wide. Pycnidia immersed, with colourless wall and ostiole, *ca* 90 × 50 µm; conidia rod-shaped, 4.1–5.7 (–6.6) × 1.2–1.6 µm. **BLS 1504**.

Widespread and often very abundant on sea shore rocks, always much more abundant than *H. aractina*, *H. oceanica* and *H. orae*. *H. maura* is usually more tolerant of drought and exposure than these species; it also tolerates freshwater influence as on dripping cliffs. Throughout Britain and Ireland on coasts with hard rocks.

The thallus is always well-developed and cracked into mostly discrete areoles, but otherwise is variable in appearance, either smooth or roughened, and with the perithecia varying from immersed to rather prominent. *H. aractina*, *H. oceanica* and *H. orae* always have a thinner thallus than *H. maura* when growing adjacent to it. In addition, the pigment of the pseudocortex is often distinctly greenish in *H. aractina* and *H. orae* (brown or at most partly greenish brown in *H. maura*).

The probably lichenicolous *Stigmidium marinum* (Deakin) Swinscow (1965) is sometimes associated with this species.

Hydropunctaria oceanica Orange (2012) **NE**

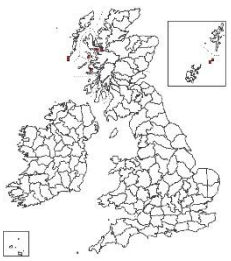


Prothallus whitish, non-fimbriate. Thallus epilithic, thin, 35–100 µm thick, dark grey-brown to brown-black, sometimes with a greenish tinge; cracks sparse to numerous, but rarely delimiting discrete areoles except in very local thicker areas; surface roughened with indistinct, concolorous punctae or short flexuose or branched ridges 20–90 × 20–40 µm in size, but often too indistinct to measure; thallus gradually thinning to margin. Pseudocortex with dilute to moderately dense pigment, the pigment brown, K– or almost so. Epinecral layer sometimes present, *ca* 4 µm thick, colourless, of collapsed cells, the structure difficult to discern. Photobiont cells 5–9 × 4.5–8 µm. Basal parts of thallus colourless to brown, living photobiont cells few or absent, densely pigmented areas (punctae) projecting from the basal into the photobiont layer, pigment dark red-brown, K+ dark grey-brown. Perithecia forming conspicuous conical-hemispherical projections 260–500 µm diam., roughened below like the thallus, above smooth, concolorous with the thallus or black, apex rounded or slightly flattened; ostiolar region concolorous, inconspicuous. Involucrellum well-developed, merging with dark basal tissue. Perithecium 170–210 µm diam. when viewed in section (few measured). Asci 8-spored, c. 45–82 × 18–29 µm. Ascospores cylindric-ellipsoidal, (12.5–) 13.5–16.5 (–18) × (5.5–)7–8 (–8.5) µm, (1.4–) 1.8–2.3 (–2.7) times as long as wide. **BLS 2596**.

On gently to steeply sloping rocks on the sea shore, often in places which are occasionally lightly irrigated by rain water; usually growing with *H. maura*, sometimes with *H. orae*. Also seen on a slightly seeping rock face 200 m from the sea, and in small quantities on boulders by freshwater lakes up to 4.5 km from the sea. Wales, Scotland, Channel Is, Ireland.

Often found contiguous with *H. maura*, which has a thicker thallus with usually discrete areoles, and with rather inconspicuous perithecia forming only low projections. The distinction between the two species is easily seen in the field. When growing with *H. orae*, the latter is greener in colour, the thallus is sometimes slightly thicker, and the perithecial mounds are slightly larger. The thallus of *H. oceanica* contains a brown pigment in the pseudocortex, but in *H. orae* the pigment is dull green. *H. aractina* differs in the usually greenish cortical pigment, but mixed collections have not been seen. *H. adriatica* (Zahlbr.) Keller & Gueidan from the Mediterranean and the Black Sea also tends to have a thinner thallus than *H. maura*; it is distinct in ITS sequence.

Hydropunctaria orae Orange (2012) **NE**



Prothallus not seen. Thallus thin to moderately thick, 40–100 µm, dull mid green to dark greenish grey, thinner areas often without cracks, thicker parts with few to numerous cracks, but rarely forming discrete 'islands' of thallus. Thallus surface minutely roughened by low punctae 20–40 µm diam., occasionally forming minute ridges up to 80 × 30 µm in size, punctae concolorous, or darker than the surrounding surface in shaded specimens. Pseudocortex present, but a surface layer *ca* 5 µm thick is sometimes pigmented, pigment dull green, K–. Lower part of thallus with no or few living algal cells, cells often with large oil droplets; densely pigmented and more or less discrete punctae projecting upward from the basal layer into the green layer, occasionally reaching the thallus surface, pigment dark reddish brown, K+ dark greyish brown. Epinecral layer sometimes present, colourless, to 5 µm thick, comprising collapsed and scarcely recognisable cell remains. Photobiont cells 5–10.5 × 3.7–9 µm. Perithecia forming low to moderately projecting, occasionally rather prominent, warts in the thallus 300–840 µm diam., apex rounded, rarely depressed, ostiole inconspicuous. Perithecia 260–270 µm diam. when viewed in section (few measured). Involucrellum well-developed, merging with dark basal tissue. Asci 8–spored, 43–52 × 21–26 µm. Ascospores cylindric-ellipsoidal, aseptate, colourless, filled with small oil droplets when mature, (13–) 14.5–17.5 (–19.5) × (6–) 7–8 (–8.5) µm, (1.7–) 1.9–2.5 (–2.8) times as long as wide. **BLS 2597**.

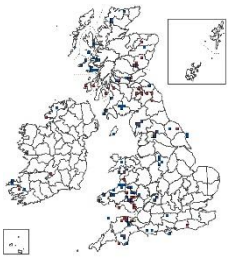
On gently sloping to steep rocks on the sea shore, especially where slightly irrigated by rain water, or in freshwater streamlets on the shore. Wales, Scotland, Ireland.

The thallus of this species is relatively thin, so that cracks are relatively few and perithecia are rather prominent. The thallus often has a green tinge, which is sometimes partly due to a green pigment in the pseudocortex, and sometimes due to loss of pigment in shade. In mixed collections, thalli of *H. maura* are thicker, more extensively cracked, less green, and with less prominent perithecia. *H. scabra* is confined to freshwater habitats and the thallus is never cracked.

H. aractina and *H. orae* cannot be reliably distinguished using morphological methods; sequencing is preferred.

Hydropunctaria rheitrophila (Zschacke) Keller, Gueidan & Thüs (2009) **Nb**

Verrucaria rheitrophila Zschacke (1922)



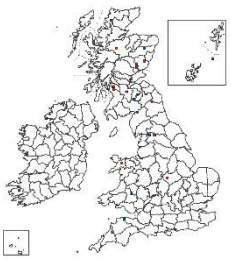
Prothallus whitish, not fimbriate; contiguous conspecific thalli often separated by thin black lines. Thallus greyish green to pale brownish green to dark brown, well-developed, 60–95 µm thick, subgelatinous, usually uncracked, but sometimes with sparse or numerous cracks which probably form only after collection; thallus surface smooth or with sparse to numerous black punctae 20–40 µm diam. at the surface. Thallus in section composed of ± distinct columns of cells; cortex poorly defined, cell walls with brown pigment (dilute or absent in shade). Lower part of thallus often forming an ill-defined medulla; in this zone living algal cells are often few, and the fungal cells contain oil drops; this zone is colourless to dilute brown, locally with intensely pigmented patches near its upper edge, often appearing as more or less discrete punctae in section. Perithecia immersed in the thallus or forming very low projections which are usually too indistinct to measure; apex appearing at the thallus surface only as a small black dot, or more usually as a black disc to 220 µm diam., often roughened or surrounded by a few punctae. Perithecia 110–210 µm diam., when viewed in section. Exciple at sides and base colourless or partly brown. Involucrellum present, well-developed in the upper half of the perithecium, often spreading outwards and downwards and grading into the punctae of the upper layer of the medulla. Ascospores ellipsoidal, (8.5–) 11–14 (–16) × (6–) 6.5–8 (–9.5) µm, length/width ratio (1.3–) 1.5–1.9 (–2.3), without a perispore. **BLS 1499**.

On long-submerged base-rich rocks in streams, streamlets and lakes, tolerant of shade, often growing with *Verrucaria aquatilis*, *V. elaeomelaena* or *V. funckii*, and the red alga *Hildenbrandia rivularis*; frequent.. Widespread in Britain and Ireland.

This species can usually be recognized in the field by the immersed perithecia visible as black dots, and often by the black punctae which give the thallus a scabrid appearance. Punctae are most easily seen in thin thalli, but are immersed in thicker thalli. The thallus is typically uncracked, 60–95 µm thick, the cortical pigment (when present) is brown, and the spores are significantly smaller than other species in the genus.

Hydropunctaria scabra (Vězda) Keller, Gueidan & Thüs (2009) **Nb**

Verrucaria scabra Vězda (1970)



Prothallus whitish, not fimbriate; contiguous conspecific thalli often separated by thin black lines. Thallus dull green to dark grey-green or dark green (sometimes blackish to unaided eye), well-developed, 35–150 µm thick, subgelatinous, uncracked (rarely with fine splits forming in dried material), surface smooth to slightly scabrid with concolorous papillae, occasionally with very local black punctae *ca* 30 µm diam. Thallus in section composed of ± distinct columns of cells; cortex poorly defined, cell walls with dull green pigment (dilute or absent in shade). Lower part of thallus often forming an ill-defined medulla, ranging from a zone with ill-defined areas of brown pigment, to a pigmented zone forming an extensive dark basal layer to the thallus; upper part of medulla often with small, upwardly projecting areas of intensely pigmented cells, appearing as ± discrete punctae in section. Perithecia usually immersed in the thallus, forming at most very low projections which are too indistinct to measure, or (when the thallus is thin) forming low to moderate projections 300–650 µm diam; apex appearing at the thallus surface either as a whitish ring 120–150 µm diam., or more usually as a black disc 200–300 µm diam., often roughened or surrounded by a few punctae, rarely radially fissured. Perithecia 275–290 µm diam. when viewed in section. Exciple with sides and base colourless or partly brown. Involucrellum present, well-developed in the upper half of the perithecium, often spreading outwards and downwards and grading into the punctae of the upper layer of the medulla; sometimes (where medulla is thin), conical and reaching the base of the thallus. Ascospores ellipsoidal to (mostly) cylindric-ellipsoidal, (11–) 14–17.5 (–21.5) × (7–) 7.5–9 (–10.5) µm, length/width ratio (1.4–) 1.7–2.1 (–2.4), without an epispore. Conidia straight or slightly curved, 3.5–5 × *ca* 1.2 µm. **BLS 2390**.

On permanently or frequently submerged siliceous rocks in streams and lakes, shaded or unshaded, up to 660 m altitude; occasional. S.W. and N. England, Wales, N.W. Scotland.

Differs from *H. rheitrophila* in the green (rather than brown) thallus pigment, the slightly larger and more cylindrical ascospores, the larger, more widely spaced and more projecting perithecia, and the tendency for the medulla to be more darkly pigmented. However, the basic morphology is very similar, with a mainly apical involucrellum which is often continued laterally as a line of punctae. The differences are striking in mixed collections from well-lit sites, but in shade the thallus pigment is poorly developed, so that there may appear to be a continuum of thallus colours from shades of green to brown. This species has been overlooked in Britain and has probably been misidentified as *H. rheitrophila*. Some thalli superficially resemble *Verrucaria praetermissa* in the green thallus and dark basal layer, but in that species the thallus is non-gelatinous and the ascospores are larger. *V. pachyderma* may be difficult to separate in the field, but it has larger ascospores and a different involucrellum.

INVOLUCROPYRENIUM Breuss (1996)

Thallus small-squamulose, almost crustose in some species, attached to the substratum by intertwined colourless or brown rhizoidal hyphae. **Photobiont** chlorococcoid. **Upper cortex** rather thin (10-30 µm), uneven in thickness and poorly differentiated from the algal layer, composed of small (5-8 µm diam.), roundish-angular cells; **lower cortex** indistinct. **Ascomata** perithecia, emergent between the squamules. **Involucrellum** present, apical, dimidiate or entirely encircling the perithecium. **Exciple** composed of tangentially arranged ± elongated cells, pigmented around the ostiole, lower part pale to blackish. **Hamathecium** of periphyses, interascal filaments absent. **Asci** 8-spored, clavate, thin-walled, non-amyloid and without an ocular chamber. **Ascospores** biseriately arranged, colourless, aseptate, ellipsoidal or ovoid. **Conidiomata** not known. **Chemistry**: no lichen products detected by TLC. **Ecology**: on soil or over decaying bryophytes and plant debris, non-British species also on calcareous rock.

The genus was introduced for species with a more or less squamulose thallus, and ascomata positioned between the squamules; *I. waltheri* is the type, and the only one from our region. *I. waltheri*

was shown to belong within the *Endocarpon* group of *Verrucaria* s.lat. by Prieto *et al*. (2012), but the genus seems likely to be heterogeneous, and more molecular data are needed.

Verrucaria romeana B. de Lesd. (1911) (syn. *V. squamulosa* Brand & van den Boom 2003) was placed in *Involucropyrenium* by Breuss (2016). However, preliminary sequence data suggest that it might be close to *V. macrostoma* and *V. nigrescens* (these also fall within the *Endocarpon* group according to Prieto *et al*. 2012), and so it is retained in *Verrucaria* for the present.

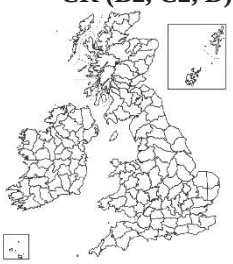
Literature

Breuss (2009b, 2010, 2016), Breuss & Türk (2004), Prieto *et al*. (2010a, 2012), Van den Boom & Brand (2003).

Involucropyrenium waltheri (Kremp.) Breuss (1996) **CR (B2, C2, D)**

Thallus minutely squamulose, squamules 0.5–1.5 mm diam. and rarely more than 0.2 mm thick, firmly appressed and confluent to form a continuous, crust-like cover over the substratum, forming a dense dark hypothallus; upper surface fawn to dark brown, matt, not pruinose; rhizoidal hyphae brown,. Perithecia between the squamules, often aggregated in groups or lines, black, spherical, semi-emergent; exciple brown-black; the involucrellum entirely surrounding perithecia. Asci clavate. Ascospores 17–21 × 8–10 µm, ± ovoid to clavate, biseriately arranged. **BLS 1862**.

On soil and humus, confined to high altitudes; known from a single collection. Scotland (Westerness, Ben Alder).



MERISMATIUM Zopf (1898)

Lichenicolous or **algicolous**, with vegetative tissues immersed in the host thallus and not visible externally. **Perithecia** semi-immersed to ± sessile and scattered or in small groups, spherical to pyriform, black, often glossy, surface of the ascomatal wall around the ostiole smooth; ostiolar region conical and sometimes slightly papillate. **Involucrellum** absent. **Exciple** of tangentially flattened to somewhat angular cells, brown, sometimes with bluish or violet pigment in the ostiolar region (probably also overlapping with the brown pigment, and then not discernible). **Hamathecium** consisting of short periphysoids with periphyses lining the ostiolar canal; interascal filaments not present. **Asci** broadly cylindrical to slightly clavate, *Verrucaria*-type, (6-) 8-spored. **Ascospores** broadly ellipsoidal to cylindric-ellipsoidal, brown, often slightly asymmetric, with multiple transverse septa or submuriform to muriform, in optical section with 4–18 cells, with transverse septa laid down after a vertical septum; ascospore wall thin, sometimes with a distinct perispore. **Conidiomata** unknown. **Chemistry**: lichen substances absent. **Ecology**: parasitic on lichens or algae, or possibly sometimes lichenized.

Distinguished from *Polyblastia* mainly by the lichenicolous habit and its more strongly pigmented ascospores. The host specificity of most species needs further investigation.

The genus *Halospora* was separated from *Merismatium* by Hafellner (2011), distinguished morphologically by the ascospores surrounded by a gelatinous perispore ("halo"), and with longitudinal septa laid down secondarily after the transverse septa are formed. Comparative molecular data have not been obtained to date, and the two genera are united here pending further studies. *M. deminutum* has often been regarded as lichenised, and was previously placed in *Polyblastia*. The placement of the genus in Verrucariaceae is uncertain; two ITS-LSU sequences prepared from *M. deminutum* suggest a possible placement in Chaetothyriales.

Literature

Hafellner (2011), Orange (2009c), Roux *et al*. (2002), Triebel (1989).

1 Ascospores thick-walled, with a distinct perispore visible at at least some stages of development; longitudinal septa formed at a late stage of development....2
Ascospores thin-walled; perispore not present; longitudinal septa formed at an early stage of development....3

2(1) Ascospores (18–) 22.5–27.5 (–31) µm long, muriform with 6–15 cells visible in optical section, perispore thick, conspicuous .... ***deminutum***
Ascospores (11–) 13–15.5 (–16.5) µm long, submuriform, divided by oblique septa into a total of *ca* 4 cells; perispore thin, inconspicuous.... ***discrepans***

3(1) Ascospores submuriform, with 4–6 cells visible in optical section....4
Ascospores (14–)15–25(–32) µm long, submuriform to muriform, (8–) 10–18 cells visible in optical section .... ***nigritellum***

4(1) Ascospores (8.5–) 11–17 (–19) × (5–) 6.5–8 (–9.5) µm, concolorous .... ***coccisporum***
Ascospores 10–13 × 5–6.5 µm, the end cells paler than the mid cells .... ***heterophractum***

Merismatium coccisporum (Norman) Vouaux (1913) **NE NR**

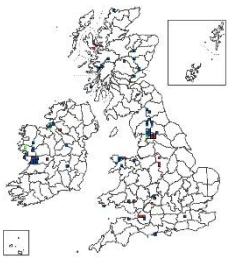
Non-lichenized. Perithecia 110–200 µm in diam., semi-immersed to sessile. Asci 45–60 × 14–20 µm. Ascospores orange-brown (walls and septa often much darker than the lumina), broadly ellipsoidal to ovoid, apices acute or occasionally obtuse, with 3–6 transverse septa (usually with at least one oblique) and 0–3 longitudinal septa in central segments, (8.5–) 11–17 (–19) × (5–) 6.5–8 (–9.5) µm, length/width ratio 1.6–2.2. **BLS 2686**.

On the crustose basal thallus of *Stereocaulon plicatile*, W. Scotland (Argyll, Glen Coe). Reported from elsewhere on unrelated lichens, including species of *Amygdalaria*, *Cladonia* and *Euopsis*.

The species is poorly known and could represent an aggregate.

Merismatium deminutum (Arnold) Cl. Roux & Nav.-Ros. (2002) **Nb**

Halospora deminuta (Arnold) Tomas. & Cif. (1952)



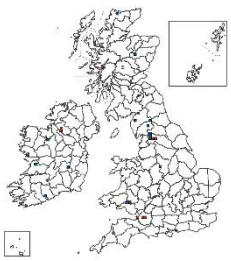
Thallus immersed. Perithecia in pits in limestone, not projecting, or projecting from the pit by up to a third, 0.20–0.28 mm diam. (few measured). Involucrellum absent; exciple pigmented throughout, brown to dark brown, K+ darker brown, with faint violet pigment around the ostiolar region; hyphae surrounding the exciple colourless to brownish, I− to I+ violet. Asci 8-spored. Ascospores medium to dark brown, muriform, 6–15 cells visible in optical section, (18–) 22.5–27.5 (–31) × (10.5–) 11.5–14 (–16.5) µm, length/width ratio (1.2–) 1.8–2.1 (–2.4); perispore conspicuous, 1.5–2.5 µm thick, but often much thicker in immature spores. **BLS 1152**.

On limestone; frequent. Throughout Britain and Ireland in areas with suitable rock.

Studies have suggested that this species is non-lichenized and is lichenicolous on species of *Polyblastia*, *Thelidium* and *Verrucaria* that have an endolithic thallus, but British material that has been examined has the appearance of a lichenized species with no trace of a host. However, Hafellner (2011) observed that "lichenicolous behaviour is mostly not obvious but is indicated by the ascomata mostly developing in the pits that remain after the ascomata of the host lichen have fallen out, but usually the *Halospora* ascomata do not fit in size, i.e. the holes are too large."

Merismatium discrepans (J. Lahm) Triebel (1989) **Nb**

Halospora discrepans (J. Lahm) Hafellner (2011)



Non-lichenized. Perithecia one-third to half-immersed in the host, 0.19–0.22 mm diam.; peridium brown throughout, K+ darker brown; ostiolar region dull greenish blue. Ascospores dark brown, submuriform, divided by oblique septa into (3-) 4 cells, (11–) 13–15.5 (–16.5) × (8.5–) 9–10 (–11.5) µm, length/width ratio (1.1–) 1.4–1.6 (–1.7), with a narrow perispore that may degenerate by maturity. **BLS 1154**.

On the thallus of *Protoblastenia calva* and *P. rupestris* on limestone; widely distributed but overlooked. Scattered throughout the British Isles.

Distinguished from *H. deminuta* most easily by the slightly smaller ascospores with oblique septa.

Merismatium heterophractum (Nyl.) Vouaux (1913) **NE**

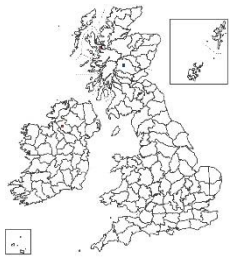
Non-lichenized. Perithecia black, minute, semi-immersed; ascospores 10–13 × 5–6.5 µm, ovoid, mostly 3-septate (more rarely with four or five transverse septa), with one or two additional longitudinal (occasionally oblique) septa, without a perispore. The two outer cells are conspicuously paler than the two inner cells and have thinner walls. **BLS 2771**.

On thallus of *Bacidia herbarum*, on limestone soil of a quarry. Scotland (Mid Perthshire); known only from a single site in GBI.

Reported from elsewhere on *Bilimbia sabuletorum*, *Biatora vernalis*, *Cladonia rei* and "*Lecidea*" *berengeriana*. The related *M. decolorans* (not yet recorded from Britain) has larger spores, 13.5–16.5 µm long.

Merismatium nigritellum (Nyl.) Vouaux (1913) **NE NR**

Polyblastia gothica Th. Fr. (1865)



Non-lichenized. Perithecia (150–) 200–250 (–300) µm diam., accompanied by roundish goniocysts (15–) 25–40 µm diam. (possibly not connected). Asci 65–115 × 20–27 µm. Ascospores broadly ellipsoidal to ovoid, submuriform to muriform, with (8–) 10–18 cells visible in optical section, (14–) 16–24.5 (–32) × (6.5–) 8–12 (–15) µm, length/width ratio 1.9–2.4, perispore not present. **BLS 2110**.

On thallus of *Placidium lachneum* and *Leptogium burgessii*; very rare. Scotland (Ben Lawers, Creag Megaidh, Cairngorm, Skye).

Additional hosts are reported from outside the British Isles; this species could also represent an aggregate.

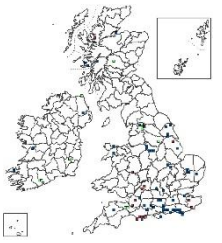
NESOTHELE Orange (2022)

Thallus endolithic to more usually superficial, grey-green to brown, of lobed goniocyst-like units, convex areoles, or tightly adnate squamules. **Photobiont** chlorococcoid. **Ascomata** perithecia, sometimes partly immersed in the thallus but without a discrete thalline covering, in one species immersed in convex squamules; black, the ostiolar region often pale and conspicuous in several species. **Involucrellum** present or indistinct. **Hymenial gel** I+ red. **Hamathecium** of periphyses; interascal filaments absent. **Hymenial algal cells** 3–8.5 µm long, 1.0–4.5 times as long as wide. **Asci** *Verrucaria*-type, I−, 4- to 8-spored. **Ascospores** colourless, ellipsoidal to narrowly ellipsoidal, 25–59.5 × 12.5–31.5 µm, muriform, without a perispore. **Conidiomata** unknown. **Ecology**: on usually damp calcareous rock.

A monophyletic segregate from *Staurothele* (s. str.), differing in the colourless ascospores and 4- to 8- (rather than 2-) spored asci. Five species are currently known (Orange & Chhetri 2022) of which three occur in our region. They are included in the key to *Staurothele* s. lat. below.

Nesothele hymenogonia (Nyl.) Orange (2022) **Nb**

Staurothele hymenogonia (Nyl.) Th. Fr. (1865)

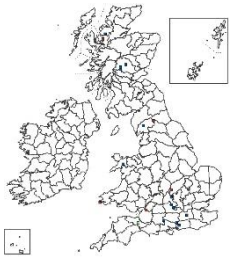


Thallus endolithic, grey. Perithecia forming conical-hemispherical projections 0.3–0.6 mm diam., black (or dusted with rock fragments), the surface often rough or radially fissured, ostiole flat or in a small depression; base of perithecium often within a shallow pit in the rock; involucrellum present; hymenial algal cells 3.3–7.5 × 2.5–3 µm, cylindrical, 1.3–2.5 times as long as wide. Asci 8-spored. Ascospores colourless, ellipsoidal, (23–) 25.5–29 (–30) × 12.5–6 (–17) µm. **BLS 1344**.

On limestone rocks and pebbles; locally common. Most records are from England, also in N. Wales, Scotland, Ireland.

Nesothele rugulosa (A. Massal.) Orange (2022) **NT**

Staurothele rugulosa (A. Massal.) Arnold (1897)

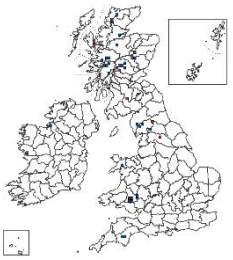


Thallus epilithic, well-developed, dirty cream or greenish grey; areoles strongly convex, crowded, thallus becoming secondarily cracked. Perithecia blackish, to *ca* 0.5 mm diam., half to completely immersed amongst the areoles; involucrellum present; hymenial algal cells 3.3–5.7 (–7) × *ca* 3 µm, 1.1–2 (–2.4) times as long as wide. Asci 8-spored. Ascospores colourless, ellipsoidal, 31–34.5 × 18–20.5 µm. **BLS 1346**.

On calcareous sandstone and limestone, sometimes in small streams; rare. S. England, Wales (Pembrokeshire), C. & N.W. Scotland.

Nesothele succedens (Rehm ex Arnold) Orange (2022) **Nb**

Staurothele succedens (Rehm ex Arnold) Arnold (1880)



Thallus superficial, grey-green to brown (often growing with a black film of cyanobacteria), not cracked, the surface roughened or with an almost micro-squamulose appearance, composed of lobed and branched goniocyst-like units 0.35–0.5 mm diam. Perithecia one quarter to half immersed in the thallus, forming projections 0.3–0.52 mm diam., black, naked or with a few thallus granules, black, the surface sometimes rough; hymenial algal cells 3–7.5 × 1.6–2.5 µm, 1.3–4.5 times as long as wide. Asci 8-spored. Ascospores colourless, ellipsoidal, (29.5–) 34–42.5 (–46) × (15–) 17–21.5 (–23) µm, (1.3–) 1.5–2.5 (–3.1) times as long as wide. **BLS 1348**.

On damp calcareous rocks, including sandstone, limestone and basic metamorphic rocks, sometimes on soft and unstable rock; local. N. & W. Britain, N.W. Ireland.

NORMANDINA Nyl. (1855)

Thallus crustose to squamulose and then broadly attached to the substrate by numerous hyphae; soralia sometimes present. **Upper cortex** well-developed or indistinct, cells similar in shape to those of the photobiont layer. **Photobiont layer** of ± isodiametric hyphal segments. **Medulla** of filamentous hyphae. **Lower cortex** absent. **Photobiont** *Myrmecia* (Trebouxiophyceae). **Ascomata** perithecioid, subglobose or conic-globose, black. **Exciple** of tangentially slightly flattened angular cells, the outer layers reddish brown, K+ dark grey, pigment unequally distributed in the cell walls. **Involucrellum** absent. **Hamathecium** of periphyses, interascal filaments absent; hymenial gel I+ red (yellowish or blue at very low concentrations of I), K/I+ blue. **Asci** clavate, 8-spored, the wall thickened above, K/I–. **Ascospores** ellipsoidal-fusiform, usually 7-septate, rarely a proportion submuriform, slightly constricted at the septa, colourless or faintly brownish, smooth. **Conidiomata** unknown. **Chemistry**: terpenoids present in some species. **Ecology**: on bark or rock, often overgrowing bryophytes or other lichens.

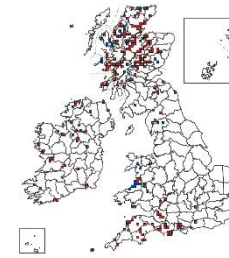
Literature

Frisch & Ohmura (2015), Lücking & Moncada (2017), Muggia *et al*. (2010), Orange (2022), Orange & Aptroot (2009), T*et al*. (2011).

1 Thallus squamulose, squamules large, to 1.7 mm diam. ..... ***pulchella***
Thallus crustose, sometimes with very small subaquamulose marginal areoles..... 2

2(1) Thallus with very young areoles that are often subsquamulose in appearance; two unidentified terpenoids by TLC; on bryophytes over rock..... ***acroglypta***
Thallus with very young areoles convex or irregular in shape but not subsquamulose; zeorin or no substances by TLC; on bryophytes over bark ..... ***chlorococca***

Normandina acroglypta (Norman) Aptroot (1995) **LC**



Thallus crustose, uneven, grey-green; very young areoles have a subsquamulose appearance, being somewhat lobed at the margin, and either flat or slightly convex; thallus composed of goniocyst-like units; soralia usually present, scattered, diffuse, concolorous with the thallus; soredia 60–250 µm diam. Ascomata 0.20–0.43 mm diam., 25–75% immersed in the thallus. Ascospores (3-) 5- to 7-septate, (23.5–) 27.5–37 (–43) × (5–) 6—7.5 (–8.5) µm. Two unidentified terpenoids by TLC. Thallus K–, C–, Pd–. **BLS 1835**.

On dead cushions of bryophytes, rarely lichens, over rock. Also seen as an associate of *Pectenia cyanoloma*, itself growing on *Corylus*, in rainforest in one wood in Skye. Distribution poorly known due to confusion with *N. chlorococca*; the map shown here is a composite of the two species. Confirmed records are from England (Westmorland), Wales (Brecon, Caernarvon) and Scotland.

The subsquamulose nature of the areoles is often ill-defined. *N. chlorococca* is distinguished by growing over bark, by the lack of subsquamulose areoles, and by chemistry.

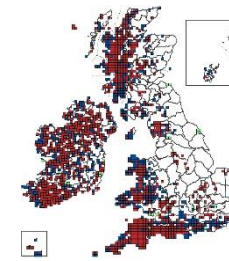
Normandina chlorococca (Leighton) Orange (2022) **NE**

Thallus crustose, uneven, grey-green; very young areoles have the form of convex granules without any subsquamulose appearance, rapidly becoming irregular in shape and coalescing with other areoles; soralia ill-defined, local. Ascospores 5- to 8-septate, (22.5–) 27.5–36 (–39.5) × (6–) 6.5–8 (–9) µm. Zeorin in trace amounts by TLC, or secondary substance not detectable. **BLS 2837**.

On dead cushions of bryophytes over bark, especially where base-rich. Mainly with a westerly distribution, but distribution is poorly known due to confusion with *N. acroglypta*. Confirmed records are from England (Oxfordshire, Somerset), Wales (Caernarvon, Merioneth), Scotland (Kirkudbright) and Northern Ireland (Antrim, Down).

On the basis that most GBI records of *N. acroglypta* s.l. are from corticolous substrata, *N. chlorococca* appears to be the commoner of the two species.

Normandina pulchella (Borrer) Nyl. (1861) **LC**



Thallus squamulose; squamules glaucous to pale grey or greenish grey, much greener when wet, to 5 mm diam., composed of one to several broadly rounded shell- or ear-like lobes to 1.7 mm diam., upper surface concentrically ridged, margins sharply raised, 50–100 µm wide; squamules scattered or crowded; soralia often present on lobe surface and margins, green or concolorous with the lobes; soredia granular, 40–80 µm diam.; lower surface whitish, slightly felted, broadly attached by numerous hyphae. Ascomata occasional, embedded in the thallus, strongly projecting on the underside of the thallus; similar in structure to those of *N. acroglypta*, but the exciple with more evenly distributed pigmented areas, thus not tending to break into 'plates' in squash preparations. Ascospores 29–37 × 6–7 µm, mostly 7-septate. Zeorin by TLC, spot tests negative. **BLS 0920**.

On mossy deciduous trees or rocks in woodland and parkland, growing over bryophytes or other lichens (especially *Pannaria, Parmeliella* and *Pectenia*), rarely on bare bark; frequent and increasing in distribution. S. & W. Britain, throughout Ireland.

The neat squamules with sharply raised margins are distinctive; the squamules of *Lichenomphalia hudsoniana* are superficially similar, but lack soralia, have an upper and lower cortex, and grow on peaty soil or rotten wood. In shaded, humid habitats the soralia may be more conspicuous than the squamules. Fruiting material is more common in the tropics than in temperate regions, where it is often sturdier and often lacks soredia; several species may be involved.

Host-specific parasites include: *Capronia normandinae* R. Sant. & D. Hawksworth (1990), with black superficial setose perithecia; *Cladophialophora normandinae* (Diederich & Etayo) Diederich (2013) with black sporodochia; and *Tremella normandinae* Diederich (1996) forming pale galls.

PARABAGLIETTOA Gueidan & Cl. Roux (2009)

Thallus crustose, endolithic or superficial; endolithic thalli with the upper cortex of hyphal tissue intermingled with microcrystals, sometimes with one layer of slightly pigmented cortical cells at the top and a hyphal medulla without oil cells; when superficial continuous to rimose, grey-green to grey-brown. Soralia and isidia absent. **Perithecia** superficial to half or three-quarters immersed, globose and sometimes ± flat on the top or slightly depressed. **Involucrellum** present, often rather thick, reaching half to all the way down the exciple. **Exciple** colourless to pale brown. **Hymenium** colourless, K/I + blue. **Hamathecium** consisting of periphyses and short periphysoids, the latter abundant or not, but never spreading and detachable as in some species of *Baglietoa*. **Asci** clavate, 8-spored. **Ascospores** colourless, ellipsoidal to cylindric-ellipsoidal, aseptate or 1-septate. **Conidiomata** sometimes present, immersed. **Conidia** colourless, aseptate, bacilliform. **Chemistry**: acetone-soluble substances absent; pigment in involucrellum dark reddish brown, K+ dark brown or dark grey-brown. **Ecology**: on limestone.

A small monophyletic genus sister to *Baglietoa* (Gueidan *et al*. 2009), which differs in the involucrellum that is lid-like (when present), the presence of oil cells in the medulla, and the lack of conidiomata. The pigment in the involucrellum is darker and more reddish, and more likely to be dark grey in K, than in many species of Verrucariaceae.

Literature

Gueidan *et al*. (2009), Krzewicka (2012), Orange *et al*. (2009b).

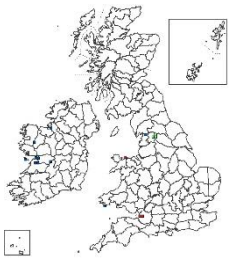
1 Ascospores 1-septate, (9–) 11–14.5 (–15.5) µm long ..... ***impressa***
Ascospores aseptate (rarely 1-septate when over-mature), usually larger 2

2(1) Perithecia immersed or forming small projections, 200–280 µm diam., ascospores (13.5–) 14–17 (–18.5) µm long ..... ***cyanea***
Perithecia forming projections 140–440 µm diam., ascospores often larger 3

3(2) Thallus endolithic (at most with minute brown dots where photobiont-containing units reach the surface), pycnidia frequent, often easily visible as small brown pits ..... ***dufourii***
Thallus epilithic, rarely almost immersed, pycnidia absent ..... ***pinguicula***

Parabagliettoa cyanea (A. Massal.) Gueidan & Cl. Roux (2009) **Nb**

Verrucaria cyanea A. Massal. (1853)



Thallus immersed or in part also thinly superficial, whitish, uncracked; typically forming a mosaic with conspecific thalli, the neighbouring thalli separated by sunken to slightly raised brown lines. Perithecia immersed, with only the black apex visible, or forming black projections 200–280 µm diam., sometimes forming poorly defined pits in the rock; involucrellum thin, 30–40 µm thick, confined to the apex of the ascoma or spreading sideways and downwards. Ascospores (13.5–) 14–17 (–18.5) × (5.5–) 6–8 (–9) µm, length/width ratio (1.8–) 2–2.5 (–2.8). Conidiomata present. **BLS 1484**.

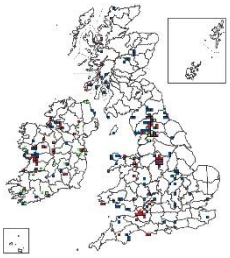
On exposed calcareous rocks; rare and usually in small quantity. S.W. England, N. Wales, locally frequent in W. Ireland.

Differs from *P. dufourii* in the smaller, less prominent perithecia and the thalli typically in a mosaic with conspecific thalli separated by dark lines; the lines produced by one thallus typically do not merge completely with those of its neighbour, so the lines often appear double.

Parabagliettoa dufourii (DC.) Gueidan & Cl. Roux (2009) **LC**

Verrucaria dufourii DC. (1805)

Thallus immersed, the surface usually level with surrounding rock or slightly lower, pale grey to brown-grey, not cracked; sometimes thallus units reaching to the rock surface as minute, brown specks; prothallus not seen,



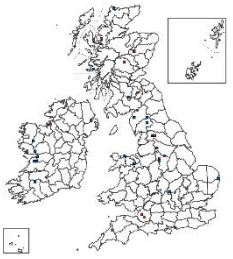
but the leading edge of the thallus is sometimes whitish; junction with neighbouring, conspecific thalli marked by a fine crack, a groove, a change in level, a whitish (rarely brown) line, or a row or double row of brown pycnidia. Perithecia forming distinct projections 280–440 µm diam., black, not covered by the thallus, the apex flat or usually concave, leaving shallow pits in the rock when decayed; ostiole inconspicuous, or appearing as a slightly paler area 30–80 µm diam., or as a paler area to 140 µm diam. and occupying much of the concavity; involucrellum well-developed, thick, flanking the upper half of the exciple, pigment dark reddish brown, K+ dark brown. Exciple pale below. Ascospores cylindrical to ellipsoidal, (15.5–) 16.5–20 (–23.5) × (6.5–) 7–8.5 (–9) µm, length/width ratio (1.9–) 2.0–2.7 (–3.4), often with a perispore to *ca* 1.5 µm thick. Pycnidia frequent, scattered, often numerous and easily seen, appearing as brown pits 60–100 µm diam. Conidia rod-shaped, 3.3–4.5 × 0.8–1.2 µm. **BLS 1487**.

On hard limestones; occasional. Widespread in limestone areas of Britain and Ireland.

Distinguished by the immersed thallus, often dotted with pycnidia, the perithecia typically with a concave apex, and the usually somewhat cylindrical ascospores. Perhaps previously over-recorded for *P. pinguicula* which is very similar, but with the thallus usually at least thinly superficial and often cracked, the perithecia less obviously depressed above and without pycnidia.

Parabagliettoa impressa (Stizenb.) Orange (2023) **Nb**

Thelidium impressum (Stizenb.) Zschacke (1920)



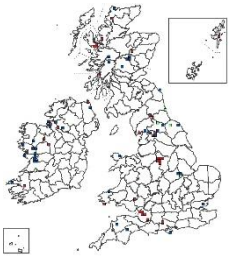
Thallus endolithic, pale grey to grey-brown, rarely thinly epilithic. Perithecia approximately half-immersed in rock, sometimes leaving shallow pits when dead, forming black projections 0.2–0.48 mm diam., sometimes flattened above; ostiole sometimes in a shallow depression; involucrellum well-developed, clasping the perithecium and often reaching to base-level, pigment dark reddish-brown, K+ dark grey-brown; perithecium in section 0.15–0.28 mm diam. Ascospores 1-septate, (9–) 11–14.5 (–15.5) × (6–) 6.5–8.5 (–9) µm, length/width ratio (1.4–) 1.5–1.9 (–2.1). **BLS 1388**.

On limestone; rare. S.W. & N. England, N. Wales, Scotland, W. Ireland.

Differs from *P. dufourii* in the small, 1-septate ascospores. Morphology and an ITS-LSU sequence suggest this belongs in *Parabagliettoa*.

Parabagliettoa pinguicula (A. Massal.) Orange (2023) **Nb**

Verrucaria pinguicula A. Massal. (1856)



Thallus superficial, rarely almost immersed, often raised above the surrounding rock, continuous to extensively cracked, whitish to pale brown; prothallus not seen, the junction with neighbouring conspecific thalli marked by a brown line; cortex without or with dilute brown pigment (the brown colour of the thallus is often partly due to cyanobacteria on the surface). Perithecia forming low to moderate projections 140–440 µm diam., black, not covered by the thallus, the apex flattened or occasionally concave, sometimes leaving shallow pits in rock when decayed; ostiole inconspicuous, or visible as a slightly paler dot or shallow pit; involucrellum well-developed, thickest beside the upper half of the perithecium, but often more or less clasping the exciple below and reaching to its base; perithecia in section 190–280 µm diam., pale below. Ascospores cylindrical to ellipsoidal, (12–) 13.5–18 (–21) × (5–) 5.5–8.5 (–11) µm, (1.5–) 2–2.7 (–3.4) times as long as wide, perispore usually not visible, rarely inconspicuous and up to 0.8 µm thick. Conidiomata not seen. **BLS 1512**.

On hard limestones; locally frequent but under-recorded. Throughout Britain and Ireland in limestone areas.

The thallus is superficial though thin, but pale uncracked thalli may appear to be immersed. Morphologically close to *P. dufourii*, which differs in the immersed thallus, often dotted with pycnidia and the more distinctly concave apex to the perithecium. Some poorly developed specimens may be difficult to name.

PLACIDIOPSIS Beltr. (1858)

Thallus squamulose. **Upper cortex** a pseudocortex, pseudoparenchymatous, thin. **Lower cortex** pseudoparenchymatous or absent, squamules attached to the substrate by intertwined colourless or brown rhizoidal hyphae, or a tuft of hyphae or rhizines. **Photobiont** *Diplosphaera* (Trebouxiophyceae). **Ascomata** perithecia, immersed in the squamules. **Involucrellum** present or absent (absent in British species). **Exciple** of tangentially arranged ± elongate cells, pigmented around the ostiole, the lower part pale or darkening. **Hamathecium** of periphyses; paraphyses absent. **Asci** 8-spored, clavate, thin-walled, apically slightly thickened with a small ocular chamber. **Ascospores** clearly 1-septate, biseriately arranged, ellipsoidal to ovoid or subfusiform, colourless. **Conidiomata** unknown. **Chemistry**: lichen products not detected by TLC. **Ecology**: mostly on soil, detritus or mosses, occasionally on rock.

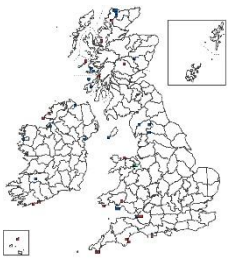
Similar to *Catapyrenium* and closely related (Prieto *et al*. 2010b), differing from that genus in morphological terms in having ascospores that are clearly 1-septate when mature, not aseptate (note that in *Catapyrenium*, over-mature or germinating ascospores can develop a septum).

Literature

Breuss (1996, 2009c, 2010), Breuss & Hansen (1988), Prieto *et al*. (2010a, b, 2011).

1 Squamules partly ascending, ± imbricate and divided, without pruina, somewhat tumid; lower cortex lacking, rhizoidal hyphae aggregated into a central tuft ..... ***custnani***
Squamules entirely firmly appressed, rounded to slightly incised, often whitish pruinose; lower cortex pseudoparenchymatous, rhizoidal hyphae forming a hyphal web ..... ***pseudocinerea***

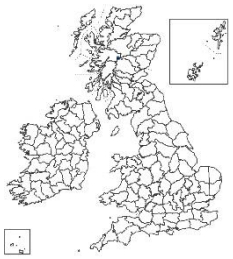
Placidiopsis custnani (Massal.) Körb. (1863) **NT**



Squamules 1–2 mm diam., ascending, clustered or crowded, often ± imbricate, spreading, sometimes forming a nodulose crust-like cover, incised or divided, ± tumid (especially on the margins), pale olive brownish to medium brown on the upper side, green-olive when wet, underside dark brown to blackish, paler towards the margins; rhizoidal hyphae brown, in the central part usually aggregated to form a tuft or rhizine-like attachment organ. Perithecia frequent, 1–5 per squamule, 0.2–0.3 mm diam., immersed with a ± elevated dark ostiole; exciple pale to blackish brown. Ascospores (12–) 14–20 × 5.5–7.5 µm, ellipsoidal to slightly ovoid. **BLS 1132**.

On ± consolidated soil, often among mosses, associated with limestones, shell-sand dunes, mica-schist, serpentines, rarely on old mortar; widespread, but rare. Coastal and inland S.W. and N.W. England, Wales, W. Scotland (up to 900 m in the Highlands), W. Ireland.

Placidiopsis pseudocinerea Breuss (1983) **CR (D)**



Squamules to 4 mm diam., entirely closely appressed, the margins rounded or slightly incised, scattered or aggregated in small groups, pale brownish and naked or weakly pruinose and then with a whitish grey tinge; underside blackish, lower cortex of isodiametric polygonal cells with dark pigmented walls, with brown rhizoidal hyphae forming a dense dark hypothallus. Perithecia three-quarters to fully immersed, 0.2–0.35 mm diam., the ostiole often slightly elevated; exciple at first colourless, soon darkening around the ostiole and eventually blackish-brown throughout. Ascospores (14–) 15–19 (–21) × (6.5–) 7.5–9 (–10) µm, ellipsoidal to slightly ovoid. **BLS 1884**.

On calcareous soil or associated humus at high altitude; rare. Scotland (Central Highlands, Ben Alder).

Closely resembles *Catapyrenium cinereum* which has aseptate, more elongate, cylindric-clavate ascospores and smaller, more deeply incised squamules (Breuss & Hansen 1988).

.

PLACIDIUM A. Massal. (1855)

Thallus squamulose or almost leafy, attached to the substrate by intertwined colourless or brownish rhizoidal hyphae, rhizines absent. **Upper cortex** distinct, composed of rather large (7–14 µm diam.) angular tightly conglutinated cells, sharply delimited against the algal layer. **Medulla** with a mix of globose and filamentous hyphae or mostly formed by filamentous hyphae. **Lower cortex** composed of roundish-angular cells, or absent. **Photobiont** *Myrmecia* (Trebouxiophyceae). **Ascomata** perithecia, immersed in the thallus. **Involucrellum** absent. **Exciple** composed of tangentially arranged ± elongated cells, pigmented around the ostiole, lower part pale or ± darkened. **Hamathecium** of periphyses; paraphyses absent. **Asci** 8-spored, cylindrical or less frequently clavate, thin-walled, non-amyloid and without an ocular chamber. **Ascospores** uniseriately arranged, colourless, aseptate, ellipsoidal. **Conidiomata** pycnidial, *Dermatocarpon*-type, immersed laminally in the squamules or forming spherical projections at their margins. **Conidia** cylindrical or shortly bacilliform. **Chemistry**: no lichen products detected by TLC. **Ecology**: mostly on soil or over decaying bryophytes and plant debris, preferring calciferous substrata, rarely on calcareous rocks or on bark.

The genus is currently restricted to species lacking rhizines; species with rhizines belong in the sister genus *Clavascidium*. Both clavate and cylindrical asci can be found in each genus, although species with clavate asci are mainly found within *Clavascidium* (Prieto *et al*. 2012).

Literature
Breuss (1996, 2009d, 2010), Prieto *et al*. (2010a, 2012).

1 Squamules usually loosely appressed or partly ascending, crowded to overlapping; pycnidia marginal 2
Squamules ± firmly appressed, not ascending, dispersed to contiguous; pycnidia laminal 4

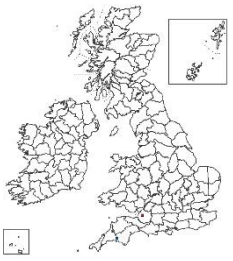
2(1) Pycnidia usually very conspicuous, globose, the walls black and friable; lower cortex of vertically arranged polygonal cells; conidia 5–7 µm long, bacilliform ..... ***lachneum***
Pycnidia less conspicuous; lower cortex of globose cells, not vertically arranged; conidia 3–5 µm long, cylindric-ellipsoidal 3

3(2) Ascospores 15–20 × 7.5–9.5 µm; squamules to 10 mm across, thick and leathery, ± wavy, with thick medullary tissue of elongate hyphae ..... ***rufescens***
Ascospores 12–17 (–19) × 5.5–7.5 µm; squamules to 6 mm across, thin; medullary tissue less well-developed, composed of a mix of globose and elongate cells ..... ***pilosellum***

4(1) Exciple brownish throughout when mature ..... ***michelii***
Exciple persistently pale, only the uppermost part around the ostiole pigmented 5

5(4) On mortar or calcareous rocks; squamules 2–4 mm across, often with dark margins; lower side black ..... ***boccanum***
On soil; squamules 2–7 mm across, not dark-margined; lower side pale to brown, rarely blackish ..... ***squamulosum***

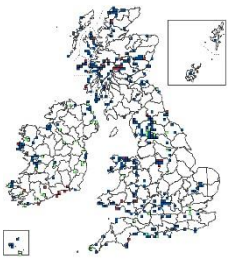
Placidium boccanum (Servít) Breuss (1996) **Nb**
Squamules 2–4 mm across, scattered to contiguous, firmly attached throughout or with slightly upturned margins, irregularly orbicular to somewhat lobed; upper surface brown, matt or slightly glossy; lower surface black up to the margin, giving a dark rim around each squamule; lower cortex of round to ± angular cells; rhizoidal hyphae colourless. Perithecia immersed; exciple pale except around the ostiole. Asci cylindrical. Ascospores 12–16 × 5.5–7.5 µm, ellipsoidal, uniseriately arranged. Pycnidia laminal, immersed; conidia 3–4 µm long, cylindric-ellipsoidal. **BLS 1861**.



Mostly on mortar, rarely on calcareous rocks; very rare. England (single collections from S. Devon and Somerset).

The dark margins to the squamules are a particular feature of this species.

Placidium lachneum (Ach.) B. de Lesd. (1932) **Nb**

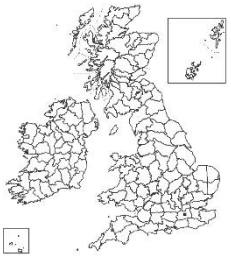


Squamules to 8 mm across, scattered or more often crowded to imbricate, ± rounded or lobed, partly ascending; upper surface brown to dark red-brown, matt; lower surface black; margins with conspicuous globular pycnidia to 0.4 mm diam.; lower cortex of thin-walled angular cells arranged vertically forming a very distinct layer; rhizoidal hyphae colourless to dark; medullary layer thick, of elongate hyphae. Perithecia laminal, entirely immersed; exciple colourless except for the ostiole. Asci cylindrical. Ascospores 14–18 × 6–8 µm, ellipsoidal, uniseriately arranged. Pycnidia marginal, usually very conspicuous, globose, the walls black and friable; conidia 5–7 µm long, bacilliform. **BLS 0301**.

On soil, humus and basic rocks, widely distributed and fairly common in upland areas. Scottish Highlands, Wales, southern, central and northern England, in Ireland mostly in the west. Recent records are sparse compared with in earlier times; it is not clear whether this is charting a decline or over-recording in the past, and there are many misidentifications for *P. squamulosum*.

The large, dark-walled pycnidia are diagnostic.

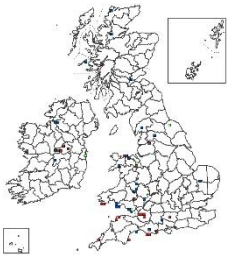
Placidium michelii A. Massal. (1855) **VU (D2)**



Squamules 2–4 mm diam., usually dispersed, rarely contiguous, firmly attached to the substrate, rounded to slightly incised, pale to medium brown above, dull; lower surface blackish, with a thin cortex composed of angular cells; rhizoidal hyphae colourless. Perithecia immersed; exciple brown in mature ascomata. Asci cylindrical. Ascospores 11–15 × 5–6 µm, ellipsoidal, uniseriately arranged. Pycnidia unknown in British specimens, elsewhere laminal with cylindric-ellipsoidal conidia. **BLS 0302**.

On chalk soils. Very rare and local, not seen recently and perhaps now extinct due to overgrowth of vegetation and human pressure. S.E. England (Surrey, Box Hill).

Placidium pilosellum (Breuss) Breuss (1996) **NT**

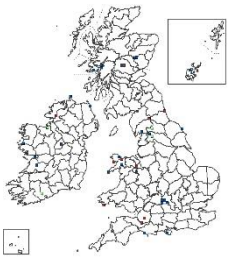


Squamules to 6 mm across, loosely attached or partly ascending, scattered to ± imbricate, rounded or lobed, pale brownish to reddish brown above, matt; younger squamules often with colourless, hair-like hyphal extensions on the margins. Medulla composed of a mix of elongate and rounded cells. Perithecia immersed in the squamules; exciple pale except for around the ostiole. Asci cylindrical. Ascospores 12–17 (–19) × 5.5–7.5 µm, ellipsoidal, uniseriately arranged. Pycnidia marginal; conidia 3–4 µm long, cylindric-ellipsoidal. **BLS 1586**.

On soil or humus, often among mosses, preferring coastal areas; localized. S.W. England to Scotland, rarer in the north.

The colourless, pubescent hyphal extensions on the lobe margins have been claimed to be distinctive, but are not an exclusive feature of this species.

Placidium rufescens (Ach.) A. Massal. (1855) **Nb**



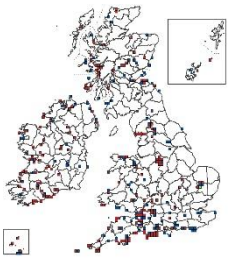
Squamules to 10 mm diam., crowded to imbricate, ± lobate, thick, leathery, usually undulate; upper surface pale to dark brown, often with a reddish tinge, dull or somewhat glossy; lower cortex of rounded to angular cells; rhizoidal hyphae colourless; medullary tissue well-developed, of elongate hyphae. Perithecia completely immersed; exciple colourless except for the ostiole. Asci cylindrical. Ascospores 15–20 × 7.5–9.5 µm, broadly ellipsoidal, uniseriately arranged. Pycnidia marginal, sparse to abundant; conidia 3–5 µm long, cylindric-ellipsoidal. **BLS 1776**.

On dry calcareous rocks or on soil; widespread but local. Scattered throughout much of Britain and Ireland.

Similar to *P. lachneum*, from which it can easily be distinguished by its larger ascospores and the different size and shape of the conidia. *P. pilosellum* has markedly thinner squamules and

smaller ascospores, while *P. squamulosum* and *P. michelii* both differ in smaller, ± appressed squamules, smaller ascospores and in lacking marginal pycnidia.

Placidium squamulosum (Ach.) Breuss (1996) **LC**



Squamules 2–7 mm across, scattered to contiguous, attached by the entire underside or with slightly upturned margins, pale to dark brown above, matt, irregularly orbicular to somewhat lobed, ± uniformly pale below; medulla composed of a mix of elongate and rounded cells; lower cortex of rounded to ± angular cells; rhizoidal hyphae colourless. Perithecia fully immersed; peridium pale, dark only around the ostiole. Asci cylindrical. Ascospores 12–16 × 5.5–7.5 µm, ellipsoidal, uniseriately arranged. Pycnidia laminally immersed in the squamules; conidia 3–5 µm long, cylindric-ellipsoidal. **BLS 1608**.

On neutral to calcareous soil and humus; widespread, the most frequent species of the genus; throughout Britain and Ireland.

PLACOPYRENIUM Breuss (1987)

Thallus crustose to subsquamulose, without vegetative propagules, always divided into areoles, these often with dark sides; sometimes upper surface pruinose; sometimes attached by localized hapters. **Prothallus** present in crustose species, absent in subsquamulose species. **Cortex** poorly defined; pigment, when present, brown; epinecral layer often present. **Photobiont** *Diplosphaera* (Trebouxiophyceae). **Ascomata** perithecia, immersed in the thallus. **Exciple** colourless to brown. **Involucrellum** absent or very weakly developed at the apex of the perithecium. **Hamathecium** of periphyses and periphysoids, interascal filaments absent; gel hemiamyloid, I + red (+ blue at very low concentrations of I), K/I + blue. **Asci** clavate, I –, with rostrate dehiscence, wall thickened above, ocular chamber usually present. **Ascospores** 8 per ascus, aseptate or partly 1-septate, colourless, ellipsoidal or cylindric-ellipsoidal, smooth, the wall thin or only slightly thickened, perispore present or absent. **Conidiomata** pycnidia, *Dermatocarpon*-type, immersed in the thallus. **Conidia** rod-shaped, aseptate, colourless. **Chemistry**: lichen products absent. **Ecology**: on rock and soil, some species in freshwater habitats, several species initially parasitic on other lichens.

One of three genera of Verrucariaceae that were formerly included in *Verrucaria* but have been found to be quite distinct in phylogenetic terms, and characterized (in most species) by their initial parasitism of other lichens. Morphological distinctions between *Placopyrenium* and *Verrucula* and *Verruculopsis*, the other two genera in this clade, are difficult to define, but the last two seem to parasitize species of *Caloplaca* s.l. while *Placopyrenium* affects other lichen genera.

Literature

Breuss (2009e), Gueidan *et al*. (2009), Krzewicka (2012), Orange (2004a, 2009d), Orange *et al*. (2009b).

1 Perispore present, ascospores (14–) 17.5–26.5 (–30.5) µm long; young thallus initially parasitic on *Aspicilia* or *Circinaria* species, later independent 2
Perispore absent or present but indistinct, ascospores (10.5–) 12.5–21 (–25.5) µm long; young thallus independent, or sometimes on *Staurothele* or *Verrucaria* species 3

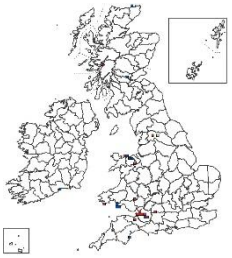
2(1) Ascospores (18.5–) 21.5–26.5 (–30.5) µm long, thallus initially parasitic on *Circinaria* (*Aspicilia*) *calcarea* ..... ***canellum***
Ascospores (14–) 17.5–22.5 (–27) µm long, thallus initially parasitic on *Aspicilia aquatica* ... ***formosum***

3(1) Ascospores (13–) 16–21 (–25.5) µm long; upper surface of areoles typically undivided or occasionally divided by a few dark lines; on regularly inundated siliceous rocks by water, sometimes parasitic on *Staurothele fissa* ..... ***cinereoatratum***
Ascospores (11.5–) 13–18 µm long; upper surface of areoles typically divided by dark lines; on calcareous rocks in terrestrial habitats, sometimes parasitic on *Verrucaria nigrescens* 4

4(3) Areoles 0.6–2 mm wide, often constricted below but not tapering into a stipe ..... ***fuscellum***
Areoles 3–8(–15) mm wide, tapering below into irregularly shaped stipes..... ***trachyticum***

Placopyrenium canellum (Nyl.) Gueidan & Cl. Roux (2007) **Nb**

Verrucaria canella Nyl. (1883)



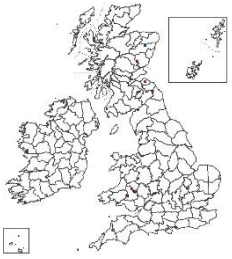
Prothallus absent or indistinct. Thallus epilithic, well-developed, 260–600 µm thick; margin thin, often ± continuous, initially not broken into discrete areas, but very early divided by cracks; thallus rapidly increasing in thickness from the margin; mature areoles discrete, 0.2–1 mm diam., separated by deep cracks; angular in outline, mostly flat, sometimes a few slightly concave or convex, pale grey or locally brownish, pruinose, the margin usually dark brown, sides black; upper surface rarely or occasionally rather frequently subdivided by dark lines. Cortex poorly defined, the cell walls with dilute brown pigment; epinecral layer to 10 µm thick; medulla colourless to darkly pigmented, but pigment often patchy, often occupying at least half the thallus thickness. Perithecia 1–5 per mature areole, immersed within the upper surface of the areole or occasionally marginal; 175–280 µm diam., the exposed part black, 100–180 µm diam., flat or occasionally slightly convex; ostiole inconspicuous or visible as a small depression *ca* 20 µm diam. Exciple thickened at the apex, colourless to brown below, dense brown above, pigment brown, K+ slightly darker or dull greenish brown. Involucrellum absent. Ascospores narrowly cylindric-ellipsoidal or ellipsoidal, (18.5–) 21.5–26.5 (–30.5) × (6.5–) 7.5–9.5 (–10.5) µm, (2.1–) 2.5–3.1 (–3.8) times as long as wide; perispore present, to 1.2 µm thick, sometimes difficult to distinguish from the ascospore wall, sometimes separating from the spore wall in K by swelling or by forming blisters. Conidiomata not seen. **BLS 1478**.

On unshaded limestone, initially growing on the thallus of *Circinaria* (*Aspicilia*) *calcarea*, later independent. S.W. and N. England, Wales, N. Scotland.

Differs from *P. fuscellum* and *Verrucaria polysticta* in the larger ascospores and the presence of a perispore. A prothallus is scarcely present, and the areoles of the mature thallus are formed by early cracking of lichenized tissue at the thallus margin. The surface of the areoles is often subdivided by dark lines, but to a much lesser extent than in *P. fuscellum* and *V. polysticta*. The typically little-subdivided areoles and the low number of perithecia per areole give a distinctive appearance to *P. canellum* and it can usually be recognized easily under the dissecting microscope. *P. formosum* is similar, but differs in the shorter ascospores, the areoles which are often convex, and the different host (*Aspicilia aquatica*).

Placopyrenium cinereoatratum (Degel.) Orange (2009) **NE NR**

Verrucaria cinereoatrata Degel. (1945)



Prothallus absent, or less frequently present but very narrow and inconspicuous. Thallus crustose to subsquamulose, free-living thalli 200–600 µm thick, margin well-defined; very young thalli entire, but soon with deep cracks reaching to the margin, dividing the thallus into discrete, sharp-edged areoles; areoles 0.5–1.2 mm diam., upper surface flat or uneven, occasionally convex when older, pale grey to mid brown, faintly to distinctly pruinose; areoles undivided or occasionally with the upper surface divided by a few dark lines; sides of areoles adjacent to cracks black; when parasitic the thallus thin, cracked and without a distinct margin. Areoles attached by the lower surface, without rhizines or hapters. Epinecral layer usually present, to 12 µm thick but sometimes scarcely developed, composed of broken cells with collapsed cell remains above. Lower parts of thallus with dense brown pigment. Perithecia immersed in the thallus, several to many per areole, 140–300 µm diam., the apex often inconspicuous in surface view, sometimes visible as a small brown dot, occasionally easily visible as a flat or slightly projecting black disc 60–120 µm diam. Exciple brown at the apex, colourless below. Ascospores (13–) 16–21 (–25.5) × (5.5–) 6.5–8 (–9.5) µm, length/width ratio (1.9–) 2.2–2.9 (–4.0), ellipsoidal,

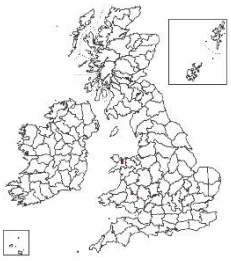
colourless, rarely faintly brown when overmature, perispore usually absent or indistinct, occasionally to 0.8 µm thick. Pycnidia immersed in the thallus, 80–105 × 25–42 µm, wall colourless or faintly brown at the ostiole; conidia aseptate, colourless, rod-shaped, 4–6 × *ca* 1.2 µm. **BLS 2531**.

On somewhat calcareous siliceous rocks beside streams and rivers, sometimes parasitic on *Staurothele fissa*; uncommon. Wales, N. England, E. Scotland.

P. formosum also grows in freshwater habitats, but in that species the ascospores are slightly larger, with a more distinct perispore, a prothallus is better developed, the areoles are more frequently gently convex, and young thalli are parasitic on *Aspicilia*. ITS sequences indicate that the two species are clearly distinct. *P. fuscellum* differs in the more strongly developed thallus, areoles which are frequently subdivided into smaller units in surface view, the slightly swollen margin of the areoles, the smaller ascospores, and the habitat usually on calcareous terrestrial rocks.

Placopyrenium formosum Orange (2009) **Nb**

Verrucaria crustulosa auct., *non* Nyl. ex Lamy (1979



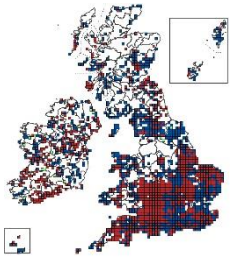
Prothallus brown, non-fimbriate, often present around areoles on rock. Thallus initially invading *Aspicilia* thalli, killing the host; superficial, well-developed, 130–400 µm thick; areoles discrete from early on, soon separated by deep cracks, at first 200–400 µm diam., later up to 1.2 mm diam., at first flat, but mature areoles sometimes gently convex, sometimes becoming subdivided by grooves; upper surface grey-brown to brown, pruinose or not, the sides black. Areoles attached by the lower surface, without rhizines or hapters. Lower parts of thallus often with irregularly shaped areas with brown pigment, tissue adjacent to sides of areoles densely pigmented with brown pigment. Perithecia immersed in the thallus, 1–22 per areole, 140–220 µm diam., the exposed part black, flat or slightly convex, to 180 µm diam. Exciple colourless or brown below, thickened and brown above. Ascospores (14–) 17.5–22.5 (–28) × (7–) 8–10 (–11) µm, length/width ratio (1.6–) 2.0–2.5 (–3.0), colourless at maturity, but often faintly brown when overmature; perispore present, 1–1.5 µm thick, compact and often difficult to distinguish from the wall. Pycnidia immersed in the thallus, detected in three specimens; conidia aseptate, colourless, rod-shaped, 3.7–5.3 × *ca* 1.2 µm. **BLS 2513**.

Initially parasitic on *Aspicilia aquatica* on siliceous rocks beside streams, later free-living; rare. N. and mid Wales, central Scotland, W. Ireland.

P. canellum differs in the larger ascospores and the different host (*Circinaria calcarea*). See under *P. cinereoatratum* for the distinction from that species.

Placopyrenium fuscellum (Turner) Gueidan & Cl. Roux (2007) **LC**

Verrucaria fuscella (Turner) Winch (1807)



Prothallus inconspicuous. Thallus epilithic, well-developed, 250–800 µm thick, often forming small patches to about 10 mm diam., but sometimes forming extensive colonies to 60 mm diam.; actively growing thallus margin usually thick, formed of discrete areoles, these often elongate and lobed, 0.3–1.4 × 0.18–0.7 mm; upper surface of areoles becoming divided into smaller units by dark lines; thallus becoming cracked into mature areoles 0.6–2 mm diam.; all areoles light brown to grey, lightly pruinose, often tinged red, often with a brown edge; sides of mature areoles black. Occasionally parts of the thallus margin have small lichenized units on a thin dark tissue; these may represent areas of regeneration following damage. Epinecral layer often present, to 6 µm thick. Cortex poorly defined, with dilute brown pigment, frequently also with a red pigment which is K+ dull blue-grey → HCl+ red ↔ K+ blue. Medulla densely pigmented. Perithecia immersed in the thallus, 1–10 (–30) within each small area separated by dark lines, but usually very numerous per mature areole; 190–225 µm diam., the exposed part 60–120 µm diam., flat to slightly convex, brown to black. Exciple thick, colourless to dilute brown below, brown above, pigment brown, K+ darker brown or greenish brown. Involucrellum absent. Ascospores cylindric-ellipsoidal, (11.5–) 13–17 (–20.5) × (4.5–) 5–6 (–7.5) µm, (1.9–) 2.3–3 (–3.7) times as long as wide; perispore absent. Conidiomata pycnidia, very rare (detected once), immersed in marginal areole, 75 × 33 µm, wall colourless, cells at ostiole faintly brown, conidia *ca* 4.5 × 1.2 µm. **BLS 1492**.

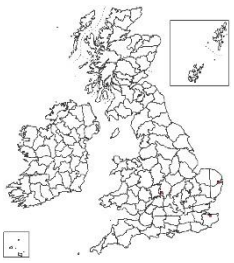
On calcareous rocks, or rocks under calcareous influence, including limestone, mortar, schist, brick and granite; on natural outcrops, but also frequently recorded from walls and buildings, possibly preferring slightly

nutrient-enriched situations; often parasitic on *Verrucaria nigrescens* when young; common. Widespread in Britain and Ireland.

The thallus margin in *P. fuscellum* is typically thick and abrupt, often giving a minutely subsquamulose appearance, and not thin as in *P. canellum* and *Verrucaria polysticta*. The lower surface of the advancing areole rapidly becomes densely pigmented. In external view the perithecia appear as dark dots in the centre of the small units that are separated by dark lines, not between them as in *V. polysticta*, and they are also less conspicuous than in that species. The mature areoles usually appear much more subdivided by lines than in *P. canellum*. An apparently unnamed acetone-insoluble pigment is frequently seen in the cortex, when it gives a red tinge to the thallus. The pigment is dull blue-grey in K, but treatment with HCl or N causes a non-reversible change, so that a further addition of K gives a distinctly blue reaction. The pigment may be mixed with, or intergrades with, the usual pigment which is brown in K. *P. trachyticum* is distinctly squamulose, with a nodular lower surface.

Host to *Zwackhiomyces lithoiceae* (B. de Lesd.) Hafellner & V. John (2006) and single reports of *Muellerella lichenicola* (Sommerf.) D. Hawksw. (1979) and an unidentified *Endococcus* (spores 7–9 × 3.5–4 µm, with somewhat pointed apices).

Placopyrenium trachyticum (Haszl.) Breuss (1987) **NE**



Prothallus absent. Thallus subsquamulose, 3–8 (–15) mm long and (0.5–) 2–5 (–8) mm wide, usually 250–800 µm thick, (but may be up to 5 mm thick including stipes), divided into secondary areoles, areoles with the upper surface divided by dark lines into few to numerous (up to 30) units, and with dark sides. Medulla (of each photosynthetic unit) without dark pigment (but units may be situated above a dark layer at the base of the thallus). Lower surface black, uneven, tapering into irregularly shaped stipes attached to the substratum. Perithecia 120–250 µm diam. Exciple colourless to pale brown. Ascospores aseptate to 1-septate, 13–18 × 5–7 µm. Conidiomata not seen. **BLS 2704**.

Reported from ironstone, limestone and concrete at the base of a church wall, England (E. Kent, E. Norfolk, Warwickshire).

Resembles *P. fuscellum* in the subsquamulose thalli, but larger, with the areoles tapering into irregularly shaped stipes below, and without dark pigment in the lower parts of the photosynthetic units. Specimens with a proportion of 1-septate ascospores have been separated as var. *subtrachyticum* (B. de Lesd.) Breuss. (2009), but the importance of this distinction needs further study.

POLYBLASTIA A. Massal. (1852)

Thallus crustose, immersed or superficial, white, green, grey or brown; rarely with vegetative propagules (soredia). **Cortex** usually poorly defined, rarely of intertwined gelatinized hyphae; pigment, when present, usually brown. **Photobiont** a green alga, cephalodia and hymenial algae absent. **Ascomata** perithecia, black, sometimes forming pits in limestone. **Involucrellum** often present. **Hamathecium** of periphyses and periphysoids, interascal filaments absent; gel hemiamyloid, I+ red (+ blue at very low concentrations of I), K/I+ blue. **Asci** clavate, K/I–, wall thickened above, ocular chamber usually present; dehiscence by extrusion of an endotunica to form a delicate rostrum. **Ascospores** (1-) 2–8 per ascus, submuriform to muriform, colourless (dark brown in one species retained here for convenience). **Chemistry**: lichen products absent. **Ecology**: on siliceous rock, limestone and on soil or over bryophytes.

Molecular studies recover *Polyblastia* in a narrow sense, as sister to the *Thelidium* group of Verrucariaceae. In this narrow sense the species share little more than a crustose thallus and small to medium, colourless, muriform ascospores (Gueidan *et al*. 2009). However, these characters also occur in some members of the *Thelidium* group, so that there is presently no morphological definition of the genus. Many species with muriform ascospores (some of them brown) have been removed from

Polyblastia and placed in genera including *Atla*, *Henrica*, *Merismatium* and *Sporodictyon*. However, the genus is still defined here in a broad sense, as molecular studies of many species are still lacking. The genus has not been well studied in Britain and Ireland, partly because some species are rather rare.

Tibell & Tibell (2017) list a number of further species as excluded from *Polyblastia*, including *P. dermatodes* (in the *Thelidium* clade and questionably distinct from *T. incavatum*, q.v.), *P. gothica* (now a synonym of *Merismatium nigritellum*, q.v.) and *P. helvetica* (of uncertain position, probably to be excluded from the Verrucariaceae).

A collection from limestone on the Isle of Skye has been provisionally identified as *Polyblastia plicata* A. Massal. (1856), but more studies are needed before the identification can be confirmed. Tibell & Tibell (2017) compared the species with *P. singularis* (Kremp.) Arnold (1868) which has smaller cruciately rather than obliquely septate ascospores and a thin whitish thallus. That species has not been recorded from Britain and Ireland.

Literature

Gueidan *et al.* (2007, 2009), Orange (2013a), Orange *et al*. (2009a), Savić & Tibell (2009, 2012), Savić *et al.* (2008), Swinscow (1971), Tibell & Tibell (2017).

Key to *Polyblastia* and similar species

1 Soralia present; perithecia 0.30–0.95 mm diam., ascospores colourless, 36–50 µm long ..... ***efflorescens***
Soralia absent 2

2(1) Perithecia at least two-thirds immersed in well-defined pits in limestone, involucrellum absent 3
Perithecia not in pits, superficial or immersed in thallus or in soil, involucrellum usually present 5

3(2) Ascospores dark brown, (18–) 22.5–27.5 (–31) µm, with a perispore usually visible at least in immature spores ..... ***Merismatium deminutum***
Ascospores colourless, perispore absent 4

4(3) Ascospores muriform, with 10–36 cells visible in optical section ..... ***albida***
Ascospores submuriform, with 3-4 transverse and 1-2 longitudinal septa, with 6-14 cells visible in optical section ..... ***Thelidium incavatum***

5(2) Ascospores brown when mature, with brown pigment visible in cell walls (immature spores may be colourless) 6
Ascospores colourless or faintly yellow-brownish when mature, brown pigment visible in cell walls only in withered or over-mature spores 13

6(5) Ascospores relatively small, (15–) 20–38.5 µm long 7
Ascospores very large, 48–150 µm long 8

7(6) Perithecia large, 0.5–0.8 mm diam., involucrellum present; thallus whitish; on rock ..... ***Henrica melaspora***
Perithecia small, 0.2–0.3 mm diam., involucrellum absent; thallus blackish; on soil ..... ***Merismatium nigritellum***

8(6) Involucrellum absent, ascospores very large, 70–160 µm long 9
Involucrellum present, ascospores smaller, 48–98 µm long 10

9(8) Asci (1-) 2-spored, spores cylindric-ellipsoidal ..... ***helvetica***
Asci (3-) 4- to 8-spored, spores ellipsoidal or cylindric-ellipsoidal ..... ***Atla wheldonii***

10(8) Thallus of strongly convex areoles; perithecia half-immersed amongst areoles, but without a covering of thalline material; exposed surface ± smooth; ascospores (51–) 53.5–63.5 (–70) µm long; cephalodia absent ..... ***Henrica theleodes***
Thallus smooth to verrucose; perithecia prominent or partly covered by a thalline layer, exposed surface often becoming rough; cephalodia present in some species 11

11(10) Ascospores (47.5–) 55–65.5 (–75) µm long, medium brown when mature but rarely opaque; thallus ± smooth to somewhat verrucose; perithecia forming projections 0.5–0.7 mm diam.; cephalodia absent ..... ***Sporodictyon cruentum***
Ascospores 50–98 µm long, dark brown and often opaque when mature, with cell outlines obscured; thallus usually verrucose; perithecia forming projections (0.44–) 0.6–1.2 mm diam. 12

12(11) Perithecia partly covered by irregular patches of thalline material, ascospores (50–) 63–73 (–76) µm long; cephalodia present ..... ***Sporodictyon schaererianum***
Perithecia partly immersed or prominent, but without a covering of thalline material, ascospores (63–) 72–87 (–98) µm long; cephalodia absent ..... ***Atla alpina***

13(5) Ascospores submuriform, with up to 3-5 transverse and 1-2 longitudinal septa 14
Ascospores muriform 16

14(13) Ascospores 12–20 µm long 15
Ascospores 30–45 (–68) µm long ..... ***verrucosa***

15(14) On terrestrial limestone, not lichenicolous; with only a few, mostly oblique septa; [not confirmed from GBI; see generic account above] ..... ***plicata***
On frequently inundated siliceous rock, lichenicolous ..... ***quartzina***

16(13) Ascospores relatively small, 17–45 µm long 17
Ascospores larger, 38–81 µm long 18

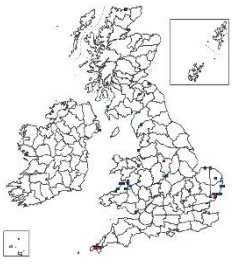
17(16) Thallus slightly cartilaginous in appearance, with a colourless hyphal cortex; ascospores (17–) 21.5–25.5 (–28) µm long; on mossy soil ..... ***sendtneri***
Thallus not cartilaginous, without a hyphal cortex; ascospores (21.5–) 26–38.5 (–45) µm long; on rock, rarely on soil ..... ***cupularis***

18(16) Asci 2-spored ..... ***agraria***
Asci 8-spored 19

19(18) Perithecia two-thirds to almost completely immersed in soil, projecting part with no thalline covering ..... ***philaea***
Perithecia forming projections which are usually partly covered by a layer of thallus ..... ***Sporodictyon terrestre***

Polyblastia agraria Th. Fr. (1864) **Nb IR**

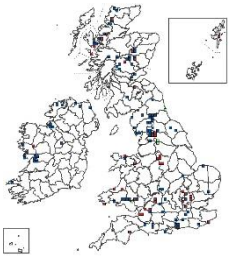
Thallus crustose, superficial, thin and film-like to uneven, green to green-brown, composed of aggregations of goniocysts with brown pigment in the surface cells. Perithecia 140–230 µm diam., smooth, sometimes collapsed when dry, half- to two-thirds immersed, or a few almost superficial, without a thalline covering. Asci 2-spored. Ascospores colourless, becoming brownish when over-mature, narrowly cylindric-ellipsoidal, muriform, (42.5–) 49–60 (–65.5) × (14–) 16–21.5 (–27) µm, length/breadth ratio (2.2–) 2.5–3.4 (–3.6).



On mossy soil on disturbed ground, old metal mines, calcareous dunes, and on stones or bone; occasional, overlooked. Scattered records throughout Britain and Ireland, especially in S.W. England, East Anglia and W. Wales.

Distinguished by the small perithecia lacking an involucrellum, the 2-spored asci and the colourless ascospores. Sérusiaux *et al*. (1999) suggested that *P. agraria* (or at least GBI material identified as that taxon) was close to *Agonimia vouauxii* (B. de Lesd.) M. Brand & Diederich (1999). Tibell & Tibell (2017) suggest that the species represents immature material of *P. helvetica*, another taxon of uncertain affinity.

Polyblastia albida Arnold (1858) **Nb**

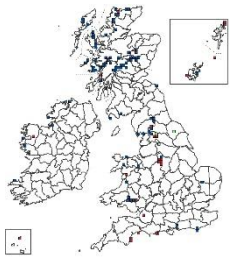


Thallus immersed. Perithecia 0.2–0.4 (–0.5) mm diam., immersed in well-defined pits in limestone, the apex of the perithecium separated from the side of the pit by a fine crack; involucrellum absent; exciple brown throughout, but often paler at the base. Asci 8-spored. Ascospores muriform, colourless, (31–) 36.5–48 (–53.5) × (13–) 18–24 (–26) µm, length/width ratio (1.6–) 1.8–2.3 (–2.6). **BLS 1148**.

On limestone, on unshaded bedrock, scree and occasionally on walls; often where the surface is damp or flushed; frequent. Throughout Britain and Ireland.

This species cannot be separated in the field with certainty from several other pit-forming species in the genera *Polyblastia*, *Staurothele* and *Thelidium*.

Polyblastia cupularis A. Massal. (1852) **Nb**



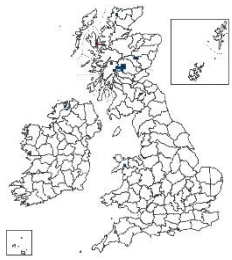
Thallus immersed, partly immersed or superficial, whitish to pale grey, often cracked. Perithecia forming moderately prominent projections 280–540 (–590) µm diam., not covered by the thallus, the apex flat or slightly depressed; involucrellum well-developed, clasping the exciple and spreading slightly. Asci 8-spored. Ascospores colourless, muriform, ellipsoidal to rather broadly ellipsoidal, (21.5–) 26–36 (–45) × (14–) 17.5–23 (–29.5) µm, length/width ratio (1.3–) 1.4–1.7 (–2.1). **BLS 1151**.

On limestone and on slightly calcareous siliceous rocks, including basic metamorphic substrata, rarely on soil. Throughout Britain and Ireland, but rare in S. England.

According to Tibell & Tibell (2017), *Polyblastia cupularis* is a southern European species and all Scandinavian material examined belongs to other species. The status of British collections is not known.

The single British record of *Nectriopsis indigens* (Arnold) Diederich & Schroers (1999) was on this host (from Sutherland).

Polyblastia efflorescens Coppins (1992) **NT**

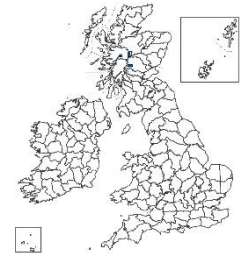


Thallus superficial, of scattered to confluent areoles, often in extensive patches; areoles 0.2–0.4 mm diam., flat to convex, grey-green, soon dissolving almost entirely into soralia; soralia irregularly convex to globose, 0.2–1 mm diam., sometimes ± stipitate and then to 0.7 mm high, pale greyish green (bright green when moist and fresh), soredia *ca* 25–50 µm diam. Perithecia rare, (0.3–) 0.4–0.8 (–0.95) mm diam. in surface view, 0.2–0.48 mm diam. in section, three-quarters to one-quarter immersed, often partly hidden by areoles or soralia; involucrellum well-developed; exciple colourless below. Asci 8-spored. Ascospores muriform, colourless, 36–50 × 22–33 µm. **BLS 1724**.

On more or less vertical rain-sheltered calcareous schist in fissures and moist overhangs; rare. N. Wales, Scotland (Highlands), N.W. Ireland.

This appears to be the only sorediate member of the genus. No molecular data are available, and its affinities need further study. It might be equivalent to *Thelidium papulare* forma *sorediatum* (q.v.)

Polyblastia helvetica Th. Fr. (1865) **Nb**

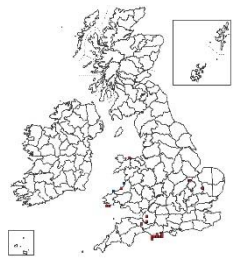


Thallus superficial, film-like, pale grey to blackish grey, often inconspicuous. Perithecia 0.3–0.5 mm diam., more or less immersed, globose; involucrellum absent; exciple densely pigmented above, dilute brown below. Asci (1-) 2-spored. Ascospores muriform, dark brown, cylindric-ellipsoidal, 70–135 × 30–60 µm. **BLS 1156**.

On base-rich mossy soil, montane; very rare. Central Scotland.

Tibel & Tibell (2017) observed that this species is not closely related to *Polyblastia* and probably does not belong in the Verrucariaceae. It is retained here pending an alternative placement.

Polyblastia philaea Zschacke (1933) **Nb**



Thallus superficial, very thin or up to 120 µm thick, pale brownish; when well-developed forming a coherent crust which is smooth to uneven or with indistinct areole-like convex areas to 0.16 mm diam.; a distinct cortex sometimes present, to 30 µm thick, composed of colourless ± elongate cells, overlying a photobiont layer with brown pigment at the top and giving a faintly cartilaginous appearance to the thallus. Perithecia two-thirds to almost completely immersed in the thallus, 0.48–0.60 mm diam.; apex black, not covered by the thallus; involucrellum absent, or at least often scarcely visible as a separate structure; exciple with a thick, darkly pigmented outer layer throughout. Asci 8-spored. Ascospores muriform, colourless, (37.5–) 44–54.5 (–58) × (17–) 19–24 (–24.5) µm, length/width ratio (1.8–) 2.1–2.5 (–2.8). **BLS 0206**.

On calcareous soil; local but probably overlooked. S. England, Wales.

Distinguished by the perithecia immersed in soil and the colourless ascospores. Its affinities are not clear, and no sequences are available. The cortex, when present, resembles that of *P. sendtneri* but is less well-developed. *Agonimia gelatinosa* has almost superficial perithecia and a thallus composed of goniocysts.

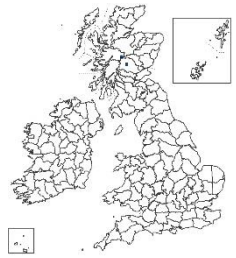
Polyblastia quartzina Lynge (1928) **Nb**

Thallus superficial, smooth or finely granular, somewhat cracked, pale to dark grey, green-grey or dark red-brown; lichenicolous. Perithecia 0.15–0.25 mm diam., half-immersed, often covered up to the ostiole by a thin layer of thallus; involucrellum well-developed, spreading; exciple colourless. Asci 8-spored. Ascospores submuriform, with 2-3 transverse and 0-2 longitudinal septa, colourless, ellipsoidal, 12–20 × 6–10 µm. **BLS 1159**.

On thalli of *Verrucaria latebrosa* and *Ionaspis lacustris* on siliceous, frequently inundated rocks in sunny streams and on *Hydropunctaria maura* in brackish seepage on sea cliffs; very rare. Wales, W., C. & N. Scotland.

Characterized by the small perithecia, well-developed involucrellum and the small submuriform ascospores. The ascospore size range is much larger than the measurements (11–13 × 6–8.5 µm) reported by Tibell & Tibell (2017), presumably from the type which was collected in Novaya Zemlya. More than one species could be involved, and British material should be compared with the collection provisionally identified as *P. plicata* (see key above).

Polyblastia sendtneri Kremp. (1855) **VU (D2)**

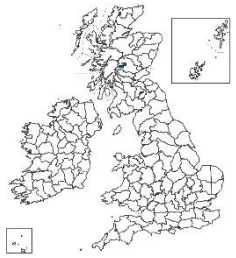


Thallus superficial, pale grey to pale brown, uneven, formed of coalescing convex units 0.15–0.5 mm diam.; surface smooth, slightly glossy, with a slightly translucent cartilaginous appearance; cortex distinct, *ca* 30 µm thick, formed of gelatinized colourless intertwined hyphae 1.5–2 µm diam., the base becoming subcellular and sometimes with brown pigment. Perithecia half- to three quarters-immersed in the thallus and substratum, sometimes a few more exposed, often clustered; apex of the perithecium exposed as a blackish projection to 0.3 mm diam.; involucrellum present, mainly near the apex of the perithecium, scarcely spreading. Asci 8-spored. Ascospores colourless, muriform, (17–) 21.5–25.5 (–28) × (10.5–) 12–14.5 (–16.5) µm, length/width ratio (1.2–) 1.6–2 (–2.2). **BLS 1160**.

On exposed mossy soil over metamorphic rocks, over 900 m, very rare. N. Scotland (Highlands: Ben Lawers, Ben Alder).

A distinctive species, distinguished by the uneven waxy thallus and the small colourless ascospores. The convex thallus granules sometimes have a subsquamulose appearance, resembling species of *Catapyrenium* and *Placidiopsis*.

Polyblastia verrucosa (Ach.) Lönnr. (1848) **Nb**



Thallus superficial, thin and inconspicuous to thick, uneven and cracked; pale grey to pale brownish grey. Perithecia forming projections 0.4–0.7 mm diam., up to half-immersed in thick thalli. Involucrellum well-developed. Asci 8-spored. Ascospores colourless, submuriform with 3-5 transverse and 1-4 longitudinal septa, with 6-10 cells in total, 30–45 (–68) × 15–20 µm. **BLS 1163**.

On calcareous rocks and mica schist at 600 m; very rare. C. Highlands (Breadalbane), N.W. Highlands (Ben Hope), Lake District.

This species should be compared with *Thelidium papulare*, which can have a proportion of submuriform ascospores.

PSOROGLAENA Müll. Arg. (1891)

Thallus crustose or minutely filamentous, cortical cells often with small papillae. **Photobiont** *Auxenochlorella* (Trebouxiophyceae). **Ascomata** perithecia, usually pale brown, rarely dark brown; surface smooth or rarely with projecting hyphae or a ring-shaped collar. **Involucrellum** absent. **Exciple** usually pale, rarely with some brown pigment; cells periclinally elongate in section, sometimes with a surface layer of isodiametric cells. **Hamathecium** of periphyses, interascal filaments absent, gel I+ red. **Asci** 1- to 8-spored, clavate-cylindrical, thickened at the apex when young, I–, K/I–. **Ascospores** transversely septate to muriform, ellipsoidal, smooth, without a perispore, colourless. **Conidiomata** unknown. **Chemistry:** lichen products not detected. **Ecology:** on bark, evergreen leaves, bryophytes on leaves, rock and mossy soil.

The species are inconspicuous and often overlooked, and are united by the crustose to minutely filamentous thalli, usually pale ascomata (rarely dark) and septate to submuriform ascospores. The genera *Leucocarpia* and *Macentina* are synonyms, according to Orange (2013a) and Lücking *et al*. (2016). *Agonimia* is similar, sharing the papillate cortical cells of the thallus, but has dark-pigmented ascomata. Muggia *et al*. (2010) found however that the genera are distinct in phylogenetic terms, and that *P. abscondita* is not closely related to *P. biatorella* and *P. stigonemoides*. The type of *Psoroglaena* has not yet been sequenced.

There is an additional undescribed species growing amongst thin moss and lichen crusts over calcareous rock, with 1(–3?)-septate ascospores (10.5–) 11.5–13.5 (–14.5) × 5.5–6.5 (–7) µm; it was referred to as *P. infossa ined*. by Orange (2013a) and is included in a key to the genus by Lee & Hur (2022).

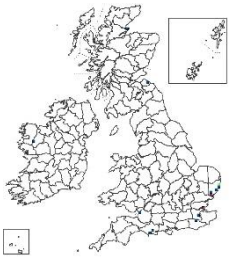
Literature

Lee & Hur (2022), Lücking (2008), Muggia *et al*. (2010), Nyati *et al*. (2007), Orange (2009, 2013a).

1 Amongst bryophytes and other lichens over rock, montane; perithecia three-quarters to completely immersed in the substratum; ascospores muriform..... ***biatorella***
On bark; perithecia prominent; ascospores transversely septate 2

2(1) Thallus minutely filamentous, often disintegrating into soredium-like granules; perithecia 0.2–0.38 mm diam.; ascospores 3- to 5-septate .....***stigonemoides***
Thallus immersed or thin and leprose; perithecia 0.08–0.12 mm diam.; ascospores 1- to 3-septate ..... ***abscondita***

Psoroglaena abscondita (Coppins & Vězda) Hafellner & Türk (2001) **LC**
Thallus superficial, very thin, leprose, dull green, the cortical hyphae with inconspicuous papillae. Photobiont cells globose, 8–12 µm diam, in glomerulose clusters. Perithecia numerous, crowded, minute, globose, 80–120 µm diam., without an involucrellum, somewhat collapsed, pale brown and rather pellucid when dry but assuming their regular globose shape and becoming almost translucent and colourless when wetted. Exciple 10–12 µm thick, composed of thin-walled colourless or pale yellowish angular cells. Asci cylindric-clavate or sometimes pyriform, 45–50 × 10–

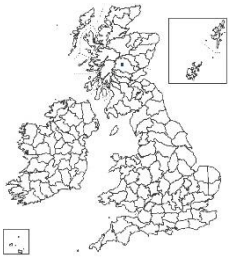


15 µm, 8-spored. Ascospores fusiform-ellipsoidal, ± attenuated at the lower end, at first aseptate but later becoming 1- to 3-septate, 12–20 × 3.5–4.5 µm. **BLS 0860**.

In fissures of bark of *Sambucus* or on stems of shaded *Juniperus* in coastal scrub, also from a cultivated shrub in an urban setting, even found inside a glasshouse; occasional, often overlooked. Probably dispersed throughout England and Scotland.

Psoroglaena biatorella (Arnold) Lücking (2008) **DD**

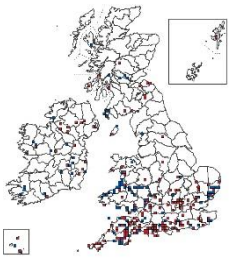
Leucocarpia biatorella (Arnold) Vězda (1969)



Thallus crustose, thinly granular-verrucose, greenish to yellowish white, effuse. Perithecia immersed in the thallus and substrate, with only the pinkish or yellowish ostiolar region exposed, globose or with a slightly elongated ostiolar region, 0.4–0.6 (–0.8) mm diam. Asci 8-spored, 50–70 × 20–30 µm, clavate. Ascospores ellipsoidal, colourless, (25–) 28–38 (–45) × (10–) 11–14 µm, muriform, with up to 9 transverse septa. Conidiomata unknown. Lichen products not detected by TLC. **BLS 1774**.

On bryophyte mats over mica-schist at 1000 m altitude; very rare. Scotland (Perth: Ben Lawers).

Psoroglaena stigonemoides (Orange) Henssen (1995) **LC**



Thallus minutely fruticose, 0.05–0.4 (–0.6) mm thick, densely branched, branches 12–35 µm diam., cylindrical, frequently ascending, sometimes prostrate; cortical cells often with one or more papillae *ca* 1 µm high; thallus locally disintegrating into soredium-like granules 15–40 µm diam. Perithecia 0.20–0.38 µm diam., pale brown, ovoid or obpyriform; exciple 30–80 µm thick, the median layer of elongated cells, the outer layer of isodiametric cells. Asci fusiform-cylindrical. Ascospores (13–) 16–21 × (4–) 5–6 µm, 3-4 (-5)-septate. **BLS 1630**.

On shaded bark in species- and nutrient-poor bryophyte-dominated communities, on *Sambucus* and *Ulmus* and in wound tracks on other trees, in humid situations; frequent. Throughout Britain and Ireland, commoner in the south.

Frequently sterile and easily overlooked as an alga or as moss protonemata. The cylindrical, papillose branches are, however, readily identifiable under the microscope. Sterile granular morphs have bulging cells on the surface of the granules and frequently short lengths of branches intermixed with them.

SPORODICTYON A. Massal. (1852)

Thallus crustose, superficial, grey, greenish grey or brownish, thin to thick, smooth to rimose or areolate or sometimes almost missing. **Photobiont** a green alga, with cyanobacteria (*Nostoc* sp.) occurring as an additional symbiont in cephalodia in some species; hymenial algae absent. **Ascomata** perithecia, medium-sized to rather large, hemispherical and forming projections from the thallus, with a thalline cover at least in the lower part; in section spherical, dark brown throughout or sometimes pale at the base. **Involucrellum** well-developed, in the upper part fused with the peridium. **Asci** very variable in shape, ellipsoidal to clavate, 8-spored or sometimes with fewer spores. **Ascospores** ellipsoidal or often slightly curved with one end being somewhat broader, sometimes ovoid, when mature colourless or ± yellowish to medium or dark brown, muriform. **Conidiomata** unknown. **Chemistry**: lichen products absent. **Ecology**: on siliceous rocks, often where calcareous or moist, more rarely secondarily overgrowing soil and mosses.

Included within *Polyblastia* by Orange *et al*. (2009a), but demonstrated to be phylogenetically distinct by Gueidan *et al*. (2009) and Savić & Tibell (2009). The genus occupies a clade with *Atla* and *Henrica*, and also – surprisingly – with the type species of *Verrucaria*, *V. rupestris*. These genera cannot be reliably separated by morphology.

Species differ morphologically from *Polyblastia* by the ascomata which are overlain, at least partially, with thalline material. Cephalodia, when present, are usually easily identified as brown verrucose well-delimited structures on the surface of the thallus; loose associations with cyanobacteria can occur in *Atla*, but there are no well-defined cephalodia.

In addition to the key here, the species are included in the key to *Polyblastia* and similar species above.

Literature

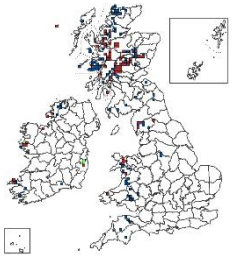
Gueidan *et al*. (2009), Hafellner (2010), Orange (2013a), Orange *et al*. (2009a), Savić & Tibell (2009), Savić *et al*. (2008), Tibell & Tibell (2017).

1 Ascospores brown when mature, with brown pigment visible in cell walls; cephalodia present or not ... 2
Ascospores colourless to yellowish when mature; cephalodia usually present ..... ***terrestre***

2(1) Thallus thin, the perithecia forming projections 0.5–0.7 mm diam. with a typically smooth or slightly verrucose thalline covering; ascospores (47–) 55–65 (–75) µm long, medium brown when mature; cephalodia absent..... ***cruentum***
Perithecia forming projections (0.45–) 0.7–1.2 mm diam., with an irregular and typically coarsely verrucose thalline covering, ascospores (50–) 63–73 (–76) µm long; cephalodia frequent ..... ***schaererianum***

Sporodictyon cruentum (Körb.) Körb. (1863) **LC**

Polyblastia cruenta (Körb.) P. James & Swinscow (1971)



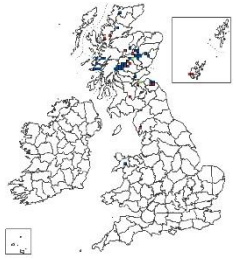
Thallus superficial, usually well-developed, thin, smooth or uneven and with small areole-like convexities, continuous or somewhat cracked, grey-green in shade to brown when well-lit; cephalodia absent. Perithecia forming projections 0.5–0.7 mm diam., often covered to the apex by a thin, smooth or somewhat irregular layer of thallus, often partly lost and exposing the black perithecium. Ascospores muriform, medium brown when mature, occasionally dark brown but with the cell outlines rarely obscured, (47–) 55–65 (–75) × (24–) 29–36 (–42) µm, length/width ratio (1.4–) 1.6–2.1 (–2.5). **BLS 1150**.

On damp siliceous rock; in streams, on flushed bedrock and on stones on damp ground; particularly in the uplands, locally frequent. S.W. and N. England, Wales, montane Scotland, W. Ireland.

Often recognizable in the field by the brown thallus and large, prominent perithecia. The thallus is sometimes verrucose, but not as strongly as in *S. schaererianum* which has darker and larger ascospores. *S. terrestre* differs in the colourless ascospores and usually the presence of cephalodia.

Sporodictyon schaererianum A. Massal. (1852) **Nb**

Polyblastia schaereriana (A. Massal.) Müll. Arg. (1862)



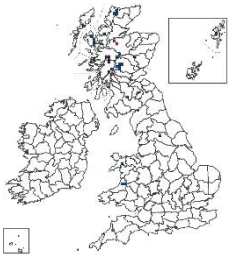
Thallus superficial, well-developed, often of areole-like or lobed convexities 0.1–0.3 mm broad, verrucose or rugose-verrucose, pale grey to pale brown; cephalodia frequent. Perithecia forming projections (0.45–) 0.7–1.2 mm diam., with an irregular and usually incomplete covering of thallus; exposed parts of perithecium ± smooth to strongly roughened. Ascospores muriform, dark brown when mature, the cell outlines often obscured, (50–) 63–73 (–76) × (29–) 33–41 (–47) µm, length/width ratio (1.4–) 1.6–2 (–2.2). **BLS 1162**.

On damp calcareous rock on cliffs and below overhangs, mainly upland. Rare in S.W. & N. England, Wales, Ireland; occasional in Scotland.

Often recognizable in the field by the large perithecia partly covered by irregular patches of thallus. This species has been confused with *Atla alpina*, which differs in the absence of any thalline covering to the perithecium, the slightly larger ascospores, and the absence of cephalodia. *Henrica theleodes* differs in the strongly convex areoles, smooth perithecia and smaller ascospores. Most old records of *H. theleodes* are likely to be *S. schaererianum*.

Sporodictyon terrestre (Th. Fr.) Savić & Tibell (2008) **NT**

Polyblastia terrestris Th. Fr. (1860)



Thallus superficial, sometimes slightly uneven but usually verrucose, of indistinct areole-like units 80–300 µm diam., pale grey to brown; cephalodia frequent. Perithecia forming projections 0.4–0.8 mm diam., covered by an uneven to verrucose layer of thallus, or this layer partly lost. Ascospores muriform, colourless or faintly yellowish, with little or no colour visible in the cell walls except in withered and overmature spores, (39–) 51–68 (–81) × (22–) 26–34 (–40) µm, length/width ratio (1.5–) 1.7–2.3 (–3). **BLS 1157**.

On damp siliceous rocks, occasionally on soil, stones and bryophytes; upland, rare. N. England, N. Wales, Scotland, Ireland.

Distinguished from *S. cruentum* and *S. schaererianum* by the ascospores which are ± colourless when mature and healthy. *S. cruentum* also differs in the absence of cephalodia; the thallus of that species is often darker and smoother than in *S. terrestre*, but the two species overlap in these features.

STAUROTHELE Norman (1853)

Thallus crustose, immersed or superficial, very rarely of narrow, ascending squamules; grey, green or brown. **Cortex** ill-defined. **Medulla** poorly defined or absent. **Prothallus** whitish or brown. **Photobiont** *Diplosphaera* (Trebouxiophyceae). **Ascomata** immersed in the thallus, or prominent, or forming pits in limestone. **Exciple** with or without dark pigment. **Involucrellum** present or absent. **Hymenium** containing living cells of the photobiont. **Hymenial gel** I+ red (I+ blue at very low concentrations of iodine), K/I+ blue. **Hamathecium** of periphyses and periphysoids; interascal filaments absent. **Asci** 1- to 8- spored, verrucarioid; clavate, wall thickened above, with an ocular chamber, after dehiscence with a delicate extruded endotunica, I–, K/I–. **Ascospores** muriform (very rarely 3-septate?), colourless to dark brown, ellipsoidal to cylindrical. **Conidiomata** pycnidia, immersed in the thallus. **Conidia** rod-shaped. **Chemistry**: lichen substances not detected by TLC; brown, K+ darkened or K+ green-brown, acetone-insoluble pigments in thallus and ascomata. **Ecology**: on rock, especially calcareous and damp siliceous rocks, and on soil.

The genus is used here for crustose species with brown muriform ascospores, and with photobiont cells in the hymenium. *Staurothele sens. str.* comprises a number of species with an epilithic thallus and brown ascospores (including the type species *S. clopima*), whereas at least some of the endolithic species (including *S. rupifraga*) belong in the *Thelidium* group of taxa (Gueidan *et al*. 2009, 2014). Species with colourless ascospores and 4- to 8-spored asci are now included in the segregate genus *Nesothele* (Orange & Chhetri 2022). Species with hymenial algae also occur in the *Endocarpon* group, which includes *Endocarpon* (q.v.), *Willeya* Müll. Arg. (1883), and a number of well-known species lacking hymenial algae that are currently retained in *Verrucaria*. *Willeya* is a crustose genus with colourless to pale brown ascospores; species are known from E. Asia, Australia and N. America, but one species has been found on imported rock in the Netherlands (Aptroot 2016). One squamulose species of *Staurothele* s. str. has been confirmed (Heiðmarsson *et al*. 2017).

The algae in the thallus may differ in shape and colour from those in the hymenium, but they belong to the same taxon. According to Thüs *et al.* (2011) the photobiont in at least most species of *Staurothele* belongs to *Diplosphaera*. The precise shape of individual algal cells in the hymenium depends, in part, on whether the cell has recently divided, but the range of shape in each *Staurothele* species is constant and is a useful character in identification. Some reports state that species with 2-spored asci have an I+ blue hymenial gel, but this could not be confirmed using iodine reagents with 0.5-1.5% iodine. *Polyblastia* differs in the absence of hymenial algae.

An apparently undescribed species is known from calcareous soil in lowland grassland in S. Wales (Orange 2013a), which differs from *S. geoica* in its thallus of grey-green areoles, narrower hymenial algal cells and smaller ascospores (23–28 µm in length versus 34–36.5 µm in *S. geoica*). It may be close to *S. maculosa* Breuss & Berger (2022), known from gypsum soils in southern Spain, but that species has ascomata with a well-developed involucrellum.

Literature

Aptroot (2016), Breuss & Berger (2022), Gueidan *et al*. (2007, 2009, 2014), Heiðmarsson *et al*. (2017), Morse & Ladd (2019), Orange (2013a), Orange & Chhetri (2022), Orange *et al*. (2009c), Savić *et al*. (2008), Thüs *et al*. (2011).

Key to species of *Nesothele* and *Staurothele*

1 Perithecia completely or almost completely immersed in well-defined pits in limestone; involucrellum absent; thallus endolithic (rarely thinly epilithic in part) 2
Perithecia not immersed in well-defined pits; sometimes base of perithecium in a shallow pit, but then involucrellum present; thallus various 5

2(1) Ascospores dark brown when mature (often opaque), 4(-5) per ascus ..... ***rupifraga***
Ascospores colourless when mature (rarely brown in *S. bacilligera*?), 2 or 8 per ascus 3

3(2) Hymenial algal cells cylindrical in outline, 2–4 times as long as wide ..... ***bacilligera***
Hymenial algal cells isodiametric to shortly cylindrical or cylindric-ellipsoidal, 1–2 times as long as wide 4

4(3) Asci 8-spored when mature ..... ***caesia***
Asci 2-spored when mature ..... ***guestphalica***

5(1) Ascospores brown; asci 2-spored 6
Ascospores colourless; asci 8-spored 10

6(5) Perithecia ± sessile, without a thalline covering 7
Perithecia with a thalline covering at least at the base, or immersed in thalline warts 8

7(6) Hymenial algal cells oblong to narrowly oblong in outline; thallus grey-brown ..... ***arctica***
Hymenial algal cells isodiametric to broadly ellipsoidal; thallus cream ..... ***rufa***

8(6) Perithecia forming distinct projections above the general level of the thallus, covered by a thalline layer at least in the lower half, but not immersed in swollen thalline warts; hymenial algal cells subglobose to cylindric-ellipsoidal, 1–1.6 times as long as wide ..... ***fissa***
Perithecia immersed in swollen thalline warts which are not strongly raised above the sterile parts of the thallus 9

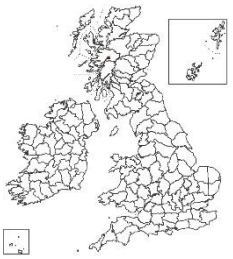
9(8) Hymenial algal cells oblong to narrowly oblong in outline, 2–4.3 times as long as wide ..... ***areolata***
Hymenial algal cells isodiametric to shortly cylindric-ellipsoidal, 1–1.4 times as long as wide ..... ***frustulenta***

10(5) Involucrellum absent; on soil ..... ***geoica***
Involucrellum present; on rock (*Nesothele*) 11

11(10) Thallus endolithic; base of perithecium often in a shallow pit in rock; hymenial algal cells cylindrical, 1.3–2.5 times as long as wide ..... ***Nesothele hymenogonia***
Thallus epilithic, of goniocyst-like units or convex areoles 12

12(11) Thallus of crowded convex cream to grey-green areoles; perithecia half to mostly immersed in areoles ..... ***Nesothele rugulosa***
Thallus of grey-green to brown, often lobed or branched, goniocyst-like units; perithecia usually prominent, one quarter to half immersed in thallus ..... ***Nesothele succedens***

Staurothele arctica Lynge (1937) **Nb**

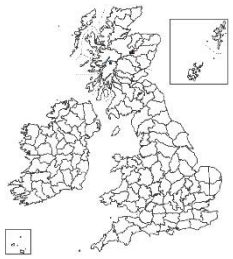


Thallus immersed or superficial and warty, grey-brown, effuse or composed of minute thin areoles. Perithecia sessile, conical, to 0.5 mm diam.; involucrellum present, dark brown to black, paler in the ostiolar region, nearly surrounding the pale brown-walled perithecia; hymenial algal cells oblong to narrowly oblong in outline, 5–8 (–12) × *ca* 4 µm. Asci 2-spored. Ascospores becoming dark brown, ellipsoidal, muriform and many-celled, 32–48 × 12–18 µm. **BLS 1808**.

One record from a snowbed in W. Scotland (Ben Nevis).

The species is characterized by its sessile perithecia on a poorly developed thallus, and ± elongate hymenial algae. The British record must represent one of the southernmost populations of this species, and thus highly vulnerable to climate change.

Staurothele areolata (Ach.) Lettau (1912) **VU (D2)**

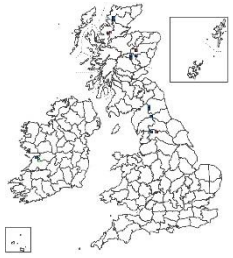


Thallus superficial, brown, areolate, areoles becoming strongly convex; fertile areoles larger than sterile, often constricted below; thallus secondarily cracked into single or small groups of areoles. Perithecia immersed in the thallus, mostly one per areole; either completely immersed and inconspicuous, or with the apex visible as a black disc, or projecting slightly as a low black mound; involucrellum present, confined to the apex of the exciple; hymenial algae oblong to narrowly oblong in side view, 5.7–8 × 2.5–3 µm, 2–4.3 times as long as wide. Asci 2-spored. Ascospores brown, cylindric-ellipsoidal to narrowly cylindric-ellipsoidal, (43–) 45–63.5 × 14–22 µm. **BLS 1679**.

Reported from boulders in melt-water streams from late snow patches; rare. Scotland (Central Highlands).

Distinguished from *Staurothele fissa* by the strongly convex areoles with immersed perithecia. *S. frustulenta* differs mainly in the short hymenial algae. The status of this species in the British Isles needs to be reviewed; a specimen identified as this from Cairn Toul is in very poor condition and is not this species; possibly it is *S. clopima* (Wahlenb.) Th. Fr. (1861).

Staurothele bacilligera (Arnold) Arnold (1885) **NT**

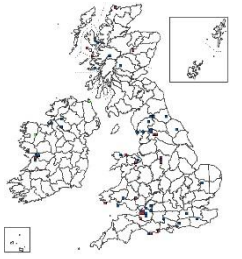


Thallus endolithic, pale grey-brown (the thallus may be exposed as minute brown specks). Perithecia 0.28–0.39 mm diam., immersed in well-defined pits in rock, occasionally projecting slightly when old; exciple brown, darker in the ostiolar region and pale brown below; involucrellum absent; hymenial algal cells 4–8 × 1.5–2 µm, oblong to narrowly oblong in outline, 2–4 times as long as wide. Ascospores colourless (sometimes ± brown later?), muriform, 8 per ascus, ellipsoidal to ovoid, (30–) 32–37.5 × (13–) 14–16.5 (–17) µm. **BLS 1340**.

On unshaded limestone rocks; very local. N. England, C. & N. Scotland, W. Ireland.

Perhaps a species of *Nesothele* (q.v.) but sequences are needed to explore this hypothesis.

Staurothele caesia (Arnold) Arnold (1885) **Nb**



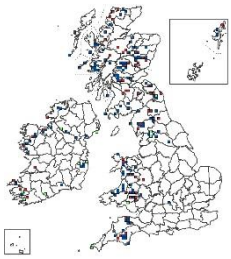
Thallus endolithic, also rarely (perhaps in shade) with a thin epilithic layer, pale grey to brownish grey, the thallus sometimes exposed at surface as brown specks *ca* 30 µm diam.; adjacent thalli sometimes separated by dark lines. Perithecia immersed in well-defined pits, 0.38–0.5 mm diam.; involucrellum absent; hymenial algal cells 3–5 × 3–3.5 µm, isodiametric to shortly cylindrical, 1–2 times as long as wide. Asci 8-spored. Ascospores colourless, to dilute brown when overmature, ellipsoidal, (32.5–)

35–44 (–49) × 20–24.5 (–28) µm. **BLS 1341**.

On mostly unshaded limestone, rarely on mortar; locally frequent. Local in Britain, W. Ireland.

Distinguished by the pale ascospores, 8-spored asci and short hymenial algae. *S. guestphalica* differs in the 2-spored asci.

Staurothele fissa (Taylor) Zwackh (1862) **LC**



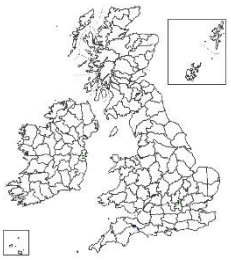
Thallus superficial, continuous or more usually cracked or strongly cracked into islets, pale brown (in shade) to brown; prothallus whitish. Perithecia forming distinct conical-hemispherical projections, the apex brown to black, half to almost completely covered by a layer of thallus; involucrellum present, often confined to the apical part of the exciple, appressed or slightly divergent; hymenial algal cells subglobose to cylindric-ellipsoidal, single cells 3.3–6.5 × 3–5 µm, 1–1.6 times as long as wide, but cells frequently in pairs or tetrads. Asci 2-spored. Ascospores cylindric-ellipsoidal to narrowly cylindrical, pale to mid brown (cell outlines never obscured), (31–) 37–48.5 (–55) × (15–) 16–20 (–25.5) µm, (1.5–) 2–3 times as long as wide. Pycnidia frequent, *Dermatocarpon*-type; conidia rod-shaped or slightly curved, 3–4 × *ca* 1.2 µm. **BLS 1343**.

On frequently or permanently submerged siliceous rocks in unpolluted streams and lakes, avoiding the most acidic waters; locally frequent. N. & W. Britain, almost absent from C. & S.E. England, scattered records in Ireland.

The perithecia are covered, at least partly, by a layer of thallus, but they form distinct mounds above the level of the rest of the thallus; in *S. areolata* and *S. frustulenta*, the perithecia are more or less immersed in swollen areoles which are not as distinct from the sterile parts of the thallus. *S. fuscocuprea* (Nyl.) Zschacke (1913) is an arctic-alpine species which could occur in Britain; currently it is distinguished from *S. fissa* only by the hymenial algal cells which are cylindrical to narrowly cylindrical in outline (cells single or in pairs, never in tetrads?), but the small number of ITS sequences currently available supports the existence of two species.

Sometimes host to the lichenicolous lichen *Placopyrenium cinereoatratum* (q.v.).

Staurothele frustulenta Vain. (1921) **DD NR**

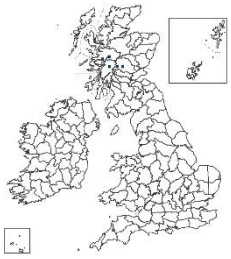


Thallus superficial, brown, areolate, areoles becoming strongly convex; fertile areoles larger than sterile, often constricted below; thallus secondarily cracked into single or small groups of areoles. Perithecia immersed in the thallus, mostly one per areole; either completely immersed and inconspicuous, or with the apex visible as a black disc, or projecting slightly as a low, black mound; involucrellum present, confined to the apex of the exciple or slightly spreading and reaching to base-level; hymenial algae almost isodiametric to shortly cylindric-ellipsoidal, 3.7–5.7 × 3.3–4.5 µm, 1.1–1.4 times as long as wide. Asci 2-spored. Ascospores brown, cylindric-ellipsoidal, (29–) 33.5–46 (–48) × (13–) 14.5–21 µm. **BLS 1981**.

On dry and somewhat nutrient-enriched rocks, concrete or roof tiles; very rare. England (Devon, Essex, Oxford), Ireland (Dublin).

Close to *S. areolata*, which differs mainly in the elongate hymenial algae. See also *S. fissa*.

Staurothele geoica Zschacke (1918) **Nb**

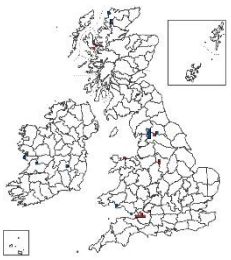


Thallus superficial, dark brown, thin, minutely roughened, comprising goniocyst-like units with brown pigment at the surface. Perithecia forming projections 0.28–0.38 mm diam., one third to two thirds immersed in the thallus, mostly naked but the surface sometimes bearing small patches of thallus; peridium pigmented throughout; involucrellum absent; hymenial algal cells isodiametric to shortly cylindrical. Ascus 8-spored. Ascospores colourless, ellipsoidal, 34–36.5 × 17–17.5 µm. **BLS 1728**.

On soil in montane sites; rare. W. Scotland.

Morphological features suggest that this species may be better placed in *Nesothele* (q.v.) but it is poorly known and no sequences are currently available.

Staurothele guestphalica (J. Lahm ex Körb.) Arnold (1885) **Nb**

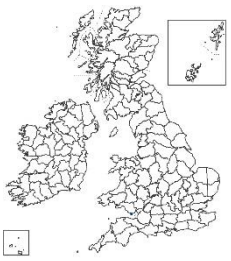


Thallus endolithic, pale grey, adjacent thalli often separated by dark lines. Perithecia immersed in well-defined pits in rock, 0.28–0.4 mm diam.; involucrellum absent; hymenial algal cells 3–6 × 3–5 µm, isodiametric to shortly cylindrical, 1–1.5 times as long as wide. Asci 2-spored when mature. Ascospores colourless, ellipsoidal to rather narrowly ellipsoidal, (33–) 41–49 (–51) × (17–) 19–23 (–25.5) µm. **BLS 1617**.

On limestone; rare. S.W. & N. England, S. and N. Wales, Scotland, Ireland.

Close to *S. caesia*, but with 2-spored asci and slightly larger ascospores. Immature asci may initially contain more than 2 spores, but only two become mature.

Staurothele rufa (A. Massal.) Zschacke (1913) **EN (D)**

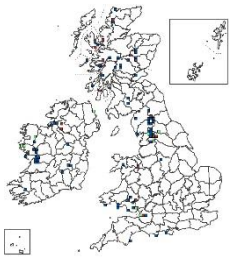


Thallus epilithic, pale cream but thin and indistinct, to 40 µm thick. Perithecia forming black conical-hemispherical projections 0.36–0.48 mm diam., without a covering of thallus, surface rough and sometimes with indistinct radial fissures; involucrellum well-developed; perithecia forming shallow pits in rock; hymenial algal cells 2.5–3.7 × *ca* 2.5 µm, isodiametric to broadly ellipsoidal, 1–1.5 times as long as wide. Asci 2-spored. Ascospores brown, cylindric-ellipsoidal, (34.5–) 36–40.5 (–42) × (11.5–) 12–18 (–20) µm. **BLS 1345**.

On Liassic limestone in a disused coastal quarry; rare. S. Wales (near Porthkerry).

The single British specimen was collected in 1964 and the species has not been collected since, despite searches of likely sites.

Staurothele rupifraga (A. Massal.) Arnold (1880) **Nb**



Thallus endolithic, pale brownish grey, sometimes with minute brown specks on the rock surface. Perithecia immersed in well-defined pits in rock, 0.32–0.38 mm diam.; involucrellum absent; hymenial algae isodiametric to shortly cylindrical, 3–4 × *ca* 3 µm. Asci 4(-5)-spored. Ascospores ellipsoidal, brown, usually becoming opaque when mature so that only cells at the apparent margin of the spore can be seen, (38.5–) 44–55.5 (–62) × (18–) 20–25 (–27.5) µm. **BLS 1347**.

On unshaded or slightly shaded limestone, typically on more or less north-facing or slightly damp (but not flushed) surfaces; locally frequent. Throughout Britain and Ireland.

THELIDIUM A. Massal. (1855)

Thallus crustose, immersed or superficial, white, green, grey, or brown; pigment, when present, brown or dull green, rarely orange-yellow or purple; rarely with soredia. **Cortex** poorly defined. **Photobiont** a green alga. **Ascomata** perithecia, black, superficial or immersed in thallus or rock. **Involucrellum** often present. **Hamathecium** of periphyses and periphysoids, interascal filaments absent; gel I+ red (+ blue at very low concentrations of I), K/I+ blue. **Asci** narrowly ellipsoidal to clavate, K/I–,wall thickened above, ocular chamber usually present; dehiscence by extrusion of a delicate endotunica as a long rostrum, 8-spored. **Ascospores** 1- to 3 (-7)-septate (occasionally a small proportion of ascospores with 1-2 longitudinal septa), colourless, broadly to narrowly ellipsoidal or cylindric-ellipsoidal, smooth, wall thin or only slightly thickened, perispore not detected. **Conidiomata** unknown. **Chemistry**: a quinone-like, acetone-soluble pigment present in one species; a small range of acetone-insoluble pigments present, including (1) brown, K+ darker brown or greenish brown, (2) reddish brown, K+ dark grey-brown. **Ecology**: mostly on rock, including

limestone and siliceous rock, mainly where damp or calcareous, including freshwater habitats; occasionally on soil.

Traditionally defined by the crustose thallus, lack of hymenial algae, and septate ascospores. Species with these characteristics are found mainly in the *Thelidium* group of Verrucariaceae (Gueidan *et al.* 2009), together with species traditionally placed in *Polyblastia* and others, but *T. methorium* and *T. papulare* are related to *Verrucaria latebrosa*. *T. impressum* belongs in *Parabagliettoa*.

Literature

Gueidan *et al.* (2009), Orange (2009e, 2013a), Savić *et al.* (2008), Thüs *et al.* (2011), Thüs & Nascimbene (2008).

1 Perithecia immersed in pits in calcareous rock, involucrellum absent, thallus endolithic 2
Perithecia prominent, or immersed in a thallus, at most forming shallow depressions in rock 4

2(1) Ascospores 1-septate ..... ***decipiens***
Ascospores 3-septate 3

3(2) Ascospores (20–) 27.5–35 (–47) µm long; perithecia 160– 340 µm diam.; a yellow, K+ violet pigment often present in the thallus ..... ***fontigenum***
Ascospores (28.5–) 36–46 (–54) µm long, perithecia (170–) 260–520 (–660) µm diam.; yellow, K+ violet pigment absent ..... ***incavatum***

4(1) Involucrellum absent 5
Involucrellum present 7

5(4) Ascospores 1-septate 6
Ascospores 3-septate ..... ***zwackhii***

6(5) Thallus with the photobiont arranged irregularly, in at most weakly defined goniocyst-like units; involucrellum thin, fused with the upper exciple but clearly exterior to it ..... ***rehmii***
Thallus with the photobiont cells arranged in small groups, in goniocyst-like structures; involucrellum absent ..... ***minutulum***

7(4) Ascospores 1-septate 8
Ascospores 3(–5)-septate 15

8(7) Ascospores (9–) 11–14.5 (–15.5) µm long; thallus endolithic ..... ***Parabagliettoa impressa***
Ascospores >16 µm long (mean spore size over 20 µm long) 9

9(8) Involucrella confluent to form a dark layer underlying the green parts of the thallus; pigment in the involucrellum reddish-brown, K+ dark grey-brown; ascospores (24–) 25.5–30.5 (–34) µm long ..... ***fumidum***
Involucrella not confluent; pigment in involucrellum brown, K– or K+ darker brown 10

10(9) Perithecia forming projections which are covered except at the apex by a layer of thallus..... 11
Perithecial projections not covered by thallus 12

11(10) Thallus thin, pale grey-green to dark brown; perithecial projections conical-hemispherical, 0.24–0.45 (–0.5) mm diam.; on siliceous rocks in streams ..... ***pluvium***
Thallus thick, brown, usually densely white pruinose and then looking bluish grey; perithecial projections 0.5–0.6 mm diam., often constricted at the base; on limestone or siliceous rock affected by shell sand ..... ***dionantense***

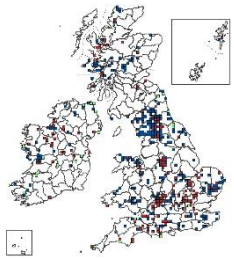
12(10) Ascospores 26–46 µm long; thallus usually light grey-brown to dark brown 13
Ascospores (16.5–) 21–28.5 (–36.5) µm long; thallus usually white, grey or grey-green 14

13(12) Perithecial projections (0.3–) 0.4–0.7 (–0.74) mm diam.; ascospores (25–) 30–38 (–49) × (10–) 13–16.5 (–20) µm ..... ***methiorum***
Perithecial projections 0.25–0.51 µm diam.; ascospores 26–39 × 9–18 µm ..... ***submethiorum***

14(12) Perithecial projections 160–240 µm diam. ..... ***rehmii***
Perithecia projections (240–) 300–700 (–860) µm diam. ..... ***pyrenophorum***

15(7) Ascospores (20–) 27.5–35 (–47) µm long; perithecial projections 100–360 µm diam.; a yellow, K+ violet pigment often present in the thallus ..... ***fontigenum***
Ascospores (27–) 36–50 (–65) µm long; perithecial projections (360–) 400–800 (–880) µm diam.; yellow, K+ violet pigment absent ..... ***papulare***

Thelidium decipiens (Nyl.) Kremp. (1861) **LC**



Thallus endolithic, white, grey or cream, or discoloured brown. Perithecia 0.2–0.4 mm diam., immersed in well-defined pits in rock, the apex occasionally projecting when old and usually separated from surrounding rock by a thin crack; ostiole inconspicuous; involucrellum absent; exciple brown throughout (blackish in thick section, translucent brown in squash preparation), K– to K+ slightly darker brown or greenish-brown. Ascospores 1-septate, (19.5–) 25–32.5 (–41) × (9.5–) 11.5–14.5 (–19) µm, length/width ratio (1.5–) 1.9–2.6 (–3.2). **BLS 1385**.

On limestone, mortar and calcareous sandstone; frequent. Widespread in Britain and Ireland.

Reported as a host for *Lichenothelia renobalesiana* and *Opegrapha hochstetteri*.

Thelidium dionantense (Hue) Zahlbr. (1921) **NE**

Thallus epilithic, brown, glossy but usually densely white pruinose and then looking bluish grey. Perithecia immersed in superficial thallus warts which often have a constricted base, 0.5–0.6 mm diam.; involucrellum carbonized only in the upper half, clypear region visible from above up to 0.3 mm diam. Asci 8-spored. Ascospores colourless, ellipsoidal, (0-)1-septate, 23–32 × 12–15 µm. **BLS 2844**.

On granite overblown by shell sand in machair, Scotland (Iona); in Europe reported from dry limestone.

Known from a single record in Britain and Ireland, misidentified as a saxicolous morph of *Thelotrema lepadinum* which is superficially similar but has larger ascomata with broader openings, and quite different microscopic features. *Thelidium pyrenophorum* is similar but has perithecial projections that are not covered with thalline tissue, and *T. pluvium* has smaller conic-hemispherical projections that are not constricted at the base, and occurs in streams and on dripping rock faces.

Thelidium fontigenum A. Massal. (1856) **Nb**

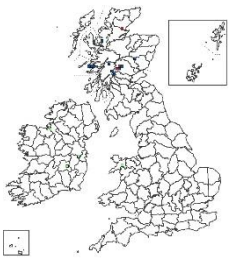
Thallus immersed or superficial, thin, continuous or in small flecks; white, grey, dark brown, orange-yellow or purple-red; often with flecks or extensive patches of a yellow, K+ violet pigment. Perithecia immersed in pits in rock, or forming projections 0.10–0.36 mm diam.; involucrellum absent, or developed around the ostiole in immersed perithecia; or thin, spreading down from the apex and often reaching down to the substrate in projecting perithecia; perithecia 0.16–0.34 mm diam., colourless to brown below. Ascospores 3-septate, (20–) 27.5–35 (–47) × (9–) 11–14 (–17) µm, length/width ratio (1.8–) 2.2–2.8 (–4). Thallus (yellow areas) K+ purple (quinone-like pigment). **BLS 1900**.

On limestone, mortar, tufa and on siliceous stones, especially where damp; local. Widespread in Britain and probably also in Ireland.

Distinguished by the small perithecia which are either in pits or which have an involucrellum when projecting, and the 3-septate ascospores; there is a gradation between specimens with immersed perithecia on limestone and

those with projecting perithecia on siliceous rock. *T. zwackhii* differs in the prominent perithecia without an involucrellum, *T. papulare* differs in the larger perithecia with a more massive involucrellum. A yellow, K+ violet or purple pigment is usually present, at least in small quantities; this pigment is absent or extremely rare in other species of the genus; in the thallus it can appear either orange-yellow or purple-red. See also *T. incavatum*.

Thelidium fumidum (Nyl.) Hazsl. (1884) **NT**



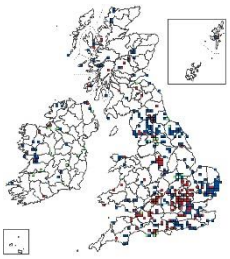
Thallus superficial, dark brown to blackish brown, to 0.21 mm thick, cracked, with a thick dark basal layer. Perithecia partly immersed in the thallus, forming low to moderate projections 0.26–0.63 mm diam., covered by a layer of thallus below but free above; involucrellum thick, enclosing the perithecium, upper margin spreading sideways and downwards, continuous with the basal layer of the thallus, pigment dark reddish brown, K+ dark grey-brown; perithecium in section 0.18–0.36 mm diam. Ascospores 1-septate, (24–) 25.5–30.5 (–34) × (9–) 10–12.5 (–15) µm, (1.7–) 2.2–2.9 (–3.8) times as long as wide. **BLS 1386**.

On damp, slightly calcareous mica-schist rocks above 550 m altitude; rare. Scottish Highlands.

Distinguished from other *Thelidium* species by the well-developed basal layer of the thallus (perhaps better interpreted as spreading and confluent involucrella); the pigment in the basal layer and involucrellum also differs subtly from other species (similar to the pigment in *Parabagliettoa*). The description applies to British material; specimens seen from Europe (including the type of *T. fumidum*) occur on distinctly calcareous rocks and lack a dark basal layer and are probably not the same species.

Thelidium incavatum Mudd (1861) **LC**

? *Polyblastia dermatodes* A. Massal. (1855)



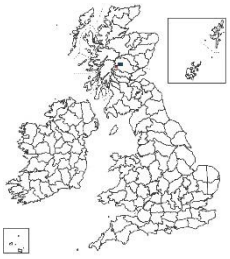
Thallus endolithic, white, grey or discoloured brown. Perithecia (0.17–) 0.26–0.52 (–0.66) mm diam., immersed in well-defined pits in rock, occasionally the apex projecting; involucrellum absent; exciple brown throughout (blackish in thick section, translucent brown in squash preparation), K– or K+ slightly darker brown or greenish-brown. Ascospores 3(–5)-septate, occasionally with 1(-2) longitudinal septa, (28.5–) 36–46 (–54) × (11–) 13.5–16.5 (–20) µm, length/width ratio (1.8–) 2.5–3 (–3.9). **BLS 1389**.

On limestone and other calcareous rocks; frequent. Throughout Britain and Ireland.

Characterized by the relatively large perithecia immersed in pits, absence of an involucrellum and mostly 3-septate spores. *T. fontigenum* differs in the smaller perithecia, smaller ascospores and frequently by the presence of an orange, K+ violet pigment.

Polyblastia dermatodes is said to differ in the submuriform ascospores, but the number of longitudinal septa is variable even within a single specimen and it is difficult at present to make a clear distinction between the two species. There appears to be little or no correlation between the number of septa, the size or length/width ratio of the ascospores and the size of the perithecia; in addition, many of the collections which have submuriform spores appear to be in poor condition and some spores are clearly abnormal. This group of taxa requires careful revision, and if the synonymy is confirmed the epithet *dermatodes* would have nomenclatural priority.

Thelidium methorium (Nyl.) Hellb. (1875) **Nb**



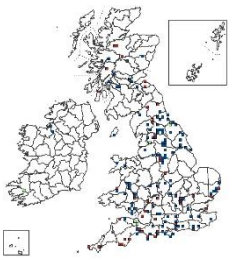
Thallus epilithic, pale grey- to dark brown (rarely greenish-grey in shade), usually rimose, 0.08–0.24 mm thick. Perithecia forming projections (0.3–) 0.4–0.7 (–0.74) mm diam., black, sometimes appearing grey or brown due to a very thin, pale surface layer; not covered by the thallus; ostiole inconspicuous or visible as a pale dot, depressed or not; involucrellum well-developed, sometimes reaching to the level of the base of the perithecium; perithecium in section 0.3–0.5 mm diam., the wall almost colourless to pale brown or green-brown (dark in thick section), K+ greenish brown to green. Ascospores 1-septate, (25–) 30–38 (–49) × (10–) 13–16.5 (–20) µm, length/width ratio (1.6–) 2–2.7 (–3.5). **BLS 1729**.

On mica-schist on a damp outcrop and in a stream; very rare. Scotland (Central Highlands).

The description applies mainly to material from outside Britain; in parts of N. Europe this is a frequent and

conspicuous species of wet siliceous rocks. Usually easily identified by the brown, epilithic thallus, large perithecia and the large, 1-septate ascospores. *T. submethorium* from C. Europe and Finland (and recently recorded from Britain; q.v.) is morphologically similar though not closely related; it has smaller perithecia (250–510 µm diam.) and marginally smaller ascospores 26–39 µm in length. *T. pyrenophorum* differs in the smaller spores, the thallus often white or grey even when well-illuminated and it occurs on rocks which are usually not irrigated. *T. papulare* differs in the 3 (-5)-septate ascospores.

Thelidium minutulum Körb. (1863) **LC**

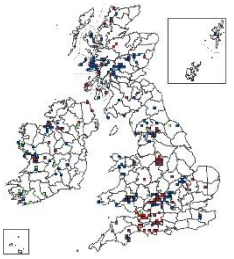


Thallus superficial, pale grey-green to dark brown, in numerous small patches or continuous, usually not cracked, thin, 30–160 µm thick. Perithecia very prominent or up to half-immersed in the thallus, (0.08–) 0.1–0.26 (–0.34) mm diam.; ostiole inconspicuous; involucrellum absent; exciple brown above, K– or K+ slightly darker brown or greenish brown, usually colourless at the base. Ascospores 1-septate, (12–) 19–25 (–30.5) × (5–) 8.5–10.5 (–13) µm, length/width ratio (1.2–) 2.1–2.6 (–3.3). **BLS 1391**.

On siliceous rocks, limestone, brick and soil; often on small stones; in woodland, beside streams, or on waste ground; frequent. Widespread in Britain and Ireland.

Distinguished by the prominent perithecia without an involucrellum and the 1-septate ascospores. *T. zwackhii* differs in the 3-septate ascospores.

Thelidium papulare (Fr.) Arnold (1885) **LC**



Thallus immersed to superficial, white, grey or brown, superficial thallus 0.05–0.15 (–0.2) mm thick. Perithecia forming projections (0.35–) 0.4–0.8 (–0.9) mm diam., blackish or appearing grey or brown due to a very thin pale surface layer, not covered by the thallus; ostiole often visible as a pale dot, sometimes shallowly depressed; involucrellum well-developed; perithecium in section (0.22–) 0.25–0.55 (–0.62) mm diam., wall brown, K– or K+ slightly darker brown or greenish brown. Ascospores 3(-5)-septate, occasionally with 1 or more longitudinal septa, comprising 4(–7) cells, (27–) 36–50 (–65) × (10.5–) 14–18.5 (–23) µm, length/width ratio (1.7–) 2.3–3 (–3.9). **BLS 1394**.

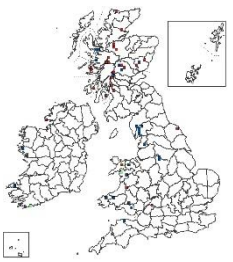
On limestone, mica-schist, calcareous sandstone and mudstone; often on damp rocks; locally frequent. Widespread in Britain and Ireland.

Characterized by the relatively large perithecia, well-developed involucrellum and 3(-5)-septate ascospores. Specimens from limestone, with an immersed thallus, tend to have smaller ascospores with fewer septa than specimens from siliceous rocks which have a superficial thallus. *T. methorium* and *T. pyrenophorum* are similar but differ in the 1-septate ascospores. See also *T. fontigenum*. *Polyblastia verrucosa* has consistently submuriform ascospores.

A host for *Stigmidium tetrasporum* Etayo (1994).

Thelidium papulare forma **sorediatum** Coppins (1992) [**BLS 1394**] has a cracked grey-brown to mid brown thallus; soralia are present, mainly scattered and irregularly linear, developing along cracks in the thallus, brown, abrading to dull pale-green. Perithecia as in forma *papulare*. It is recorded from slightly calcareous schist or on limestone, at altitudes of 120–900 m; rare. Wales (Caernarvonshire), N.W. & C. Scotland, Outer Hebrides (Lewis).

Thelidium pluvium Orange (1991) **Nb**

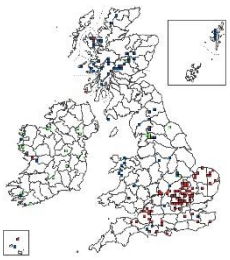


Thallus epilithic, 35–85 µm thick, pale grey-green to dark brown, continuous to sparingly rimose. Perithecia forming conical-hemispherical projections 0.24–0.45 (–0.5) mm diam., covered except at the apex by a layer of thallus, lacking at the apex; ostiole inconspicuous, not depressed; involucrellum relatively thin and weakly developed, present only surrounding the upper half of the exciple and scarcely spreading, or spreading sideways and downwards and nearly reaching to base-level, brown, K– or K+ darker brown or greenish-brown; perithecia in section 0.2–0.35 mm diam., brown at the apex, colourless below. Ascospores 1-septate, (19.5–) 24–30 (–37) × (7–) 10.5–14 (–18) µm, length/width ratio (1.7–) 1.9–2.5 (–3.1). **BLS 1812**.

On siliceous rocks in streams or on dripping rock-faces; local. Wales, S.W. and N. England, Scotland, W. Ireland.

Characterized by the thalline covering to the perithecia, the presence of an involucrellum and the 1-septate spores. Possibly overlooked as *Verrucaria hydrophila*.

Thelidium pyrenophorum (Ach.) Mudd (1861) **Nb**



Thallus superficial, white or grey, rarely brownish, or immersed, cracked or not. Perithecia forming projections (0.24–) 0.3–0.7 (–0.86) mm diam., not covered by the thallus, black or sometimes grey due to a superficial colourless layer; ostiole inconspicuous or somewhat depressed; involucrellum well-developed; exciple colourless to brown below. Ascospores 1-septate, (16.5–) 21–28.5 (–36.5) × (7.5–) 10–13.5 (–16.5) µm, length/width ratio (1.5–) 1.9–2.4 (–3.3). **BLS 1395**.

On limestone, mortar, mica-schist and base-rich siliceous rocks; occasional. Widespread in Britain and Ireland.

The species is variable in the degree of development of the thallus, the size of the perithecia and the size of the ascospores, but there appears to be little correlation between these features. See also *T. methorium* and *T. papulare*.

Thelidium rehmii Zschacke (1921) **NE**

Thallus grey-green, diffuse, continuous, uncracked or with local irregular cracks; algae arranged in at most weakly defined goniocyst-like units. Perithecia black, forming moderately convex projections 160-240 µm diam., ostiole inconspicuous or visible as a very small depression; involucrellum thin, the pigmented part *ca* 30 µm thick at its widest point, appressed to the upper exciple but clearly exterior to it, reaching to the level of or just below the thallus surface; pigment brown, K+ darker brown. Ascospores 1-septate, (20–) 21.5–25 (–26.5) × (10–) 10.5–12 (–12.5) µm, (1.7–) 1.9–2.2 (–2.5) times as long as wide. **BLS 2652**.

On siliceous stones and old tile fragments in shaded but not particularly moist habitats; probably widespread but overlooked. Scotland (W. Inverness), Wales.

Although the involucrellum is thin, its presence can already be suspected under the dissecting microscope; the perithecia are less prominent than in *Thelidium minutulum*, and are never collapsed when dry as in some specimens of that species. The thallus is more continuous than in *T. minutulum*, less granular, and with a weaker organisation into goniocyst-like units.

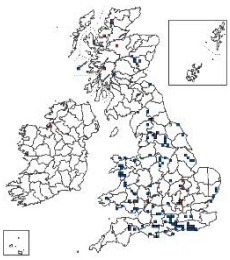
Thelidium submethiorum (Vain.) Zschacke (1920) **NE**

Thallus olive, brown or brown-grey to dark blue-grey, thin to thick (10–130 µm thick), smooth or sometimes slightly rimose-cracked, ± subgelatinous when wet, the margin hardly pigmented; cortex and basal layer absent. Perithecia prominent, 150–275 µm diam., with a well-developed involucrellum 250–510 µm diam., either confined to the apical region or reaching down to the base of the perithecium, the perithecial projections ± hemispherical with a prominent sunken ostiole. Ascospores 1-septate, 26–39 × 9–18 µm, without a perispore. **BLS 2811**.

One recent British record; on siliceous stone in lead mine, Wales (Caernarvon).

Differs from *Thelidium methiorum* in the size of perithecia and ascospores, though there is some overlap in both characters. The description has been abstracted from Thüs & Schultz (2009), which is apparently the only recent account of the species.

Thelidium zwackhii (Hepp) A. Massal. (1855) **Nb**



Thallus superficial, grey-green to dark brown, diffuse, thin, in small flecks or forming a continuous or slightly cracked crust, formed of goniocyst-like units 20–45 µm diam., often with brown pigment in surface cells. Perithecia prominent or half-immersed in thallus, 0.1–0.29 mm diam. in surface view, sometimes collapsing into a concave shape when dry; involucrellum absent; perithecia 0.14–0.3 mm diam. in section, brown above, usually colourless at the base. Ascospores 3-septate, (20–) 26.5–33 (–39) × (8.5–) 10.5–13 (–15) µm, (1.8–) 2.3–2.8 (–3.5) times as long as wide. **BLS 1392**.

On limestone, chalk and siliceous rocks, usually on small stones and on soil; in moist situations, apparently a rapid colonizer of short-lived niches; in woodland, waste ground and by streams; frequent. Widespread in Britain, W. Ireland (but there probably under-recorded).

Distinguished by the small, prominent perithecia without an involucrellum and the 3-septate ascospores. *T.*

fontigenum differs in the perithecia being either immersed in pits, or with an involucrellum; *T. minutulum* differs in the 1-septate ascospores.

TRIMMATOTHELE Norman ex Zahlbr. (1903)

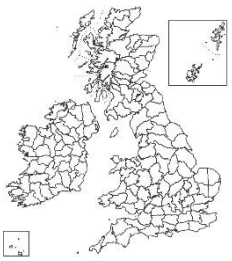
Thallus crustose. **Photobiont** chlorococcoid. **Ascomata** perithecia, black. **Hamathecium** of periphyses; interascal filaments absent; hymenial gel I± yellowish, K/I+ blue. **Asci** ± clavate, multispored, *Verrucaria*-type, K/I–. **Ascospores** ± ellipsoidal, aseptate, colourless. **Conidiomata** not known. **Chemistry**: lichen substances absent. **Ecology**: on rock or bark.

Similar to *Verrucaria* except for the multispored asci. A little-known genus, with two European species, only one of which occurs in our area. Considered to be a synonym of *Verrucaria* by Ertz & Diederich (2004), but found to occupy an independent clade (along with an an unnamed species assigned to *Verrucaria*) by Savić *et al*. (2008) and Gueidan *et al*. (2009).

Literature

Coppins (2009), Ertz & Diederich (2004), Gueidan *et al*. (2009), Savić *et al*. (2008).

Trimmatothele perquisita (Norman) Norman ex Zahlbr. (1903) **Nb**



Thallus endolithic to epilithic and then areolate, to 0.12 mm thick, brown (but often overgrown by black cyanobacterial cells), matt, cracked and secondarily areolate; photobiont cells 5–10 × 5–8 µm, dividing by binary fission. Perithecia 0.25–0.5 mm diam., half to three-quarters immersed in the thallus; involucrellum well-developed, more or less conical, reaching to the base of the perithecium; exciple dark brown throughout, 70–80 µm thick above, 50–60 µm thick at the sides and base; periphyses to 30 µm long, *ca* 1.5 µm diam. Asci 50–65 × 13–17 µm, *ca* 64-spored, cylindric-clavate. Ascospores (4.5–) 5.5–8 (–11) × 2.5–3.5 (–5.5) µm, ellipsoidal to cylindric-ellipsoidal. **BLS 1439**.

On crystalline limestone at *ca* 1000 m; very rare. N. Scotland (E. Inverness: Ben Alder; Argyll: Ben Sgulaird).

The ascospores of the Scottish collections are slightly longer than those of the type from Norway.

VERRUCARIA Schrad. (1794)

Thallus crustose, immersed or superficial, white, green, grey, dark brown, black or purplish; rarely with vegetative propagules (blastidia). **Cortex** poorly defined; pigment, when present, usually brown, more rarely green, blue-green or red-purple; epinecral layer sometimes present. **Photobiont** green, including *Diplosphaera* and *Elliptochloris* (Trebouxiophyceae), *Dilabifilum* (Ulvophyceae) and *Heterococcus* (Xanthophyceae); occasionally absent (in species that probably do not belong in Verrucariaceae). **Ascomata** perithecia, black (except for rare albino forms), sometimes forming pits in limestone. **Involucrellum** often present. **Hamathecium** of periphyses and periphysoids, interascal filaments absent; gel hemiamyloid, I+ red (+ blue at very low concentrations of I), K/I + blue. **Asci** clavate, I–, the wall thickened above, ocular chamber usually present; dehiscence by extrusion of an endotunica to form a delicate rostrum. **Ascospores** 8 (very rarely 4) per ascus, aseptate, colourless, broadly to narrowly ellipsoidal or cylindric-ellipsoidal, smooth, the wall thin or only slightly

thickened, perispore often present, or very rarely with a small gelatinous appendage at each end. **Conidiomata** pycnidia, immersed in the thallus. **Conidia** rod-shaped, aseptate, colourless. **Chemistry**: lichen products absent except for a quinone-like red pigment occurring very rarely; a small range of acetone-insoluble pigments present, including (a) brown, K+ darkening, (b) reddish brown, K+ dark grey-brown, (c) dull green, K–. **Ecology**: mostly on rock, including limestone and (often damp) siliceous rock, including freshwater and littoral maritime habitats; occasionally on soil or bark, or parasitic on lichens.

A polyphyletic genus with at least 300 currently accepted species, but many are poorly known. Various groups treated under *Verrucaria* by Orange *et al*. (2009b) are now recognized as phylogenetically distinct genera, including *Baglietto*a for *V. baldensis*, *V. calciseda* and *V. parmigerella*; *Hydropunctaria* for freshwater and marine species with black thalli; *Parabagliettoa* for *V. cyanea* and *V. dufourii*; *Placopyrenium*, *Verrucula* and *Verruculopsis* for clades that mostly contain lichenicolous species; and *Wahlenbergiella* for the marine species *V. mucosa* and *V. striatula.*

The type of *Verrucaria*, *V. rupestris* Schrad. (1794) has been shown by Savić *et al.* (2008) and Gueidan *et al.* (2009) to occupy an isolated position within the *Sporodictyon* clade in the Verrucariaceae, sister to the genus *Henrica*. *V. rupestris* has not been reported from Britain and Ireland, and it is possible that there are no genuine species of *Verrucaria* present in our area. Numerous other species are known to belong to a range of groups of taxa in the Verrucariaceae, primarily those referred to as the *Endocarpon* and *Staurothele* clades, but the generic limits in these clades need further study and the necessary combinations have not been made. They are retained in *Verrucaria* here for convenience, with notes on phylogenetic position provided for those species for which molecular data are available.

There are few clear-cut morphological characters to assist identification and these are rather variable in response to the environment. It is recommended that each specimen is carefully examined and the structure understood before identification is attempted. Despite this, most species can be recognised in the field or under a dissecting microscope. Characters to note include: thallus immersed or superficial to various degrees, subgelatinous or not; size of perithecia and degree of immersion in the thallus or in pits in limestone, degree of development of involucrellum if present (in section), size of ascospores. So-called ‘subgelatinous’ thalli are found in some freshwater and maritime species; the thallus is often translucent when fresh and wet (preserved specimens should not be rewetted), very smooth when dry, and uncracked (but fine cracks can develop in dried collections). In section the photobiont and fungal cells are often in distinct columns, the fungal cells tightly coherent and without intercellular spaces and sometimes with thickened walls (the distinction is less clear in some maritime species, which have a cracked thallus but a ‘subgelatinous’ cell arrangement). Non-gelatinous thalli tend to have the cells irregularly arranged, with some small air-spaces between the cells; these air-filled spaces often look dark in a section mounted in water. In some species the thallus is composed of goniocyst-like units, which appear in section as distinct or indistinct isodiametric arrangements of photobiont cells enclosed by fungal cells. Some species, mainly those with endolithic thalli, erode distinct pits in limestone in which the perithecium is contained; in such species where an involucrellum is absent there is typically a fine crack around the apex of the perithecium (but may be absent on soft substrates), representing the sides of the pit, but in endolithic species where an involucrellum is present there is usually no such crack.

Within the perithecium, the exciple is the structure which immediately surrounds the hymenium (centrum). Pigmented tissues external to the exciple are regarded as the involucrellum. Where the hymenium is surrounded by a single structure, pigmented or not, this is regarded as comprising only excipular tissue, and an involucrellum is considered to be absent. The form of the involucrellum should be studied in vertical sections of the perithecium; these are often best sectioned *in situ*.

Ascospore size is an important character, but numerous spores should be measured if possible, as abnormal, immature or overmature spores may be present. The presence of a perispore is more widespread in the genus than was thought, but requires more study; sometimes it may be overlooked as an apparently thickened spore wall; some immature spores from broken asci may have sheaths of

colourless material, but these are often ephemeral.

Vegetative propagules (blastidia) are currently known in the region only in *V. macrostoma* and *V. nigrescens*.

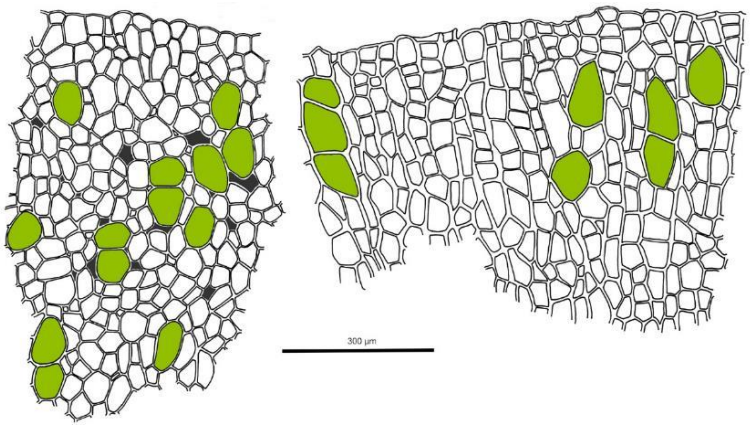
Poorly developed, abnormal or damaged specimens may be difficult to name; in this case the best approach is to measure numerous ascospores and compare the size range with the table to suggest likely species.

Verrucaria phaeosperma Arnold (1874) [**BLS 2347**] was included in Orange *et al*. (2009b) but probably does not belong in Verrucariaceae and is not included in the keys. It is lichenicolous on lichens on limestone, including *Hymenelia prevostii* and *Thelidium decipiens*; the perithecia occur in pits, the hymenial gel is I+ red, K/I+ blue (as in Verrucariaceae), the ascospores are brown, aseptate, (16–) 17–21.5 (–24) × (8–) 8.5–9.5 (–10) µm, with a thin, rough perispore. The species is listed as a synonym of *Adelococcus interlatens* (Arnold) Matzer & Hafellner 1990 by Roux *et al*. (2020), and it seems likely that GBI collections at least belong to that species.

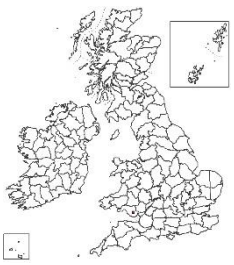
Literature

Clauzade *et al*. (1989), Gueidan *et al*. (2007, 2009), Heiðmarsson *et al*. (2017), Krzewicka (2012), Orange (2004a, b, 2013a, b, 2014, 2020), Orange *et al*. (2009b), Pérez-Ortega *et al*. (2010, 2018), Pykälä *et al*. (2017a, b, 2018, 2019), Powell (2015), Roux *et al*. (2020), Schmitt *et al*. (2009), Thüs *et al*. (2011, 2015), Thüs & Schutz (2008).

Thallus structure in epilithic species:
Left:
non-gelatinous thallus; cells not in regular columns, small spaces often present between cells (shown as dark grey) (*Verrucaria cernaensis*).
Right:
subgelatinous thallus; cells typically in columns, no spaces between cells (*Verrucaria funckii*).



Verrucaria ahtii Pykälä, Launis & Myllys (2017) **NE**

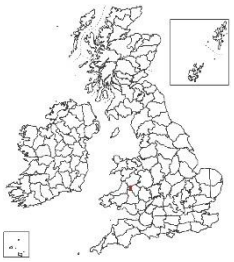


Prothallus medium brown or dark brown, fimbriate, usually rather inconspicuous. Thallus epilithic, usually thin and discontinuous, of indistinct areoles 20–150 (–250) µm diam., cracked in thicker parts, dull light to mid brown. Perithecia 0.2–0.28 (–0.4) mm diam., forming low to moderate mounds, not or rarely making pits in the substratum, with or without a thalline cover, the ostiole inconspicuous. Involucrellum well-developed, reaching half way to all the way down to the perithecial base level. Perithecia in section 0.16–0.28 (–0.32) mm diam., the wall usually dark brown. Ascospores (17–) 20.5–27.5 (–28.5) × (9–) 10–13.5 (–14.5) µm. **BLS 2697**.

On unshaded limestone and on brick, in natural habitats and on waste ground, probably widespread. Wales, Scotland.

Belongs to the *Endocarpon* group of Verrucariaceae according to Pykälä *et al*. (2017b), and closely related to *V. vitikainenii*, another species recently discovered in Wales on brick. That species lacks the fimbriate prothallus and usually has a thinner thallus that does not overgrow the perithecia. Molecular data are recommended to confirm identification.

Verrucaria alpicola Zschacke (1927) **NE**

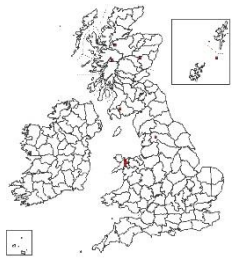


Prothallus absent. Thallus smooth, distinctly subgelatinous in specimens from shaded sites, usually cracked at least around the perithecia at exposed sites, ± subgelatinous, air filled spaces around hyphae usually not visible in anatomical sections; thallus colour light to usually dark (black-) brown or greyish, thin (15–43 µm), black basal layer rarely present; cortex with dilute to dense to brown pigment. Perithecia forming distinct projections 465–675 µm diam., covered by a thin thalline layer, rarely with the area surrounding the ostioles exposed; involucrellum 17–38 µm thick. Perithecia in section 200–350 µm diam., exciple with brown pigment reaching the base of the peridium in specimens from sun-exposed sites. Ascospores (19–) 24.5–32.5 (–43.5) × (9.5–) 12.5–16 (–19) µm, length/width ratio (1.5–) 1.7–2.3 (–3.6). Conidiomata not observed. **BLS 2653**.

Typically found in the splash zone of turbid stretches in streams, on both calcareous and siliceous rocks; confirmed records only from Mid Wales, but probably more widespread.

Part of the *Verrucaria elaeomelaena* (q.v.) aggregate, with larger ascospores than the rest of the group; apparently broadly monophyletic but genetically variable and may be split in the future. One of the Welsh collections listed as *V. alpicola* by Thüs *et al*. (2015) clusters outside of the *V. alpicola* clade and may represent a novel species. The morphological distinction from *V. margacea* is not clear at present, but that species is not part of this complex.

Verrucaria anziana Garov. (1865) **NE**

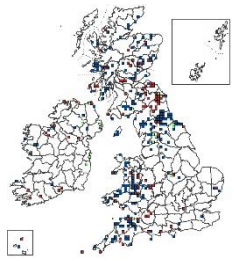


Thallus pale grey-brown to mid (rarely rather dark-) brown, non-gelatinous, 60–480 µm thick, cracks sparse to usually numerous, surface smooth, matt to slightly glossy; thallus cells not or very weakly and locally in columns, not tightly adherent, with air spaces between the cells; cortex weakly developed, with brown pigment; thallus surface sometimes abraded, the surface cells broken. Perithecia immersed in the thallus, the apex visible as a black disc, or the black apex projecting by up to one-quarter the height of the perithecium (rarely more); in section 210–380 µm diam., the wall brown throughout or colourless below. Involucrellum absent or very weakly developed around the apex of the perithecium, not spreading. Ascospores (24–) 26–31.5 (–36.5) × (10.5–) 11.5–13 (–14.5) µm, length/width ratio (2.1–) 2.3–2.6 (–3.0), perispore often distinct, 0.8–2.5 µm thick. Conidiomata not detected. **BLS 2526**.

On rocks in unshaded streams, rivers and lakes, usually on siliceous rock, one record on limestone, recorded at 100–715 m alt.; occasional in upland Britain, including North Wales, N. England and C. and W. Scotland.

Related to *Verrucaria latebrosa* but usually differing in the thicker, paler, more extensively cracked thallus, and the weaker development of the involucrellum. Specimens with a thick, pale thallus and immersed perithecia are often easily recognised in the field. However, occasional specimens may be difficult to assign.

Verrucaria aquatilis Mudd (1861) **LC**



Prothallus very inconspicuous, perhaps brown. Thallus thin, 20–55 µm thick, diffuse, dark greyish brown or dark greenish brown to brownish black (blackish with the unaided eye), uncracked or cracks very few, surface smooth or slightly roughened; upper layer of thallus (and sometimes also elsewhere) with greenish brown to dull brown pigment; lower part of thallus unpigmented, or with brown pigment sparse to extensive, but not forming a well-defined basal layer; rarely with a few intensely pigmented punctae within the thallus. Perithecia forming low to moderate conical-hemispherical projections 100–240 µm diam., ± concolorous with the thallus, covered at least when young by a layer of thallus; ostiole inconspicuous, sometimes visible as a minute pit to 20 µm diam. Perithecia in section 120–160 µm diam., colourless at the sides and base, the ostiole often dull blue-grey or blue-green. Involucrellum conical, often not reaching the base of the thallus, but sometimes merging into pigment in lower part of thallus; pigment in involucrellum red-brown, K+ grey. Ascospores broadly ellipsoidal, without a perispore, (6.5–) 7.5–9 (–10) × (4.5–) 5.5–6.5 (–8) µm, (1.1–) 1.2–1.5 (–1.8) times as long as wide. Conidiomata not detected. **BLS 1476**.

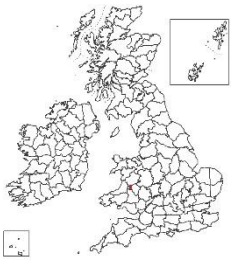
On long-submerged rocks, widespread in N. and W. Britain and Ireland, very local in C. and S.E. England.

Molecular data are sparse but the species appears to occupy an isolated clade without close relatives. Its protobiont is *Dilabifilum* (Thüs *et al*. 2011), in common with species of *Hydropunctaria* and *Wahlenbergiella*, but those genera are not closely related.

Usually easily distinguished in morphological terms from other freshwater species by the thin blackish thallus and the very small, broadly ellipsoidal ascospores. *Hydropunctaria rheitrophila* is green or brown, the perithecia are immersed, the ascospores are slightly larger, and the thallus usually contains black punctae. *V. madida* differs in the larger perithecia and ascospores, and the dark green thallus. The thin blackish crust of *V. aquatilis* could be overlooked as a dead lichen, even under the dissecting microscope.

The main host for *Stigmidium rivulorum* (Kernst.) Cl. Roux & Nav.-Ros. (1994).

Verrucaria aranensis P.M. McCarthy (1988) **NE**

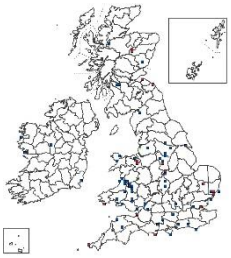


Thallus superficial, brown to black, mostly thin, 40–120 µm thick, with sparse to numerous cracks. Perithecia semi-immersed in the thallus, forming projections 0.2–0.3 mm diam., partly covered by a thin thalline layer; involucrellum more or less semicircular in section or somewhat spreading, 0.20–0.30 mm diam.; perithecia in section 0.15–0.2 mm diam., brown. Ascospores ellipsoidal to subglobose, 7–11 × 5.5–7 µm. **BLS 1643**.

On shaded limestone at the base of a wall; very rare, W. Ireland (Aran Islands).

Endemic, and only known from a single collection. Molecular data are not available; in morphological terms differing from *V. aquatilis* in the slightly larger perithecia, cracked thallus and habitat.

Verrucaria bryoctona (Th. Fr.) Orange (1991) **LC NS**

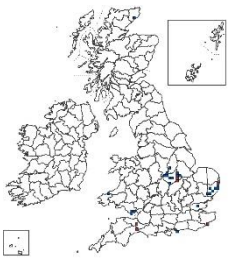


Thallus superficial, grey-green, granular-verrucose, composed of goniocyst-like units 15–40 µm diam., without pigment in cell walls. Perithecia (0.3–) 0.5 (–0.75)-immersed in the substrate, 0.11–0.31 mm diam., black or grey; exciple pigmented throughout; involucrellum absent. Ascospores narrowly ellipsoidal, initially aseptate but often becoming 1- (-3)-septate when overmature, (15–) 19.5–24.5 (–29) × (5–) 6–7 (–8) µm, length/width ratio (1.9–) 3–3.9 (–4.5), the apices rounded or narrowly truncate, frequently with a small gelatinous appendage 2–3.5 µm diam. and 1 µm long. Conidiomata not detected. **BLS 1539**.

On more or less basic soil, usually with acrocarpous mosses, in dunes, dry grassland, waste ground, spoil heaps and wall tops; occasional. Widespread in Britain and Ireland.

The only British species to have gelatinous appendages on the ascospores (other species may have a perispore surrounding the whole spore). The species was compared with *Verrucaria xyloxena* by Orange *et* al. (2009b), but differs in the less elongated spores without appendages and the presence of brown pigment in the thallus. Molecular data from Pykälä *et al*. (2019) demonstrate that the two species are not closely related.

Verrucaria bulgarica Szatala (1930) **LC NR**



Thallus thin or very thin, uncracked, greenish to dark brown. Perithecia forming hemispherical to prominent projections 60–140 µm diam., black, not covered by a thalline layer; involucrellum appressed to the exciple except at the base, not spreading, reaching to the base-level of the perithecium. Ascospores (7–) 8–9.5 (–10) × 4.5–5 (–5.5) µm, length/width ratio (1.5–) 1.6–2.0 (–2.2). **BLS 1736**.

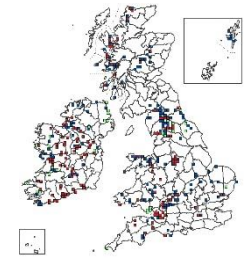
On fragments of shaded limestone, mortar or brick, lying on the ground in woodland, in a garden and a churchyard; common but overlooked. Wales, England, Scotland.

A minute species with small ascospores. Careful vertical sections distinguish it from *V. simplex* which lacks an involucrellum, but the distinction is not always easy to make. No molecular data are available, so its phylogenetic position is unknown.

Verrucaria caerulea DC. (1805) **LC**

Thallus superficial, 100–300 µm thick, or also partly immersed at the base, often raised above adjacent endolithic species or bare rock, pale grey to dull grey-brown, closely and finely cracked, often into discrete areoles, sides of cracks not or little pigmented; surface of areoles with a slightly translucent appearance or often with a whitish

compact pruina. Epinecral layer present, the cortex with dilute brown pigment when well-lit, without a dark basal layer. Perithecia three-quarters to completely immersed in the thallus, the apex black, flat or appearing as a shallowly convex projection 120–220 µm diam. Perithecia in section 150–195 µm diam., colourless or lightly pigmented below. Involucrellum appressed to the exciple in the upper half or extending to the base. Ascospores (12–) 13–17.5 (–23.5) × (5–) 5.5–7 (–9.5) µm, length/width ratio (1.9–) 2.2–2.7 (–3.4). **BLS 1481**.



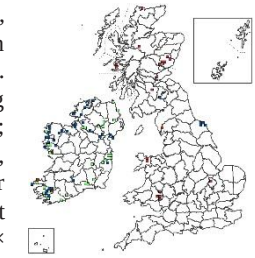
On limestone, local. Widespread in Britain and Ireland.

Distinguished by the epilithic, usually closely cracked thallus, and the mostly immersed perithecia. The epinecral layer is responsible for a very slight translucent appearance sometimes possessed by the thallus surface, at other times it appears as a whitish layer partly hiding the brownish cortex below. *Parabagliettoa pinguicula* differs in the more projecting and larger perithecia.

Assigned to the *Staurothele* clade with reservations by Gueidan *et al*. (2009), its position needs clarification.

Verrucaria cernaensis Zschacke (1927) **LC**

Thallus superficial, well-developed, 100–300 µm thick or more, non-gelatinous, greyish brown to dark brown, strongly cracked, often into discrete areoles; cortex with brown pigment; lower part of thallus often with ill-defined areas of brown pigment. Perithecia two-thirds to completely immersed in the thallus, not projecting or forming low to moderate projections 120–360 µm diam. when measurable, apex black; perithecium in section 220–320 µm diam.; involucrellum usually well developed, sometimes mainly apical, but often reaching to the base of the exciple; often more or less appressed to the exciple and the sides steeply conical or even vertical. Pigment dark brown, K + darker brown or greyish brown. Ascospores (15–) 18–22 (–27) × (7.5–) 9.5–11.5 (–14) µm, length/width ratio (1.5–) 1.7–2.1 (–2.4); perispore absent. Conidiomata often present, scattered, visible as brown dots 40–60 µm diam., conidia straight or slightly curved, 4–8 × *ca* 1 µm. **BLS 1910**.



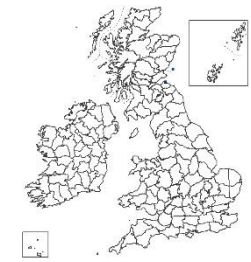
On frequently submerged rocks beside lakes and rivers, and on seeping or sometimes only seasonally damp rocks; frequent on siliceous rock but also on limestone and concrete; frequent in N. and W. Britain and much of Ireland, but local in lowland areas.

Detected in the field by the brown, regularly cracked thallus and little-projecting perithecia. Some specimens of *V. latebrosa* are similar in morphological terms, but differ in the larger spores with a distinct perispore.

A member of the *Endocarpon* group according to Pykälä et al. (2017b), and probably in need of a new generic name.

Verrucaria ceuthocarpa Wahlenb. (1803) **LC NR**

Prothallus absent or forming a very narrow, white border. Thallus epilithic, thin to usually thick, to 400 µm thick, often thinning rapidly to a well-defined margin; surface matt, grey- or green-brown to black; deeply cracked to the margin, often into discrete areoles, areoles often separated by wide cracks; sides of areoles black when mature; surface of areoles flat to gently convex, the edge sharply delimited and sometimes slightly raised; surface without punctae or ridges; thallus in section with the fungal cells in columns. Perithecia usually completely immersed in the thallus, occasionally slightly projecting. Ascospores 8.5–10.5 × 6–7.5 µm. **BLS 2469**.



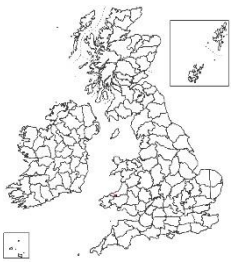
On siliceous rocks on the sea shore, very rare. N. & E. Scotland (Outer Hebrides: Rona; East Lothian).

Sequences of Icelandic material suggest that this is a member of the genus *Wahlenbergiella* (Heiðmarsson *et al*. 2017), but the typically dull brown to black, deeply cracked thallus gives this species an appearance unlike the other species of that genus. *Verrucaria degelii* differs in the presence of dark ridges on the upper surface and margins of the areoles; it also may belong in *Wahlenbergiella*.

Verrucaria consociata Servít (1951) **NE**

Thallus composed of goniocyst-like clusters. Perithecia forming projections 170–240 µm diam., often prominent, covered by thallus or the thalline cover almost absent; ostiole pale or visible as a low papilla to 40 µm diam. Involucrellum weakly developed, appressed and scarcely distinguishable from the exciple, or possibly sometimes

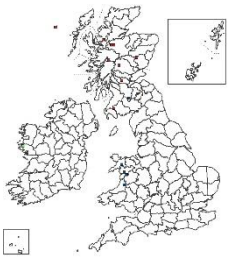
slightly spreading at the base; perithecia in section 150–210 µm diam. Ascospores aseptate, colourless, (17–) 19.5–24 (–26.5) × (8–) 9–11 (–12) µm, length/width ratio (1.9–) 2.0–2.3 (–2.6). **BLS 2626**.



On stones in streams, probably also on damp stones elsewhere, rare. Wales (Cardigan).

Distinguished by the small perithecia which are often prominent, and by the lack of a distinct involucrellum. The thallus is typically thin, though sometimes covering the base of the perithecium. Poorly known; a collective species which needs more study. The description is based only on the holotype. No molecular data are available; Orange (2013b) contrasted *Verrucaria rosula* with this species, but their interrelationships are unknown.

Verrucaria conturmatula Nyl. (1879) **NE**

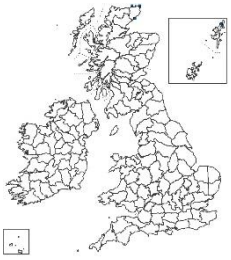


Non-lichenised; forming infection spots to 3.3 mm diam. on the host thallus, these darker than healthy host tissues; infected parts becoming thinner then disappearing or falling away. Perithecia immersed in the host thallus, visible as flat or slightly convex black dots to 170 µm diam., often confluent in small groups, forming black areas to 400 µm diam.; perithecia in section 85–140 µm diam., colourless or locally brown. Involucrellum disc-shaped, extending laterally from the apex of the perithecium along the surface of the host, 85–270 µm diam., often confluent with other involucrella. Ascospores cylindrical to cylindric-ellipsoidal, sometimes slightly constricted in the mid portion, (11.5–) 12.5–15.5 (–18) × (3.5–) 5–6 (–6.5) µm, length/width ratio (1.8–) 2.3–2.9 (–3.5). **BLS 2346**.

Parasitic on *Ionaspis lacustris*; probably frequent. N. & W. Wales, Scottish Highlands, W. Ireland.

Other species of *Verrucaria* s.l. (now mostly assigned to *Placopyrenium*, *Verrucula* and *Verruculopsis*) develop an independent thallus after an initial parasitic stage; *V. conturmatula* seems to be unique in completing its life cycle as a parasite. No molecular data are available, and so its phylogenetic position is unknown; it is probably not a member of the Verrucariaceae. Hawksworth (1989) considered that the species represented immature material of a species of *Polycoccum*, and it should also be compared with *V. phaeosperma* that typically occurs on a related host [see notes in the generic account above].

Verrucaria degelii R. Sant. (1939) **LC NR**



Prothallus white. Thallus superficial, to 1 mm thick, dull black-green, scabrid, finely and regularly cracked; areoles with thickened sharply raised black edges, combining into low black ridges forming a network on the upper surface. Perithecia immersed, becoming prominent with age, *ca* 100 µm diam. Involucrellum small, plate-like. Ascospores 7–10 × 4–7 µm. **BLS 1485**.

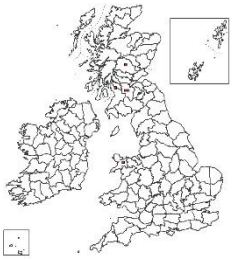
On littoral rocks on sheltered sea shores, amongst other maritime lichens; rare. N. Scotland (Shetland, Caithness).

Resembles *Wahlenbergiella mucosa* but is abundantly cracked with black raised edges to the areoles. *V. ceuthocarpa* lacks the dark ridges on the thallus. Both *V. degelii* and *V. ceuthocarpa* appear to be members of the genus *Wahlenbergiella*, based on sequences from Heiðmarsson *et al.* (2017). *Hydropunctaria amphibia* has larger ascospores, is largely uncracked and the fine ridges resemble fingerprints.

Verrucaria devensis (G. Salisb.) Orange (2014) **NE**

Prothallus white, non-fimbriate. Thallus superficial, pale grey, dull grey-green or greenish grey, mid greyish brown or mid brown, smooth, almost subgelatinous, continuous or usually locally or extensively cracked; cracks partially or sometimes completely delimiting secondary areoles; thallus margin continuous, smooth, without visible primary areoles; secondary areoles 40–600 µm diam., containing 1–7 perithecia, surface of the areoles typically slightly convex or uneven; thallus 40–70 µm thick away from perithecia, to 140 µm thick near perithecia; cells irregularly arranged or in weak vertical columns, air spaces between cells absent or very few; epinecral layer absent or thin, indistinct, to 10 µm thick, comprising a few dead, uncompressed cells; a dark basal layer present either locally or extensively. Perithecia immersed in the thallus, forming very low projections which are too ill-defined to measure, at first the apex visible only by the ostiole which forms a grey dot *ca* 20 µm diam.,

later visible as a grey or black disc to 180 µm diam. Involucrellum conical at first, becoming very wide-spreading and confluent with other involucrella, forming the dark basal layer of the thallus. Perithecia in section 120–210 µm diam., colourless at the sides and base. Asci 8-spored. Ascospores colourless, cylindric-ellipsoidal, (16–) 18.5–22 (–23) × (7.5–) 8.5–9.5 (–10.5) µm, length/width ratio (1.7–) 2.2–2.4 (–2.6). Conidiomata not detected. **BLS 0850**.



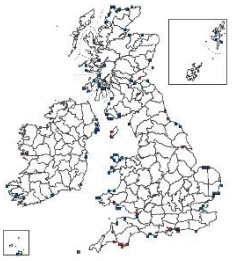
On shaded or unshaded bedrock or cobbles beside streams and rivers or on flushed rocks, frequently to occasionally submerged. Wales, N.W. England, Scotland (Mid Perths and the central belt). Probably widespread.

Related to *Verrucaria praetermissa*, which it resembles in the well-developed, often cracked thallus, the wide-spreading, often confluent involucrella, and the medium-sized ascospores. It differs in the more strongly pigmented thallus which is generally slightly thinner and often more uneven, and in the more compact, almost subgelatinous thallus structure. When the two species grow together, the differences are easily seen, even in the field. However, both are variable in appearance so that some individual specimens may be difficult to name without sequencing. The often uneven surface of *V. devensis* thalli is partly due to the tendency for the thallus to become thinner between the perithecia, but in some specimens also due to the occurrence of thinner, sterile and thicker, fertile areas of thallus adjacent to each other. In *V. praetermissa* the thallus surface is often even, but some specimens are also uneven. In shade *V. praetermissa* is typically pale grey-green, whereas *V. devensis* is darker, although it varies from pale grey green to mid brown; in good illumination *V. praetermissa* can be dull pale brown, and here *V. devensis* is dull grey to mid brown. Both species can sometimes lack any cracks, even when material is fertile and healthy.

The type is an albino morph, hence its original placement in *Leucocarpopsis*. The clade to which *V. devensis* belongs is included within the broad *Staurothele* clade, according to Gueidan *et al*. (2009).

Verrucaria ditmarsica Erichsen (1937) **Nb**

Thallus dark greenish brown to blackish brown, thin, cracks usually absent or few; surface smooth, or roughened with numerous minute dark dots and irregular ridges 10–100 × 10–60 µm in size. Perithecia small, forming low to medium conical-hemispherical projections 120–280 µm diam.; involucrellum more or less conical, or contiguous with the upper exciple and somewhat spreading. Ascospores (7.5–) 8.5–10.5 (–12) × (5–) 6–7.5 (–8) µm, length/ width ratio (1.2–) 1.3–1.7 (–2.4). **BLS 1486**.



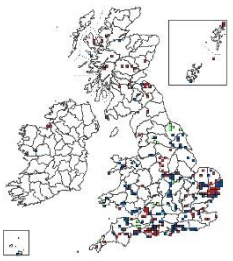
On intertidal rocks and stones, often abundant on sheltered shores and in estuaries. Widespread in Britain and Ireland.

The dark dots in the thallus may be very sparse. Differs from thin morphs of *Hydropunctaria maura* in the smaller perithecia and ascospores. *V. ditmarsica* may grow close to freshwater species where streams meet the coast; here it could be mistaken for *V. aquatilis*, which has slightly smaller ascospores and lacks punctae in the thallus.

The position of this species within *Verrucaria* s.l. is uncertain. Pérez-Ortega *et al*. (2018) found that *Turgidosculum ulvae*, an unusual species with a multicellular algal photobiont, clustered with a specimen of *V. ditmarsica*, but they occupied a clade with a long branch length and only a LSU sequence was available. ITS sequences of Welsh collections suggest that two species may be involved.

Verrucaria dolosa Hepp (1860) **LC**

Thallus superficial, thin, 25–50 µm thick, smooth to uneven, often patchy or present as small flecks, grey-green to brown. Perithecia forming low to moderate projections 140–360 (–400) µm diam., without a distinct covering of thallus when mature. Involucrellum shallowly conical. Ascospores (11–) 14–18 (–21.5) × (5–) 6–8 (–9) µm, length/width ratio (1.9–) 2.1–2.6 (–3.1), perispore not seen. Conidiomata not detected. **BLS 1619**.



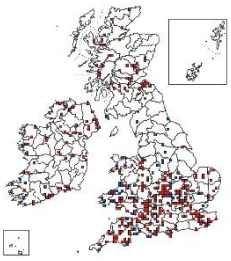
On siliceous and limestone rocks and pebbles, or on concrete or brick, tolerant of shade, frequent and widely distributed.

Distinguished by the small perithecia, small ascospores, and more or less conical involucrellum. *V. sublobulata* differs in the thicker thallus and mostly immersed perithecia. An undescribed *Verrucaria* sp. has been identified which differs from *V. dolosa* in the thallus which is composed of goniocyst-like units; more work is needed to establish it as a formal new taxon. *V. murina* differs

in the larger ascospores (but there is a broad overlap), and the more prominent perithecia which have an appressed involucrellum which is rarely distinctly conical. Weakly developed morphs of *V. elaeina* have slightly larger ascospores, a thin but rather extensive thallus not formed from goniocysts, and a conical perithecium which is often partly covered by thallus below.

The position of *V. dolosa* within the broader *Verrucaria* tree is not clear, but according to Orange (2013b) and Pykälä *et al.* (2018) it appears to cluster with *V. hydrophila*.

Verrucaria elaeina Borrer (1830) **LC**



Prothallus white; adjacent thalli of the same species often separated by dark lines. Thallus crustose, epilithic, non-gelatinous, light grey-green to pale brownish green, rarely mid-brown, thin to moderately thick, 25–90 (–105) µm thick, rimose; cracks usually numerous, but often few in young or poorly developed areas of thallus; surface smooth; surface of cracks unpigmented. Epinecral layer absent; cells of thallus irregularly arranged or in very weak vertical columns; cortex ill-defined, comprising only of an alga-free zone 5–10 (–15) µm thick; pigment absent or dilute in upper cortical cells. Medulla absent or weakly developed as a more or less alga-free zone, colourless. Perithecia numerous, one-quarter to three-quarters immersed, rarely completely immersed in the thallus, usually varying in the same specimen, forming low and indistinct to conical-hemispherical projections; projections 220–400 µm diam. when prominent enough to measure; perithecia sometimes covered with thallus to near the apex, or usually with the upper part naked; apex black, rounded or frequently somewhat flattened, often irregular and appearing either as a black ring, a ring of black dots separated by whitish areas, or as a black ring separated by a whitish ring from the black ostiolar region (the whitish areas are composed of unpigmented tissue overlying the pigmented part of the involucrellum; ostiolar region flat or slightly concave but not in a distinct depression, inconspicuous or more frequently appearing as a pale grey dot 20–120 (–160) µm diam., sometimes with a small darker spot in the centre (caused by dilute pigment immediately surrounding the ostiole). Involucrellum well-developed, conical-hemispherical to conical, thus usually ± spreading from the peridium below, usually ± flat-topped, 350–500 (–720) µm diam., pigmented throughout or pale below; pigment dark reddish-brown, K+ dark greyish-brown; outlines of pigmented cells often visible in thin section in the lower part of the involucrellum; lower cells often with large oil droplets within. Perithecia in section 160–280 µm diam., usually unpigmented except for the ostiolar region with dilute brown or greenish-brown, K+ slightly darker pigment; sometimes the outer part of the exciple is pigmented below with a similar pigment to the involucrellum. Ascospores ellipsoidal to cylindric-ellipsoidal, (15–) 16.5–22.5 (–24) × (6–) 7–9 (–9.5) µm, length/width ratio (1.7–) 2.0–2.9 (–3.5); perispore absent. Conidiomata not detected. **BLS 1871**.

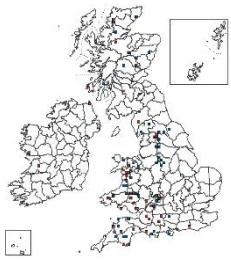
On limestone, concrete, siliceous rock and brick, in woodland or beneath herbaceous vegetation, in natural habitats or on waste ground, in gardens or on damp walls, frequent on terracotta pots in gardens; particularly characteristic of weakly calcareous rock in shade; common and locally abundant. Throughout Britain and Ireland.

The pale grey-green thallus on shaded rocks is characteristic and often easily recognised with the unaided eye; the apex of the involucrellum is often irregular, showing as a ring of dark dots surrounded by the pale opaque thallus. Some weakly developed morphs have a much less distinctive appearance and could be confused with *V. dolosa* or with *V. hydrophila*. *V. praetermissa* differs in the thicker thallus, more immersed perithecia, slightly larger ascospores, and usually distinctly freshwater habitat.

The clade to which *V. elaeina* belongs is included within the broad *Staurothele* clade, based on data from Gueidan *et al*. (2009) and Orange (2014).

Verrucaria elaeomelaena (A. Massal.) Arnold (1868) **LC NS**

Verrucaria andesiatica sensu Orange *et al*. (2009b)



Prothallus whitish, smooth, thin to absent. Thallus greenish-grey to grey (shade forms), light to dark brown (more or less exposed sites), thin to moderately thick (20–115 µm), when on limestone sometimes in patches raised above the level of the surrounding rock (due to dissolution of the limestone not protected by the thallus), making the thallus look thicker than it really is; medulla not differentiated or forming a thin to thick (5–75 µm) black basal layer (often in specimens on limestone), subgelatinous with algal cells often arranged in vertical lines and air-filled spaces around hyphae not visible in anatomical sections. Perithecia forming distinct projections in thin thalli, only slightly

projecting in thick thalli, usually covered by a thin thalline layer; involucrellum thin (17–25 µm), vertical extension variable, sometimes even in perithecia from the same thallus ranging from near apical to wide-spreading and reaching the bottom of the thallus, algae in thalline mantle present throughout or thinning out to absent towards the ostiole; perithecia in section 210–320 µm diam., exciple pale at the base. Ascospores (16–) 21–27.5 (–30) × (9.5–) 11–16 µm, length/width ratio (1.3–) 1.7–2.3 (–2.6), a perispore present in some fresh collections. Conidiomata not detected. **BLS 1488**.

On siliceous or limestone rocks and stones in streams and seepages, tolerant of shade; frequent on siliceous rocks in N. and W. Britain, local in limestone areas of England and Scotland, one confirmed record for Ireland; many other records need confirmation.

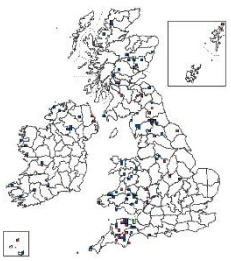
The name *Verrucaria andesiatica* Servít was considered as of uncertain application by Thüs *et al*. (2015), and in the interpretation of Orange *et al*. (2009b) it refers to populations of *V. elaeomelaena* agg. on siliceous rock rather than limestone. Molecular data suggest that the species might occur on either rock type, although the taxon was treated as a species aggregate by Thüs *et al*. (2015) and the GB specimens sequenced did not fall into *V. elaeomelaena* sensu stricto. Further studies may result in recognition of further species in this aggregate.

V. hydrophila is similar, though unrelated, and differs in the smaller ascospores, and the smaller and more crowded perithecia. *Verrucaria margacea* differs in the non-gelatinous thallus. *V. funckii* differs in the thicker thallus, and the often wide-spreading involucrella which locally form a dark 'basal layer'.

Lichens from two clades within the *V. elaeomelaena* aggregate have been recognized as distinct species, *V. alpicola* and *V. humida*. *V. alpicola* has rather larger ascospores and usually darker thalli. *V. humida* has slightly smaller perithecia and ascospores, and the perithecia are not typically overlain by a thalline layer.

Reported as a host for *Stigmidium rivulorum*.

Verrucaria funckii (Spreng.) Zahlbr. (1921) **LC NS**



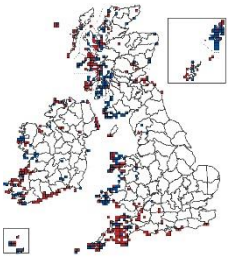
Prothallus whitish, not fimbriate, or absent; in eroded thalli, the black basal layer can be exposed on the thallus margins and is easily mistaken for a black prothallus. Thallus light grey-green to grey-brown, subgelatinous, well-developed, (20–) 80–160 (–240) µm, uncracked or rarely with a few cracks, surface smooth. Cells of thallus arranged in strongly marked columns; cortex poorly developed, with brown pigment in well-lit specimens; basal layer absent to more or less continuous. Perithecia not projecting, or forming shallowly conical, rarely conical-hemispherical projections 300–600 µm diam., usually completely covered by the thallus, the apex visible at the surface only as a small grey dot, or exposed by abrasion to form a small black disc. Perithecia in section 180–390 µm diam., colourless at the sides and base, often dilute brown at the ostiole. Involucrellum well-developed, reaching to the base of the thallus, distinctly conical with straight or even slightly concave sides, or sometimes the sides convex; often wide-spreading at the base, and merging into the basal layer of the thallus when present. Pigment in involucrellum red-brown, K+ grey. The thallus often completely covers the involucrellum, and then an alga-free ostiolar region extends to the thallus surface. Ascospores ellipsoidal to narrowly ellipsoidal, (19.5–) 22.5–25.5 (–28.5) × (8–) 9–11 (–13) µm, (1.8–) 2.1–2.6 (–3.1) times as long as wide, a thin perispore *ca* 0.5 (–2) µm thick present on at least some spores. **BLS 1490**.

On frequently or permanently submerged siliceous rocks in rivers and lakes, in small streams and in springs; frequent. Upland areas of Britain and Ireland.

The very smooth, uncracked thallus with very shallow perithecial projections is distinctive. *V. elaeomelaena* s.l. differs in the thinner thallus, higher perithecial projections, absence of a basal layer and slightly broader ascospores. The species was shown by Thüs *et* al. (2015) to belong in a clade with *V. elaeomelaena*, but distinct from that aggregate.

Verrucaria fusconigrescens Nyl. (1872) **LC**

Prothallus dark brown to blackish. Thallus superficial, areoles arising on the prothallus, soon rimose and coalescing; thallus mid to dark brown, sometimes locally pruinose, thin to medium, 50–150 µm thick, non-gelatinous; areoles matt, flat to gently convex, rarely convex or swollen, or even produced as irregular clavate structures; cortex scarcely differentiated, brown; edges of areoles also sometimes lightly browned; epinecral layer sometimes present, to 15 µm thick, composed of crushed remains of cells and appearing as pruina; medulla absent or indistinct, no dark basal layer. Perithecia immersed in the thallus, but forming low to moderate projections 130–400 µm diam., rarely prominent and exposed, the apex projecting, black, not covered by a thalline layer; apex rounded, rarely somewhat flattened; ostiole inconspicuous, or appearing as a faint pale dot



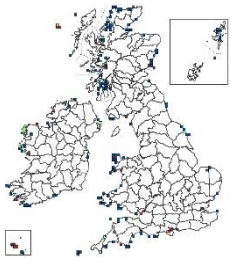
or a small papilla, or rarely in a depression; involucrellum well-developed, conical but sometimes steep-sided. Perithecia in section 200–380 µm diam., the wall colourless or locally pigmented. Ascospores cylindric-ellipsoidal, (17–) 19.5–23.5 (–26) × (6.5–) 8–9.5 (–11) µm, length/width ratio (2.1–) 2.3–2.6 (–2.8). Vegetative propagules and conidiomata not seen. **BLS 1491**.

On siliceous rocks on or near the coast, or on slightly calcareous rocks inland; frequent. N. & W. Britain, Ireland.

Distinguished by the well-developed (though not thick) brown thallus on a black prothallus, absence of thalline layer over perithecia, more or less conical involucrellum and medium sized spores. Some specimens from small, rocky hollows that fill with rain differ in the sometimes convex or irregularly produced areoles, the less areolate thallus and the more prominent, even exposed, perithecia; these seem to be an 'exuberant' expression produced by the habitat. *V. nigrescens* differs in the more immersed perithecia, inconspicuous prothallus and usually occurs on calcareous rocks.

No sequences are available for this species, so its phylogenetic position is unknown. Orange (2013a) suggested that *V. fusconigrescens* may comprise a species aggregate.

Verrucaria halizoa Leight. (1871) **LC**



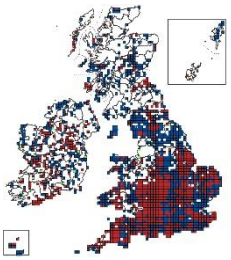
Thallus superficial, thin, 40–80 µm thick, usually uncracked, pale olive-green, to brown when well-lit, subgelatinous, translucent when wet and fresh, without ridges or punctae; cortical pigment, when present, brown. Perithecia forming regular conical-hemispherical projections 140–260 µm diam.; involucrellum spreading; exciple pale at the base. Ascospores cylindric-ellipsoidal, (7–) 8–10.5 (–12) × 3.5–4.5 (–5.5) µm, length/width ratio (1.3–) 1.7–2.8 (–3.5). Conidiomata occasional, visible as black dots *ca* 40 µm diam.; conidia straight to slightly curved, 2.9–3.3 × *ca* 1 µm. **BLS 1493**.

In crevices and shade on rocks on the sea shore, in the mid-littoral zone, usually amongst *Wahlenbergiella mucosa*, *W. striatula* and the crustose red alga *Hildenbrandia*. Local throughout coastal Britain and Ireland.

Distinguished by the thin olive-green thallus without ridges or punctae and neatly hemispherical perithecia. The pycnidia, when present, could be mistaken for punctae, causing confusion with *Verrucaria ditmarsica* or *W. striatula*.

Perez-Ortega *et al*. (2010) showed that a sequence from a Chilean specimen clustered within *Wahlenbergiella*, and the morphology and ecology of the species is consistent with that genus. However, Gueidan *et al*. (2022) added further sequences and established that Perez-Ortega's collection belonged to a neighbouring clade that included *Verrucariopsis suaedae* and *V. halophila* [the correct name for *Verrucaria halizoa* according to some authors]. *V. halizoa* is retained in *Verrucaria* pending further sequencing.

Verrucaria hochstetteri Fr. (1831) **LC**



Thallus endolithic, white to pale grey, without cracks. Perithecia 375–700 µm diam., immersed in well-defined pits in rock; exciple pigmented throughout; involucrellum absent. Ascospores ellipsoidal to broadly ellipsoidal, (24.5–) 29–34.5 (–41.5) × (14–) 16–20 (–24.5) µm, length/width ratio (1.2–) 1.5–2 (–2.4); perispore often present, 0.8–1.2 µm thick, surface compact, often with a distinct fine ornamentation of short simple or branched ridges. Conidiomata not seen. **BLS 1495**.

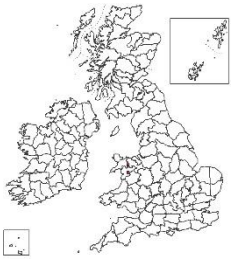
On calcareous rocks; common. Throughout Britain and Ireland.

Identified by the immersed thallus, large perithecia sunken in pits, absence of an involucrellum and large ascospores. The perispore may be confused with the ascospore wall; the distinct ornamentation is unusual in the genus.

Phylogenetic studies have shown that *V. hochstetteri* is not close to any other sequenced *Verrucaria* s.l. species, and it clusters within the main *Thelidium* clade (Gueidan *et al*. 2009). It should perhaps be transferred to that genus, but *Thelidium* itself needs reorganization. It is not closely related to *Bagliettoa* and *Parabagliettoa*, other groups with thalli immersed in limestone.

The type host of *Opegrapha hochstetteri*.

Verrucaria humida Orange (2015) **NE**



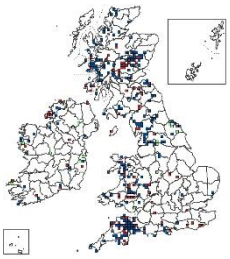
Prothallus not seen. Thallus very thin, 12–25 µm thick, smooth, continuous, grey-green or brown (pale specimens green and translucent when fresh and wet). Perithecia prominent, black, forming conical-hemispherical to hemispherical projections 200–360 µm diam., occasionally collapsed when dry, smooth or slightly roughened, the ostiolar region inconspicuous, or ostiole visible as a pale dot or papilla *ca* 40 µm diam.; thalline layer absent or present only at the extreme base. Involucrellum thin (11–30 µm), appressed to the exciple above, usually diverging at the base, dark brown, K+ darker brown, greyish brown or dark green. Perithecium in section 170–200 µm diam., colourless at the sides and base. Ascospores cylindric-ellipsoidal, aseptate, colourless, (20–) 22–25 (–26) × 10–12 (–12.5) µm, length/width ratio (1.7–) 2.0–2.3 (–2.5), without a perispore. Conidiomata not seen. **BLS 2654**.

On siliceous stones in streamlets and on flushed ground; North Wales.

Important features for the recognition of this species include the small prominent naked perithecia, the small- to medium-sized ascospores, a very thin smooth continuous thallus, and the habitat on wet stones. It differs markedly from the other taxa in the *V. elaeomelaena* group by the smaller, prominent perithecia without a thalline cover. It is likely to be confused with other, poorly known species with a thin thallus and small naked perithecia. It is recommended that for the time being, the identity of specimens referred to this species should be confirmed by sequencing.

Verrucaria hydrophila Orange (2013) **LC**

Verrucaria denudata Zschacke (1927), *nom. illeg.*



Thallus thin, 25–60 µm thick, more or less subgelatinous to non-gelatinous, grey-green to mid brown, cracks absent or few, dark basal layer absent. Perithecia forming conical-hemispherical mounds 240–560 µm diam., at first covered to the apex by a layer of thallus, later the black apex of the involucrellum sometimes exposed; ostiolar area inconspicuous, flat or convex, appearing as a pale dot 15–50 µm diam. Involucrellum conical, reaching to the substratum, densely pigmented in the upper part, often becoming almost colourless adjacent to the base of the perithecium; pigment dark brown to dark reddish brown, K+ darker brown to grey-brown. Perithecia in section 180–310 µm diam., colourless except at the apex. Ascospores (16–) 19.5–23 (–26.5) × (6.5–) 8–10 (–12) µm, length/width ratio (1.7–) 2.2–2.7 (–3.3), perispore not seen. Conidiomata not detected. **BLS 1496**.

On rocks and stones in streams and streamlets, and on wet banks, often in shade; frequent. Throughout Britain and Ireland, though occasional in lowland areas.

Distinguished by the conical involucrellum, covered by a layer of thallus, and rather small ascospores. The similar but unrelated *V. elaeomelaena* s.l. differs in the larger ascospores and usually larger perithecia. The thallus is often very smooth and thin, and translucent when fresh and wet, but some collections have a few cracks in the thallus and are less distinctly subgelatinous in appearance. Morphologically very similar specimens occur on shaded stones in woodland distant from water; these represent at least one distinct cryptic species.

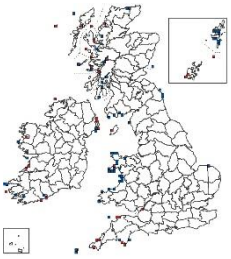
Pykälä *et al*. (2018) found that collections identified as this species occupied four separate clades, along with *V. lignicola* which has not yet been reported from Britain. However, support for some of the clades is weak, and more research on the group is needed. The position of the clade within the broader *Verrucaria* tree is not clear, but according to Thüs *et al*. (2011) the aggregate appears to cluster with *V. dolosa* and *Trimmatothele perquisita*.

A host for *Pyrenidium hetairizans* (Leight.) D. Hawksw. (1986) and *Stigmidum rivulorum*. Also for an undescribed *Opegrapha* sp. with clustered, rounded apothecia 0.12–0.2 mm diam. and dark brown, 3-septate ascospores, 16–19 × *ca* 6 µm.

Verrucaria internigrescens (Nyl.) Erichsen (1928) **Nb**

Thallus superficial, non-subgelatinous, uneven, usually cracked, white to brownish white, occasionally inconspicuous in stressed specimens; adjacent conspecific thalli sometimes separated by dark lines. Perithecia forming projections 320–780 µm diam., not covered by a thalline layer; involucrellum well-developed, reaching

to the level of the base of the perithecium, more or less clasping the exciple and spreading slightly below, to conical. Ascospores cylindric-ellipsoidal, (15–) 20–25 (–30) × (7.5–) 9–12 (–13) µm, length/width ratio (1.6–) 1.9–2.4 (–3.2). **BLS 1498**.



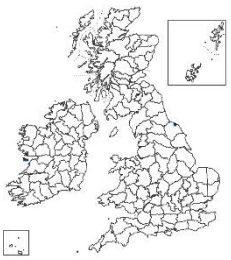
On shaded damp siliceous rocks in the supralittoral zone on seashores, or on stones embedded in coastal turf; common. Widespread.

Distinguished by the whitish, usually superficial thallus, medium-sized ascospores and maritime habitat. Some collections virtually lack a visible thallus, and these can only be identified by the habitat or by sequencing. *V. muralis* has a superficial thallus when it grows on siliceous substrata, but this is usually less well developed. The ascospores are often broader in shape in *V. muralis*, but there is a very wide overlap.

No sequences are available, so the phylogenetic position of this species is unknown.

Verrucaria knowlesiae P.M. McCarthy (1988) **Nb IR**

Thallus more or less endolithic and inconspicuous, to thinly epilithic, brownish grey, cracked. Perithecia semi-immersed to almost superficial, not covered by a thalline layer; involucrellum hemispherical to conical, 150–250 (–300) µm diam., extending to the base-level of the perithecium; perithecium in section 100–150 µm diam., brown. Ascospores ellipsoidal, 7.5–11 × 5.5–7 µm. **BLS 1645**.



On shaded limestone; very rare. W. Ireland (Galway). Apparently endemic, known only from two collections. A record from N. Yorkshire needs confirmation.

The species differs from *V. bulgarica* in the larger perithecia. It is poorly known and no sequences are available.

Verrucaria lapidicola Orange (2014) **NE**

Prothallus not detected. Thallus diffuse, very thin, 25–35 µm thick, dull grey-green to dull grey-brown, smooth but often minutely and inconspicuously mottled or minutely uneven, both mottling and unevenness at a scale of *ca* 20–60 µm; uncracked, comprising ± distinct goniocyst-like units 18–33 µm diam., mostly in a single layer. Perithecia projecting, 160–280 µm diam., black, naked or occasionally with an incomplete thalline covering in the lower two-thirds, the apex rounded or slightly flattened, ostiolar region whitish to pale brown, flat or protruding as a low papilla 30–40 (–60) µm diam. Involucrellum conical-hemispherical, densely pigmented throughout, or densely pigmented at the surface and colourless at the base next to the exciple; perithecia in section 140–200 µm diam., the wall colourless at sides and base. Ascospores colourless, ellipsoidal, (17–) 18–21.5 (–23) × 6.5–8 (–10.5) µm, length/width ratio (2.2–) 2.5–2.8 (–2.9). **BLS 2634**.

An early colonizer of small calcareous stones (including calcareous mudstone and limestone) shaded by trees or herbaceous vegetation, in woodland or beside tracks; probably overlooked. Wales (Brecon, Carmarthen, Glamorgan), England (Cumbria).

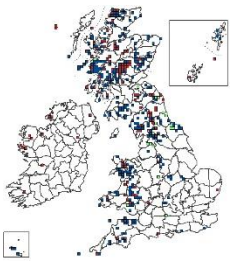
This is one of several small species, not closely related, which have not been distinguished in recent years in Great Britain, and which have generally been called *Verrucaria murina* auct. (Orange *et al*. 2009b). The thallus is thin, and composed of a layer of goniocyst-like units which are responsible for the minutely mottled or uneven surface. In the studied specimens, the ascospores may have been slightly immature. *V. dolosa* differs in the slightly smaller spores, and *V. elaeina* in the thicker, paler, often cracked thallus and larger perithecia.

The clade to which *V. lapidicola* belongs is included within the broad *Staurothele* clade, based on data from Gueidan *et al*. (2009) and Orange (2014).

Verrucaria latebrosa Körber. (1855) **LC NS**

Verrucaria aethiobola G. Wahlenberg (1803) *auct.*

Thallus epilithic, pale to dark brown, 40–200µm thick, cracks absent to numerous; thallus cells irregularly arranged or at most in very weak and local columns, either tightly adhering and with no air spaces between cells, or cells not so tightly adhering and air spaces present; cortex weakly developed, with brown pigment. Perithecia forming low to moderate conical-hemispherical projections 240–500 µm diam., apex often somewhat flattened or slightly depressed, ostiolar area inconspicuous or visible as a pale dot 40–110µm diam.; not covered by a layer of thallus, or rarely weakly so when young. Involucrellum well-developed, occupying the upper 0.3 to 0.5 of perithecium height, pigment dark brown, K+ slightly darker brown or greenish brown.



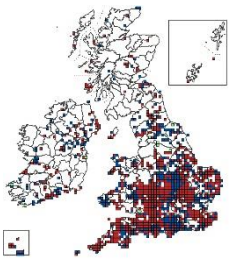
Perithecia in section 205–290 µm diam., colourless to brownish. Ascospores (23–) 25–28 (–29.5) × (8–) 10.5–13 (–14) µm, length:width ratio (1.7–) 2.0–2.6 (–3.2), a perispore often visible, gelatinous to firm, to 1.5 µm thick. Conidiomata unknown. **BLS 1473**.

On unshaded or shaded rocks by streams and lakes; occasional to frequent in upland Britain and Ireland.

Can often be identified in the field by the combination of a well-developed brown thallus, which is typically lightly cracked but smooth between the cracks, the relatively large, projecting perithecia which are typically without a thalline cover, the slightly flattened or depressed perithecial apex often with a conspicuous pale ostiolar region, and the habitat on flushed or occasionally inundated, usually siliceous rock. However, morphs may occur which are not so easily recognised; specimens on drier or more exposed rock may have a thin thallus with few cracks, and sometimes perithecia are less prominent and without a flattened apex.

Verrucaria latebrosa has been regarded as a synonym of *V. aethiobola*, but *V. aethiobola s.l.* comprises three distinct cryptic species, with *V. aethiobola s.s.* currently known from N. Norway (Orange 2020). The third species, *V. tephromela* (q.v.), cannot be distinguished reliably from *V. latebrosa* usuing morphological methods. *V. anziana* usually differs in the thicker, paler thallus which is typically more strongly cracked, and the involucrellum poorly developed or absent. The unrelated *V. margacea* typically has the perithecia covered by a layer of thallus, and the involucrellum is conical.

Verrucaria macrostoma DC. (1805) **LC**



Thallus superficial, well-developed, pale to dark brown (typically mid brown), at first comprising rounded or lobed areoles to 0.4 mm diam., these becoming crowded and often coalescing, usually with the thallus soon cracked into large secondary areoles 0.16–1.6 mm diam.; blastidia absent to abundant, 40–80 µm diam., formed on the edges of the secondary areoles; dark basal layer absent; epinecral layer often present. Perithecia forming low to moderate conical-hemispherical projections 0.3–0.52 mm diam., black, not covered by a thalline layer, not forming pits; involucrellum well-developed, often more or less reaching the base-level of the perithecium, slightly spreading to ± conical. Ascospores ellipsoidal, (21.5–) 25–31.5 (–36) × (9.5–) 11.5–14.5 (–16.5) µm, length/width ratio (1.7–) 2.0–2.4 (–2.8), perispore not seen. Conidiomata not seen in the region, but conidia said to be 3.5–4.5 × *ca* 1µm. **BLS 1502**.

On limestone, mortar and calcareous sandstone, in semi-natural habitats but also often on walls, probably favoured by slight nutrient enrichment; frequent. Widespread in England & Wales, local in Scotland & Ireland.

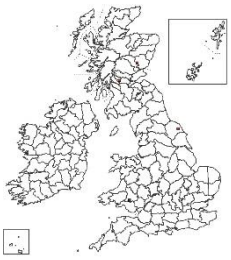
The thallus is typically mid brown but can be dark on exposed rocks and pale brown in shade. The thallus areoles are often vigorous, and in damp and shaded conditions can appear more or less subsquamulose, but there is a gradation to specimens on exposed rocks which have a neatly areolate thallus somewhat resembling *V. nigrescens*; that species differs in the usually darker colour, smaller areoles and smaller ascospores. *V. viridula* differs in the perithecia immersed in the substrate and having a less well-developed involucrellum.

Subsquamulose morphs should be compared with *V. romeana* de Lesd. (q.v.), also referred to as *V. squamulosa* van den Boom & Brand. Blastidiate specimens are referred to f. *furfuracea* B. de Lesd. (1949) [**BLS 1519**] and this is sometimes accepted at species level as *V. furfuracea* (B. de Lesd.) Breuss (2008), but it is unclear whether it deserves recognition.

V. macrostoma and *V. nigrescens* (and perhaps also *V. viridula*) form an apparently well-defined subclade within the *Endocarpon* major clade, according to Gueidan *et al*. (2009) and Orange (2013b).

A host of *Endococcus rugulosus* Nyl. (1855).

Verrucaria madida Orange (2004) **VU (D2)**



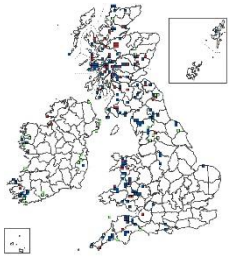
Prothallus not seen. Thallus dark green or dark greenish grey, thin, 40–60 µm thick, smooth, uncracked, subgelatinous; cells weakly arranged in columns; cortex with dull green or in part brownish pigment, medulla absent. Perithecia forming low to moderate conical-hemispherical projections 200–420 µm diam., covered by a layer of thallus at first, this layer sometimes partly lost later; apex of perithecium rounded to slightly flattened, black when the thalline layer has been eroded; perithecia in section 140–290 µm diam., colourless or brown below; involucrellum conical, or somewhat spreading at the sides and then curved down slightly. Asci (3-)4(-5)-spored. Ascospores ellipsoidal, without a perispore, (9–) 10.5–13.5 (–15) × (5.5–) 6–7 (–7.5) µm, length/width ratio (1.4–) 1.6–2.1 (–2.6). Conidiomata not detected. **BLS 2401**.

On frequently immersed siliceous rock in streams and streamlets; rare. S. Wales (Brecon Beacons), England (N.E. Yorkshire), Scotland (Angus, Stirlingshire).

Distinguished by the subgelatinous thallus with greenish pigment, conical involucrellum and small ascospores; the 4-spored asci are unique in the genus. *V. aquatilis* differs in the usually blackish thallus and smaller perithecia and ascospores, *Hydropunctaria rheitrophila* differs in the immersed perithecia and presence of punctae in the thallus, and *H. scabra* differs in the presence of immersed punctae and a dark basal layer and in the larger, cylindrical ascospores.

Molecular data indicate that this species is related to *Wahlenbergiella*, and the green subgelatinous thallus supports this hypothesis. However, the only available sequence diverges significantly from those of sequenced *Wahlenbergiella* specimens, and more research is needed into its affinities.

Verrucaria margacea (Wahlenb.) Wahlenb. (1812) **LC**



Thallus superficial, non-gelatinous, more or less continuous or with numerous cracks, pale to mid brown, smooth or somewhat uneven, giving a finely mottled appearance. Perithecia forming projections 280–540 (–700) µm diam., usually mostly covered by thallus, but often partly exposed later. Involucrellum conical, often reaching to the substratum, but sometimes weakly developed and irregularly conical; angle between involucrellum and base of perithecium colourless or with pigment evenly distributed throughout cell walls. Perithecia in section 180–320 µm diam. Ascospores (20–) 26–32.5 (–40.5) × (9–) 11–14 (–17.5) µm, length/width ratio (1.6–) 2.1–2.6 (–3.4), a perispore to 2 µm thick often present. Conidiomata not known. **BLS 1503**.

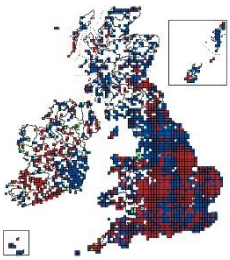
On siliceous rocks beside streams and lakes; frequent. N. & W. Britain, Ireland.

Distinguished by the non-gelatinous thallus, a conical involucrellum which is usually covered by a layer of thallus (often partly lost later) and large ascospores. *V. elaeomelaena s.l.* differs in the smooth, subgelatinous thallus, slightly smaller ascospores and occasional presence of pycnidia. *V. latebrosa* differs in the involucrellum which is rarely conical and which is typically exposed even when young (rarely almost absent), but some specimens are difficult to identify. In addition to the differences in perithecial shape, *V. margacea* tends to have a slightly uneven and mottled appearance, whereas the thallus of *V. latebrosa* tends to be smooth between the cracks, but many specimens deviate from this.

The phylogenetic position of *V. margacea* is unclear, and it appears to be a species complex; more studies are needed. Thüs *et al*. (2015) found that sequences did not cluster with those from the *V. elaeomelaena* aggregate, and it appears to occupy an isolated clade based on sequence data from Heiðmarsson *et al*. (2017). Orange (2013a) noted that British and Irish material identified as this species differs from the type.

A host for *Stigmidium rivulorum*, more frequently found on *V. aquatilis*.

Verrucaria muralis Ach. (1803) **LC**



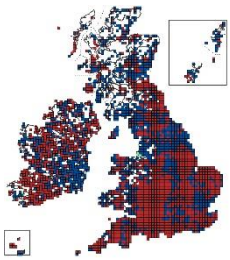
Thallus immersed to thinly superficial, white to green- or brown-white, cracks absent to numerous; cortex usually colourless, or with dilute brown pigment. Perithecia forming shallowly convex to conical-hemispherical projections 240–500 µm diam., black, or greyish below from particles of substrate, not covered by a layer of thallus, the apex rounded to slightly flattened, sometimes shallowly depressed; perithecia not in pits, or forming rather shallow pits in rock; perithecia in section 200–380 µm diam., colourless to pigmented at the base; involucrellum present around the upper half of the perithecium or reaching to base-level, ± hemispherical or sometimes spreading. Ascospores (17–) 20–24 (–27) × (7.5–) 10–12.5 (–14.5) µm, length/width ratio (1.4–) 1.7–2.3 (–3.1). **BLS 1507**.

On limestone, mortar, brick and calcareous soil, sometimes on siliceous rock, frequently on pebbles embedded in the ground; in waste ground, quarries, on walls, in grassland and beside tracks, but often sparse in semi-natural habitats. Widespread and frequent in Britain and Ireland.

Verrucaria rupestris Schrad. (1794), the type of the genus, is said to differ in the endolithic thallus. Specimens of *V. muralis* with thalli ranging from endolithic to strongly epilithic have been found to share the same ITS sequence, however, so the morphological distinction may not be useful. Indications are that the two species are not synonymous, and their phylogenetic positions need further study. There are some suggestions that *V. muralis* may belong to the *Staurothele* major clade and be related to *V. praetermissa*, or alternatively close to *V. latebrosa* (and therefore a true *Verrucaria*); see Gueidan *et al*. (2009) and Heiðmarsson *et al*. (2017).

A host of *Opegrapha hochstetteri*, and the type host of *Lichenochora coppinsii* Etayo & Nav.-Ros. (2008). Also reported are *Stigmidium tetrasporum* and two records of *Muellerella pygmaea* (Körb.) D. Hawksw. (1979) that require confirmation.

Verrucaria nigrescens Pers. (1795) **LC**



Thallus superficial, thin to thick (100–500 µm thick), dark brown, regularly cracked into areoles 200–800 µm diam., these usually polygonal, smooth, flat to slightly convex, occasionally with blastidiate margins, sides of areoles brown to blackish; prothallus absent or inconspicuous, or slightly darker than the thallus and visible between the areoles; upper cortex 10–20 µm thick, the uppermost part brown; algal layer 30–120 µm thick, the cells arranged in ± vertical columns; medulla with a black basal layer half to two-thirds of the thallus thickness. Perithecia half to three-quarters immersed in the thallus; one per areole, the apex flat to hemispherical, involucrellum 200–400 µm diam., hemispherical or extending to the base-level of the perithecium. Perithecia in section 150–250 µm diam., the exciple dark brown. Ascospores ellipsoidal, (17–) 19–27 (–30) × 8–14 µm. Conidiomata not observed. **BLS 1510**.

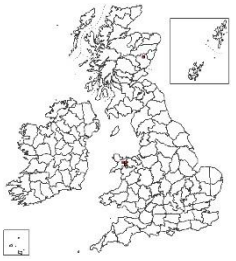
On well-lit calcareous rocks and mortar, rarely on siliceous rocks with calcareous influence; very common. Throughout Britain and Ireland.

Blastidiate specimens may be referred to *V. nigrescens* f. *tectorum* (A. Massal.) Coppins & Aptroot (2008) [**BLS 2514**] and are sometimes recognised at species level as *V. tectorum* (A. Massal.) Körb. (1863). See also *V. fusconigrescens* and *V. macrostoma*.

Apparently related to *V. macrostoma* based on the molecular evidence currently available; see Gueidan *et al*. (2009) and Orange (2013b). Orange (2013a) noted that several similar but as yet unidentified species occur in Great Britain.

The main host of *Opegrapha opaca* Nyl. (1853) and the type host of *Skyttea spinosa* D. Hawksw. & Coppins (1982). Other reported lichenicolous fungi are *Endococcus propinquus*, *E. rugulosus*, *Muellerella hospitans* Stizenb. (1863), *Stigmidium clauzadei* Cl. Roux & Nav.-Ros. (1994), *Zwackhiomyces lithoiceae*, and an unidentified *Lichenochora*. Also sometimes associated with *Lichenothelia renobalesiana*.

Verrucaria nodosa Orange (2013) **NE**



Prothallus not differentiated. Thallus superficial, grey-green (in shade) to dark brown, 70–500 µm thick, initially comprising discrete dorsiventrally flattened units which become crowded and overlapping, forming an uneven crust with sparse secondary cracks, sometimes overtopping each other to make a thick uneven crust. Surface of thallus uneven; thallus in section divided into units of variable size, 30–325 µm thick, the cells isodiametric to shortly cylindrical, 5–9 × 4–8 µm, polygonal and mostly coherent, or of somewhat rounded outline, and with numerous air-spaces between the cells; upper (and sometimes also lower) surface of units with brown-pigmented walls. Perithecia forming low to moderately convex conical-hemispherical projections 220–460 µm diam., sometimes only the lower 0.2–0.3 of perithecium height is immersed in the thallus, the projecting part naked or with an irregular thalline cover below, or sometimes the perithecium partly or almost completely overtopped by thallus units. Ostiole inconspicuous or appearing as a pale dot 20–40 µm diam., flat or slightly projecting. Involucrellum appressed to the exciple above, usually becoming broader below, rather steeply conical-hemispherical in outline, densely pigmented throughout, or with a pale area adjacent to the base of the perithecium; pigment dark brown to dark reddish brown, ostiolar area often with dark green pigment. Perithecia in section 190–310 µm diam., colourless or the outer layer pigmented throughout. Ascospores ellipsoidal, (17–) 20.5–24 (–28) × (8–) 9–10.5 (–11.5) µm, length/width ratio (2–) 2.1–2.5 (–3). Conidiomata not detected. **BLS 2616**.

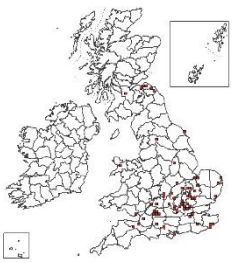
On rocks beside streams, unshaded or lightly shaded, in open woodland or unfertilized grassland, rarely on flushed rocks, rare but under-recorded. North Wales, N. England, Scotland.

This species resembles *Verrucaria rosula* in the uneven thallus composed of initially discrete units which coalesce and overlap with age. The external appearance varies considerably, probably due to differences in moisture and exposure of the different collecting sites. The initially discrete units are less finely crenulate than in *V. rosula*, and the surface is more coarsely uneven. In section, the thallus of *V. nodosa* is less clearly divided into small units than in *V. rosula*, and the cells frequently have air spaces between them. The involucrellum in

V. nodosa is more uniform in thickness than *V. rosula*. However, it is possible that some of these differences are due in part to habitat differences: the available specimens of *V. nodosa* are mostly from sunny rocks which are not permanently damp. It is likely that poorly developed specimens of *V. nodosa* and *V. rosula* will be difficult to distinguish by morphology.

More molecular data are needed to establish phylogenetic position, but it is clear from data provided by Orange (2013b) that *V. nodosa* and *V. rosula* are separate taxa, and perhaps related to the *V. macrostoma*/*V. nigrescens* clade.

Verrucaria obfuscans (Nyl.) Nyl. (1881) **NE**

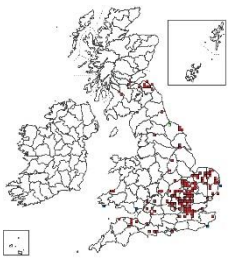


Prothallus absent or black and indistinct. Thallus superficial, well-developed, 300–1200 µm thick; areoles separated by deep cracks, angular in outline, 0.5–1.2 (–2.0) mm diam., flat or slightly concave, yellowish brown, greenish brown, pale brown or mid brown, occasionally pruinose, the sides concolorous with the upper surface or slightly darker; upper surface subdivided by inconspicuous thin lines; margin thin, initially not broken into discrete areas but very early divided by cracks; upper cortex composed of a single layer of small cells with dilute brown pigment, covered by an epinecral layer; algal layer dissected by brown pigmented areas of medulla, the cells arranged in weak columns. Perithecia forming projections 100–200 µm diam., mainly half to one-quarter or rarely three-quarters immersed; involucrellum absent; perithecia in section 180–250 µm diam., the exciple pale brown to brown throughout; ascospores colourless, sometimes two-celled, narrowly cylindric-ellipsoidal, 16–22 × 7–8 µm. Conidiomata not seen. **BLS 2649**.

On limestone, especially associated with metal-enriched run-off below window grills of churches. Common in southern England and southern Scotland, probably overlooked elsewhere; also recorded from Wales (Glamorgan, Caernarvon).

The species has not been sequenced to date, but it was contrasted with *V. macrostoma* by Powell (2015), who highlighted the lack of an involucrellum as a distinctive character. *V. ochrostoma* also lacks an involucrellum and has the peridium pigmented throughout but differs in the pale grey to grey-brown thallus with completely immersed perithecia (Krzewicka 2012).

Verrucaria ochrostoma (Borrer ex Leight.) Trevis. (1860) **DD**



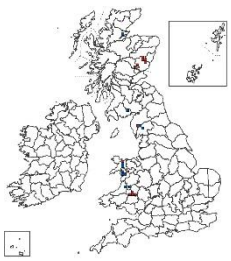
Thallus superficial, well-developed, 300–700(–1000) µm thick, pale grey to grey-brown, of more or less convex and mostly crowded areoles 0.3–0.45 µm diam., forming a crust which becomes secondarily cracked; a distinct epinecral layer present, with dilute brown pigment; medulla without a black basal layer; prothallus absent or indistinct. Perithecia completely immersed, one per areole, possibly the base immersed in the substratum, only the flat brown apex visible; involucrellum absent; exciple pigmented throughout. Ascospores narrowly cylindric-ellipsoidal, sometimes developing a septum, (15.5–) 18.5–23.5 (–27) × (8.5–) 10–13 (–14) µm, length/width ratio (1.5–) 1.6–2.1 (–2.4). Conidiomata not observed. **BLS 1511**.

On limestone, mortar and plaster; widespread and until recently overlooked. Throughout England and Wales, also southern Scotland.

Characterised by the superficial thallus and immersed perithecia without an involucrellum. The epinecral layer can give a somewhat cartilaginous appearance to the thallus. It could be mistaken for a depauperate form of *V. viridula*, and morphs with darker thalli may be similar to *V. nigrescens*. Both of those species have involucrella surrounding the perithecia. No sequences are available, so its phylogenetic position is unknown.

Verrucaria pachyderma (Arnold) Arnold (1880) **Nb**

Thallus dull to dark grey-green, sometimes with a brown tinge, subgelatinous, uncracked or with a few splits developing after collection, 40–180 µm thick, surface smooth; cells in columns, cortex weakly defined, with dull green to dull brown pigment; medulla absent or weakly defined as a zone with few living algae, but a dark basal layer not developed. Perithecia immersed in the thallus, not projecting, or forming low to moderate projections to 400 µm diam. when measurable, apex visible as a grey dot or a black disc, rarely with a black apex more



widely exposed in eroded perithecia; perithecia in section 160–350 µm diam., colourless at sides and base; involucrellum present, varying from thin and appressed to the apex of the perithecium, to conical and narrowly or widely spreading, sometimes reaching to the base of the thallus. Ascospores ellipsoidal to cylindric-ellipsoidal or narrowly so, (15–) 16–22 (–23.5) × (6–) 6.5–9 µm, length/width ratio (1.9–) 2.1–3 (–3.2), perispore absent, or perhaps thin (*ca* 0.5 µm) in some collections. Conidiomata not detected. **BLS 1477**.

On frequently submerged siliceous rocks in rivers; local. N. & W. Britain.

The very smooth dark green or brown thallus is distinctive in the field. The perithecia are often completely immersed and very inconspicuous. Differs from *V. funckii* in the smaller ascospores, the presence of green pigment in the thallus of many specimens, and in some specimens, the more weakly developed involucrellum. *Hydropunctaria scabra* can look similar in the field, but differs in the presence of punctae within the thallus and the smaller ascospores. Possibly a mixture of green and brown pigment is found in the thallus of some specimens.

According to Thüs *et al*. (2015), *V. pachyderma* occupies a clade that also includes the at least partially lichenicolous species *Verruculopsis lecideoides* (A. Massal.) Gueidan & Cl. Roux (2007) and *V. poeltiana*(Clauzade & Cl. Roux) Gueidan *et al*. (2007), but more studies are needed on the relationships of these species.

Verrucaria pallidomurina Orange (2020) **NE**

Thallus at least partly epilithic, dirty white to grey-brown, thalli often discoloured by superficial cyanobacteria, very thin to thin, to 80 µm thick, often discontinuous, cracks none to numerous, often only in thicker pockets or around perithecia; in some specimens also partly endolithic amongst rock crystals; pseudocortex unpigmented or dilute brown; thallus not composed of goniocyst-like units. Perithecia forming low and often ill-defined mounds 180–300 (–360) µm diam., black, without a thalline covering; ostiolar area inconspicuous or rarely visible as a pale dot *ca* 40 µm diam., rarely in a small depression. Involucrellum well-developed, spreading outwards and downwards, extending down a third to three quarters towards the perithecium base, brown, K+ greenish brown. Perithecia in section 160–235 µm diam., colourless or brown. Periphyses 13-30 µm long. Ascospores (19.5–) 21.5–25.5 (–28.5) × 11–12.5 (–13.5) µm, length/width ratio (1.6–) 1.9–2.2 (–2.4), perispore not detected. **BLS 2783**.

On stones of limestone or slightly calcareous siliceous rock, in unshaded, disturbed habitats. S. Wales, N. England, Ireland, probably widespread.

Difficult to distinguish from other small species of *Verrucaria* without sequencing, but the scanty thallus is only weakly pigmented even in good light conditions.

Verrucaria placida Orange (2013) **NE**

Thallus thin, 26–65 µm thick, subgelatinous, translucent when fresh and wet; smooth, more or less matt or slightly glossy, continuous, grey-green to mid brown; contiguous conspecific thalli not separated by dark lines; cells irregularly arranged or in weakly defined columns, coherent, without air spaces between cells; cortex poorly differentiated, comprising a thin layer with few or no photobiont cells (a pseudocortex sensu Gueidan *et al.* 2007), cortical pigment, when present, brown; thallus without a dark basal layer. Perithecia forming conical-hemispherical mounds 400–600 µm diam., at first covered by thallus up to the apex, later sometimes eroded to expose a black apex. Perithecia in section 250–310 µm diam. Involucrellum conical, reaching to the substratum, pigment dark brown, K+ dark grey. Ascospores aseptate, colourless, ellipsoidal, (19–) 21.5–26.5 (–30.5) × (8–) 9–10.5 (–12) µm, length/width ratio (2.0–) 2.2–2.7 (–3.0), perispore apparently absent in mature spores. Conidiomata not detected. **BLS 2544**.

On shaded siliceous rocks and stones in small streams in woodland, rare. Wales (Radnorshire).

This species is related to *Verrucaria hydrophila*, but the ITS sequence shows considerable differences. It differs in morphological terms by the smaller, more crowded perithecia and smaller ascospores. However, *V. placida* is more likely to be confused with *V. elaeomelaena* s.l. which is morphologically similar but not closely related; this differs in the broader ascospores, and the perithecia are usually a little less densely spaced.

Verrucaria policensis Servít (1946) **NE**

Prothallus indistinct, whitish. Thallus endolithic to superficial, thin, widely spreading, dirty ash grey to yellowish grey, cracked into discrete areoles but never regularly areolate, matt. Upper cortex absent, fungal hyphae forming

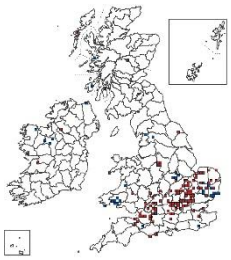
a thin, irregularly developed net surrounding the algae, colourless or yellowish, upper surface uneven, scabrid. Algal layer *ca* 60 µm thick, algal cells 8–15 µm diam. Medulla *ca* 200 µm thick, colourless. Perithecia entirely immersed in the thallus except for the ostiolar region, visible as projecting dark spots 150–200 µm diam.. Involucrellum absent or weakly developed beside the upper exciple. Exciple usually colourless except the brown ostiolar region, globose, 120–160 µm diam. Periphyses 10–15 µm in length. Asci 40–50 × 18–20 µm. Ascospores aseptate, ellipsoidal to cylindrical, 18–21 (–24) × 7.5–10 (–11) µm. Conidiomata not observed.

On a small limestone rock in woodland, England (Somerset, Cheddar Gorge). Only known from a single GBI collection.

Distinguished by the dirty white thallus that is not regularly areolate, the lack (or almost so) of an involucrellum, and the ± colourless exciple [the GBI material has an exciple that is dark throughout]. The poorly known *Verrucaria consociata* lacks and involucrellum and has ascospores that are similar in size, but the thallus is composed of goniocyst-like units and it is reported from stones in streams.

The description has been adapted mostly from Krzewicka (2012).

Verrucaria polysticta Borrer (1834) **Nb**



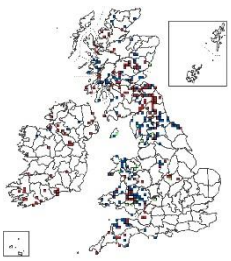
Prothallus present, usually black, non-fimbriate, rarely appearing as a very thin grey to brown film. Thallus epilithic, well-developed, 0.28–1 mm thick; the margin thin, primary areoles arising on the prothallus, these round or oblong, to 0.40 × 0.28 mm, soon becoming crowded and sometimes indistinguishable from each other, forming a crust which then becomes cracked into the mature areoles; mature areoles 0.3–1.1 mm diam., angular in outline, flat or slightly concave; upper surface grey to pale brown, pruinose or not, usually marked by dark lines; sides of mature areoles black; epinecral layer indistinct or present; cortex poorly defined, with dilute to moderately dense brown pigment; medulla densely pigmented, often occupying half or more of the thallus thickness. Perithecia immersed within the mature areoles, not or rarely marginal, 1–14 in number, arising between the delimited thallus units which are visible in surface view, rarely within one of the units; the apex appearing at the thallus surface, usually black, sometimes grey, 100–260 µm diam.; perithecia in section 180–290 µm diam., weakly to strongly pigmented below, strongly pigmented above, the pigment brown or dull greenish brown, K+ slightly darker; involucrellum absent, but the perithecia are usually flanked by dark tissue belonging to the edges of the upper thallus units, with pigment similar to that of the medulla. Ascospores cylindric-ellipsoidal or ellipsoidal, (10.5–) 12.5–15.5 (–16.5) × 5.5–7 (–8) µm, length/width ratio (1.8–) 2.1–2.5 (–3.1), perispore absent. Conidiomata not seen. **BLS 1820**.

On calcareous rock, including limestone and calcareous mudstone; on natural outcrops or on walls, once apparently parasitic on *Verrucaria cernaensis*; local. Widespread, but mainly S. and E. England.

Differs morphologically from *Placopyrenium canellum* and *P. fuscellum* in thallus growth form (distinct primary areoles arising on a prothallus) and in the perithecia mostly arising between the units which become delimited in the upper thallus. *V. polysticta* might also be compared with *Involucropyrenium* species.

According to Gueidan *et al*. (2009), *V. polysticta* belongs in the *Endocarpon* major clade, but is not closely related to other sequenced taxa; more research is needed.

Verrucaria praetermissa (Trevis.) Anzi (1864) **LC**



Prothallus whitish; adjacent thalli often separated by dark lines. Thallus superficial, diffuse, non-gelatinous, pale greenish grey to dull pale brown; surface smooth, typically with numerous cracks when well-developed, but cracks occasionally very few, especially in young areas of thallus; thallus thick when well-developed, as little as 40 µm thick near the margin, but usually up to 100–240 µm thick when mature; epinecral layer absent; cortex weak, without pigment or with brown pigment; cells of thallus irregularly arranged or in weakly defined vertical columns; thallus with a distinct extensive black basal layer, which is often absent or discontinuous in young areas. Perithecia immersed in the thallus, at most forming very low projections which are too ill-defined to measure; apex visible only as a pinkish or brownish dot 60–130 µm diam. when young, later (after abrasion?) often visible as a flat black disc or ring of black dots 60–200 µm diam.; involucrellum present, ± conical, extending laterally below, and typically contiguous with adjacent involucrella, forming the dark 'basal layer' of the thallus; perithecia in section 140–270 µm diam., the exciple thin, *ca* 10–20 µm wide at the side, usually colourless below, occasionally dilute brown in part, or brown when

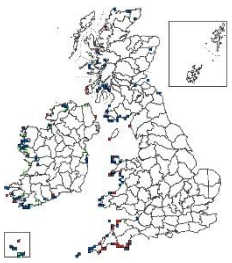
old; ostiolar region often with dark brown or dark green pigment (very rarely with dark greenish-blue pigment). Ascospores (16–) 18–25 (–28) × (6.5–) 7–10 (–10.5) µm, length/width ratio (1.7–) 2–2.9 (–3.3), often with a thin perispore *ca* 0.5 µm thick. Conidiomata not detected. **BLS 1513**.

On a variety of siliceous rocks and on limestone, on the shores of rivers and lakes subject to periodic submersion and on seepage rocks; rarely on damp rocks away from water; tolerant of shade, but also occurring in unshaded habitats; frequent except in lowland regions. Widespread in N. & W. Britain, scattered records in Ireland.

Until recently the concept of this species included *Verrucaria devensis*, which differs in the usually darker, thinner thallus, and a more compact, almost subgelatinous thallus structure. The two species often grow together, when the differences can be clearly seen. The clade to which *V. praetermissa* belongs is included within the broad *Staurothele* clade, according to Gueidan *et al*. (2009).

A host to *Endococcus rugulosus*.

Verrucaria prominula Nyl. (1861) **Nb**



Thallus superficial, often very thin, to 140 µm thick in small depressions in the substratum, white, grey or pale mauve-brown, with a slightly waxy appearance when well-developed. Perithecia moderately projecting to usually prominent, 320–520 (–800) µm diam, conical, rounded or flattened at the apex, not covered by thallus; involucrellum thick, appressed to the exciple, somewhat broadened below. Ascospores cylindrical with rounded apices, occasionally a few slightly constricted in the mid portion, (10.5–) 11.5–14 (–16) × (4.5–) 6.5–8 (–9) µm, length/width ratio (1.4–) 1.5–2 (–2.3). **BLS 1514**.

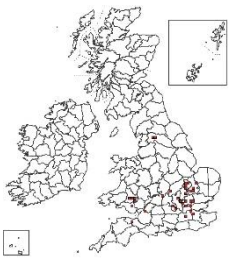
On vertical, shaded faces or in dry crevices on soft, flaking siliceous rocks on seashores, most frequently in the mesic to xeric-supralittoral zones; occasional. Mainly western coasts of Britain and Ireland, rare elsewhere.

Distinguished by the large perithecia, thin thallus and small, distinctly cylindrical ascospores. No sequences are available, so its phylogenetic position is unknown.

Verrucaria romeana B. de Lesd. (1911) **NE**

Verrucaria squamulosa van den Boom & Brand (2003)

Involucropyrenium romeanum (B. de Lesd.) Breuss (2016)



Thallus effuse, greenish grey to pale brown, areolate to irregularly cracked-areolate or sometimes continuous, areoles initially consisting as dispersed squamules, flat to somewhat verrucose, slightly lobulate with a rounded outline, becoming *ca* 1.3 mm diam. and 0.3 mm tall, densely aggregated and often overlapping and incised, subunits sometimes nearly isidium-like and 0.1–0.25 mm diam., matt, laterally discoloured; epinecral layer lacking or thin and colourless; cortex 5–20 µm thick, the upper part pale brownish; rhizoidal hyphae rare, colourless, 2–4 µm diam. Perithecia mostly half-immersed, half to completely covered by areoles, numerous, evenly distributed or in clusters of up to 5, located at the edge of areoles or between the squamules; involucrellum well-developed, 370–900 µm diam., 50–70 µm thick, black, reaching the base of the perithecia, ± contiguous with the exciple or slightly spreading; perithecia 260–360 µm diam., with a relatively short neck, exciple pale brownish below in older perithecia. Ascospores ellipsoidal to ovoid, thin-walled, smooth, (23–) 24–27 (–28) × (8–) 9–13 (–15) µm. Conidiomata inconspicuous, occasionally present, *ca* 100 µm diam. Conidia short bacilliform with rounded ends, sometimes slightly curved, 3.8–4.4 × 0.9–1.1 µm. **BLS 2621**.

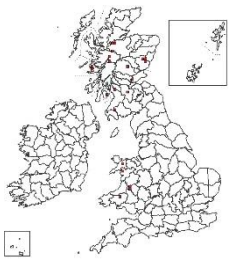
On brick, tiles, concrete etc., usually in damp sheltered situations; quite common at least in southern regions.

Overlooked until recently. *V. macrostoma* has less discrete areoles which are more crenulate and often form a regularly cracked crust. See under *Involucropyrenium* for more information.

Verrucaria rosula Orange (2013) **NE**

Thallus superficial, greenish when young, but older parts light grey-brown to dark brown, often uneven, cracks few to numerous; frequently with scattered areas of new growth in the form of greenish rosette-like patches spreading over the older, darker areas below. In section thallus composed of distinct goniocyst-like units. Perithecia forming projections 240–400 µm diam., often with an uneven covering of thallus below but naked

above, the ostiole rather frequently projecting as a pale papilla, but often flat; involucrellum hemispherical and ± appressed to the exciple except near the base, to ± conical. Ascospores (20.5–) 22.5–26.5 (–28.5) × (7.5–) 9–10.5 (–12.5) µm, length/width ratio (2.0–) 2.3–2.7 (–3.1). Conidiomata rare (seen once), conidia *ca* 5 × 1.2 µm. **BLS 2545**.



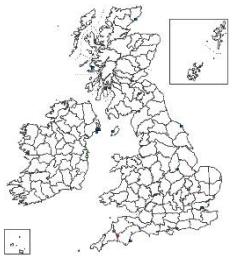
On damp siliceous rocks and stones and in or near streams, often in shade; frequent. Upland Britain, not yet recorded from Ireland.

Often easily identified by the areas of new growth forming small areas with a lobe-like or minutely placodioid appearance; sometimes seen without perithecia. Specimens without new growth areas can be much more nondescript, however. *V. consociata* has a thinner thallus and smaller perithecia.

In phylogenetic terms, *V. rosula* may belong with *V. nodosa* and the *V. macrostoma* clade, but more data are needed.

Verrucaria sandstedei B. de Lesd. (1911) **Nb**

Thallus superficial, very thin, subgelatinous, dark brown to dark green or nearly black, without ridges or punctae. Perithecia forming very small hemispherical projections to 150 µm diam., often flattened above; involucrellum rough, almost reaching the base of the exciple; exciple colourless at the base. Ascospores narrowly cylindric-ellipsoidal, 12–16 × 2–3.5 µm. **BLS 1516**.

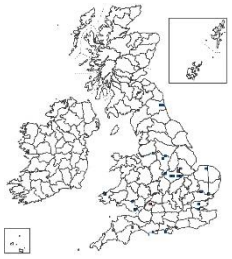


On sheltered siliceous rocks on the seashore, amongst barnacles in the mid-littoral zone; rare.

Only safely distinguished from *V. halizoa* by the very narrow ascospores. A poorly known species for which no sequences are available.

Verrucaria simplex P.M. McCarthy (1988) **LC**

Thallus very thin, brown. Perithecia forming prominent black projections 80–130 µm diam., not covered by thallus; involucrellum absent. Ascospores ellipsoidal or occasionally constricted below, (6–) 7–9.5 (–10.5) × (3.5–) 4–5 (–5.5) µm, length/width ratio (1.7–) 1.8–2.0 (–2.1). **BLS 1647**.

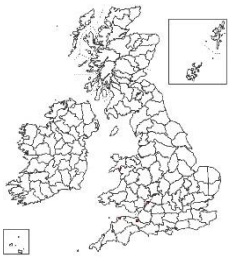


On siliceous or calcareous pebbles and on bone, in woodland or light shade; local, but doubtless overlooked. England, Wales.

A minute and easily overlooked species, for which no sequences are available. *V. bulgarica* differs in the presence of an involucrellum but this can be hard to see without careful sectioning. Perithecia with constricted ascospores may occur together with those with ellipsoidal ascospores, and need further study.

Verrucaria sphaerospora Anzi (1860) **NE**

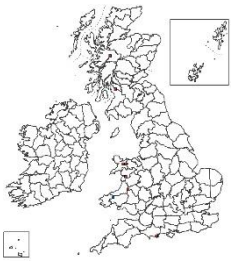
Prothallus absent. Thallus superficial, well-developed, knobbly, areolate to subsquamulose, 0.5–1 mm high, upper surface grey to brownish grey, wrinkled to finely cracked, dull, pruinose or not; areoles subangular to crenate at the margin, 0.5–2 mm diam., subdivided into smaller units by fine pale brown cracks, but never by black lines, the upper surface of areoles sometimes granular-verrucose (composed of goniocysts); sides of areoles in lower part ± dark brown, but in upper part concolorous with the upper surface; upper cortex composed of 1–2 layers of round to angular brown cells. Perithecia one to several per areole, often between smaller units, completely to rarely half-immersed; involucrellum absent (or at least indistinguishable from exciple). Perithecia 200–300 µm diam., the exciple brown to dark brown. Ascospores globose to subglobose, 9–12 × 7.5–10 µm. Conidiomata not observed. **BLS 2624**.



On sandstone, shale and slate, England (N. Devon, Gloucestershire, Somerset), Wales (Merioneth).

Easily distinguished by the small globose to subglobose ascospores (unique in terrestrial *Verrucaria* s.l.), a well-developed superficial areolate to subsquamulose thallus, and completely immersed perithecia.

Verrucaria sublobulata Eitner ex Servít (1950) **LC**



Thallus superficial, 30–200 µm thick, in delimited patches or continuous, non-gelatinous, typically uncracked, the margin typically thinning abruptly, giving a well-defined appearance to the thallus; prothallus absent or very narrow and inconspicuous. Perithecia immersed or forming only low projections, in section 105–175 µm diam.; involucrellum often confined to the apex of the perithecium, occasionally (in slightly prominent perithecia) extending down the sides of the exciple. Ascospores (13.5–) 15–18 (–21.5) × (6–) 7–8.5 (–9) µm, length/width ratio (1.8–) 2.0–2.4 (–2.7). Conidiomata rare (detected in two specimens), wall colourless. Conidia 4.5–6 × *ca* 1.2 µm. **BLS 2515**.

On siliceous rocks and stones in streams and rivers, in open and shaded sites, often occurring in less calcareous places than other freshwater *Verrucaria* spp., occasional; rarely recorded but probably frequent in N. & W. Britain, Ireland.

The small, immersed perithecia and the sharply delimited thallus margin are distinctive. Preliminary phylogenetic data indicate a possible relationship with *V. rupestris*, the type of the genus.

Verrucaria submersella Servít (1954) **NE**

Thallus non-gelatinous, superficial to semi-endolithic, thin to thick (50–150 µm thick), dirty white to greenish grey or yellowish green when wet, cracked, sometimes not adhering at the margin to the substrate but slightly elevated when dry; upper cortex ill-defined, 5–25 µm thick, upper surface scabrous; black basal layer abent; prothallus indistinct. Perithecia half to three-quarters immersed in the thallus, forming moderate projections raised above the thallus, (150–) 250–450 µm diam., naked in the upper part, forming shallow pits in the substrate; involucrellum present, enveloping the upper half of the exciple, rarely reaching to the thallus base, appressed or slightly laterally spreading into the thallus, apical part naked; exciple colourless to pale brown, 200–300 µm diam. Ascospores ellipsoidal, 18–25 (–30) × 8.5–14 µm, without a perispore. Conidiomata not observed. **BLS 2820**.

On chalk stone on a wooded hill, N. Hampshire.

The one British record has been confirmed by sequencing; the habitat is under-recorded so the species may be more widespread. In Europe it is found in riverine habitats, amphibious in splash zones (Thüs & Schultz 2009). The description is largely derived from that work and from Krzewicka (2012).

Verrucaria muralis, often found from similar soft calcareous substrata, is similar in morphological terms to *V. submersella*, and sequencing is recommended for robust identification.

Verrucaria tephromela Wahlenb. ex Orange (2020) **NE**

Prothallus white when young, then brown, or dark brown. Thallus mid to dark brown, weakly to strongly cracked, rather thin (to 90 µm thick); indistinct areoles arising on prothallus and coalescing, thereafter becoming cracked. Pseudocortex brown. Photobiont cells 7-10 × 6-9 µm. Perithecia forming moderate to mostly rather prominent projections 200-400 µm diam., the apex rounded to slightly flattened, black, without thalline covering; ostiolar region inconspicuous or visible as a slightly paler dot 20-40 µm diam. Involucrellum brown, K+ greenish brown. Exciple 190-300 µm diam. Ascospores (18–) 19–23.5 × (10–) 10.5–13 (–13.5) µm, length:width ratio (1.5–) 1.6–2 (–2.3), perispore not seen [examined ascospores were in poor condition]. **BLS 2784**.

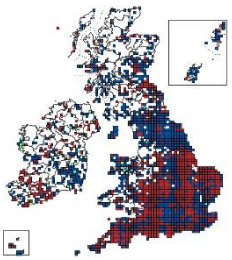
On flushed siliceous rocks above the sea shore, with *Hydropunctaria maura*; Scotland (Outer Hebrides, Shiant Is).

Only known from a single site in Britain and Ireland, and from northern Norway (Finnmark). Not distinguishable from *Verrucaria latebrosa* using morphological examination; sequencing is essential for correct identification. See Orange (2020) for more information.

Verrucaria viridula (Schrad.) Ach. (1803) **LC**

Thallus more or less immersed, visible as brown flecks at the surface of the substratum, or superficial, colour variable, often pale brown, but sometimes white, pale grey, or greenish grey; areolate, divided by cracks; vegetative propagules absent. Perithecia half to almost completely immersed in the thallus, appearing as convex to conical-hemispherical projections 150–500 µm diam., the base immersed in the substrate; perithecia in section 350–600 µm diam., the apex somewhat extended into a short beak, pigmented; involucrellum weakly developed and spreading from the apex of the perithecium, to more or less appressed to the upper half or slightly spreading. Ascospores ellipsoidal to broadly ellipsoidal, (27–) 28.5–34 (–41) × (12–) 14.5–20 (–23.5), length/width ratio

(1.3–) 1.5–2.2 (–2.6), perispore sometimes present, to 0.5 µm thick. Conidiomata appearing as dark dots to 60 µm diam. or more; conidia straight to slightly curved, 7–10 × *ca* 1 µm. **BLS 1518**.



On calcareous rock, including limestone, mortar, mudstone and brick, occasionally on soil; in semi-natural habitats or on walls; common. Throughout Britain and Ireland.

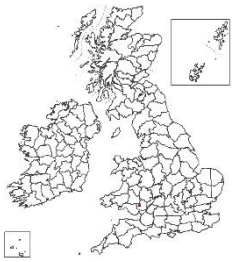
Variable, but distinguished by the large perithecia and large ascospores; the apex of the perithecium is often extended into a short beak. Often only the apex of the perithecium projects from the thallus, giving little indication of the size of the whole perithecium. The thallus is typically superficial and cracked, but can be scarcely developed. *V. hochstetteri* differs in the always endolithic thallus, the absence of an involucrellum, and, in some specimens, the presence of an ornamented perispore.

The phylogenetic position is not settled, but *V. viridula* probably belongs to the *Endocarpon* major clade that includes *V. nigrescens* and perhaps also *V. macrostoma*. Collections of *V. viridula* morphs with reduced thalli may belong to *V. ahtii* or *V. vitikainenii*.

Host to *Endococcus rugulosus*, *Muellerella lichenicola*, *Skyttea spinosa* and *Stigmidium clauzadei*.

Verrucaria vitikainenii Pykälä, Launis & Myllys (2017) **NE**

Prothallus absent or sparse, dark brown. Thallus epilithic, often poorly developed, 20–100 µm thick, discontinuous to continuous or granular, pale brown (rarely), medium brown or dark brown. Perithecia forming mounds 200–360 µm diam., one quarter to half-immersed, not leaving pits, without a thalline covering; ostiole usually inconspicuous, pale brown to dark, flat or depressed, rarely projecting and papilla-like, 20–50 (–70) µm diam., the ostiolar depression occasionally wide and to 130 µm diam; involucrellum extending down to the perithecium base, occasionally enveloping the perithecium, 30–60 µm thick, sometimes increasing in thickness towards the base to 60–80 µm thick, appressed to the exciple, more rarely slightly or moderately diverging. Perithecia in section 190–270 µm diam., wall rarely medium brown, usually dark brown or black. Ascospores (19.5–) 22–25.5 (–28.5) × (10–) 11–13 (–14.5) µm, perispore absent. Conidiomata unknown. **BLS 2698**.

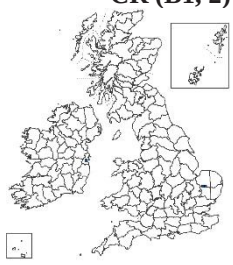


On unshaded brick in colliery spoil. S. Wales (Glamorgan), but probably widespread.

Verrucaria vitikainenii may sometimes be difficult to separate from the closely related *V. ahtii*; that species has a fimbriate prothallus, frequently a pale brown, thicker thallus and often thallus-covered perithecia. Both may be mistaken for collections of *V. viridula* with depauperate thalli.

Verrucaria xyloxena Norman (1867) **CR (B1, 2)**

Thallus superficial, granular-verrucose, brown to black-brown, composed of goniocysts 15–35 µm diam. with brown pigment on the exposed side, the algal cells algal cells 5–10 µm diam.; prothallus absent. Perithecia (0.3–) 0.5 (–0.75)–immersed, brownish black to black, 140–260 µm diam.; in section 130–220 µm diam., ostiole 20–60 µm diam., visible as pale or dark, flat or depressed discs or weakly papillate; exciple pigmented throughout; involucrellum absent. Ascospores ellipsoidal, aseptate, rarely 1-septate when overmature, (13.5–) 16.5–21 (–27) × (5.5–) 6.5–8 (–10) µm, length/width ratio (1.9–) 2.3–3.0 (–3.8), without a perispore. **BLS 1505**.



On calcareous soil, very rare England (West Suffolk, Surrey).

The spore size includes measurements from many non-British specimens. Recently revised by Pykälä *et al.* (2019), and placed within the clade that includes the *V. praetermissa* complex. The description is taken in part from that work.

VERRUCULA J. Steiner (1896)

Thallus areolate or squamulose-areolate, pale grey, greyish brown or dark brown. Cortex thin, of 1–3 layers of cells with light brown walls, generally covered by an epinecral layer that is rarely covered with crystals. Medulla of clearly filamentous hyphae, I+ blue or I–. **Perithecia** small, globose, black, generally entirely immersed except for the ostiolar area. **Involucrellum** absent. **Exciple** colourless except for around the ostiole. **Hymenium** colourless, I+ reddish. **Hamathecium** of inconspicuous periphyses and periphysoids. **Asci** ± broadly clavate, 8-spored, *Verrucaria*-type. **Ascospores** colourless, aseptate or rarely 1-septate, varying from subglobose to narrowly ellipsoidal or almost cylindrical. **Conidiomata** pycnidia, similar in appearance to the perithecia, immersed or slightly prominent, globose or pyriform, with multiple chambers, *Dermatocarpon*-type, the walls colourless except for the ostiolar region. **Conidia** aseptate, straight or slightly curved, bacilliform. **Ecology**: parasitic on thalli of anthraquinone-containing species of Teloschistaceae, subsequently developing an independent thallus.

A monophyletic genus sister to *Placocarpus*; together they form a clade basal to all other Verrucariaceae (Gueidan *et al*. 2009). Although the thalli become independent of the host, they do not seem to persist for long, and the host is usually still present. Identification of the species is not easy, relying on small differences in ascospore size and shape, the size of the areoles, the I+ reaction of the medulla, and the identity of the host. Not all the species have been sequenced, and the genus has not yet been properly studied in our region.

All British and Irish material of *Verrucula* and *Verruculopsis* used to be treated as *Verrucaria latericola* (*Verrucula latericola* (Erichsen) Nav.-Ros. & Cl. Roux), but this species in the narrow sense is said to have ascospores (9–) 10–12.5 (–13) × (4.5–) 5–6 µm, (1.7–) 1.9–2.5 (–3) times as long as wide, and to grow on *Calogaya* (*Caloplaca*) *pusilla*, and is not yet confirmed for our region. *V. latericola* should be considered as a species aggregate pending further studies of British material, and the extreme host specificity claimed by Navarro-Rosines *et al*. (2007) needs further investigation using molecular methods.

Verruculopsis Gueidan, Nav.-Ros. & Cl. Roux (q.v.) has a similar lifestyle and host preference, but has pigmented perithecial walls and affinities to *Placopyrenium*.

Literature

Gueidan *et al*. (2009), Orange *et al.* (2009b), Navarro-Rosinés *et al*. (2007).

1 Ascospores 12–16 µm long 2
Ascospores 14–19.5 µm long 3

2(1) On *Flavoplaca maritima* ..... ***maritimaria***
On *Flavoplaca calcitrapa*, *F. marina* or *F. oasis* ..... ***Verrucula sp***.

3(1) Medulla locally I + blue; ascospores 14–19.5 × 7.5–8 (–8.5) µm, 1.8–2.3 (–2.7) times as long as wide; on *Leproplaca cirrochroa* or *Flavoplaca dichroa* ..... ***helvetica***
Medulla I –; ascospores 15.5–19.5 × 5.5–7 µm, 2.5–3.4 times as long as wide; on *Variospora flavescens* and *Calogaya saxicola* ..... ***Verruculopsis flavescentaria***

Verrucula helvetica (B. de Lesd.) Nav.–Ros. et Cl. Roux (2007) **NE**

Thallus areolate or squamulose-areolate, the areoles scattered or aggregated into undivided thalli; areoles 300–600 µm diam. and 200–300 µm thick, polygonal or more rarely rounded, the upper surface ± flat to convex, irregular, greyish brown, rarely light or bright brown (in shade forms), covered with a whitish–grey pruina; cortex of 1-2 layers of cells with pale to mid brown walls, epinecral layer often discontinuous, to 5 µm thick, weakly I+ blue; medulla locally, and weakly or strongly I+ blue and K/I+ blue. Perithecia 125–160 µm diam., completely immersed or with the upper quarter exposed, 1–4 (-5) in each areole, visible from above due to pigmentation around the ostioles; exciple colourless, but brown in the ostiolar region. Ascospores ellipsoidal, 14–19.5 × 7.5–

8 (–8.5) µm, length/width ratio 1.8–2.3 (–2.7). Conidiomata completely immersed, the wall colourless except for the ostiolar region which is mid brown. Conidia bacilliform, (3–) 4–5 × 1–1.5 µm. **BLS 2759**.

Parasitic on *Leproplaca cirrochroa* and *Flavoplaca dichroa*. N. Wales, but doubtless much under-recorded.

Said to be distinguished by the distinctly I+ medulla, relatively large ascospores, and the identity of the host, but *V. granulosaria* is said to be faintly I+ blue and has spores of a similar size. British material on *L. cirrochroa* and *F. dichroa* share an identical ITS sequence.

Verrucula maritimaria Nav.-Ros. & Cl. Roux (2007) **NE**

Thallus areolate, the areoles aggregated or somewhat scattered, fairly large (0.3–1.6 mm diam.) and thick (250–350 µm), polygonal or irregularly rounded, flat or convex, light brown, pruina sparse or absent, subdivided or not by black lines, contiguous areoles often separated by black slits; cortex of 1-2 layers of cells with light brown walls, epinecral layer non-continuous; medulla I–. Perithecia 100–175 µm diam., all or nearly all immersed, (4–) 7–30 in each areole, visible from above due to pigmentation around the ostioles; exciple colourless, but brown in the ostiolar region. Ascospores narrowly ellipsoidal, (11–) 12–15 (–16) × (4–) 4.5–5.5 (–6.5) µm, length/width ratio (2.0–) 2.4–3.0 (–3.3). Conidiomata ellipsoidal, 145–160 × 55–72 µm. Conidia bacilliform, narrow, 4–5.5 × (0.5–) 1 µm. **BLS 2516**.

Restricted to *Flavoplaca maritima* according to Navarro-Rosinés *et al*. (2007); currently included in the British list but its status is unclear. Records from England (Devon, Somerset) and Scotland (Angus) on *F. maritima* may be this species.

Verrucula sp.

Areoles 400–800 µm diam., *ca* 240 µm thick; upper surface often subdivided by lines, grey-brown with a whitish surface layer, gently uneven or slightly convex, larger than uninfected host areoles, the perithecia 1–12 per areole, visible as a small rough black dot 50–80 µm diam.; cortex and sides of areoles lightly browned in section, epinecral layer present. Perithecia 100–125 µm diam., mostly colourless but brown near the ostiole. Lower parts of thallus K/I– or faintly but distinctly K/I+ lilac-blue. Ascospores 12.5–16 × 5.5–6.5 µm, 2.2–2.9 times as long as wide.

On *Flavoplaca calcitrapa*, *F. marina* and *F. oasis*. Cornwall, N. & S. Wales, probably widespread.

The only species reported on *Flavoplaca* (*Caloplaca*) *marina* by Navarro-Rosinés *et al*. (2007) was *Verrucula hladuniana* (Nav.-Ros. & Cl. Roux) Nav.-Ros. & Cl. Roux, but British specimens on different hosts share a near-identical ITS sequence, and the identity of the taxon described here is uncertain.

VERRUCULOPSIS Gueidan, Nav.-Ros. & Cl. Roux (2007)

Thallus areolate to squamulose-areolate, grey or brown. **Cortex** a thin pseudocortex, the cells with brown walls; usually covered by an epinecral layer. **Medulla** of filamentous hyphae, I–. **Ascomata** perithecia, immersed in the thallus or located between the areoles. **Exciple** dark brown above and pale brown below. **Involucrellum** present or absent. **Asci** clavate, 8-spored. **Ascospores** colourless, aseptate, ellipsoidal or cylindric-ellipsoidal. **Conidiomata** pycnidia, immersed in the thallus, *Dermatocarpon*-type. **Conidia** aseptate, bacilliform, straight or slightly curved. **Ecology**: on rock, free-living or initially parasitic on anthraquinone-containing species of *Caloplaca s.l.*

Morphologically and anatomically similar to *Verrucula* but differing by the pigmented perithecial walls, pale brown below and dark brown above, the medulla always I–, and phylogenetic affinities with *Placopyrenium* rather than *Verrucula*.

Five species are known, of which only one is known to occur in Great Britain and Ireland. It is keyed out along with *Verrucula* species (q.v.)

Literature

Gueidan *et al*. (2009), Navarro-Rosinés *et al*. (2007).

Verruculopsis flavescentaria Gueidan, Nav.-Ros. & Cl. Roux (2007) **NE**
Thallus warted-areolate, small, 2–15 mm diam., the areoles scattered or more often grouped in clusters, initially following the shape of its host but eventually taking an independent form; areoles warted or ± squamulose, 0.5–3.2 mm in maximum dimension, 0.25–0.5 mm thick, polygonal but strongly angular, often ± elongated, the upper surface convex, irregular, white to dark brown, the white parts where an epinecral layer is present, eventually becoming entirely pale greyish brown to dark brown; cortex full of crystals of 1 (-2) layers of cells; medulla I–. Perithecia 150–200 µm diam., immersed or slightly to fairly prominent, 1–4 (6) in each areole; peridium at first colourless but ± brown when mature, always ± dark brown around the neck; periphysoids 17–23 × 2–5 µm. Asci 50–56 × 12–20 µm. Ascospores narrowly ellipsoidal, 15.5–19.5 × 5.5–7 µm, 2.5–3.4 times as long as wide. Conidiomata 70–110 µm diam, conidia bacilliform, 4–5.5 × 1–1.5 µm. **BLS 2517**.

Initially parasitic on *Flavoplaca flavescens* and *Calogaya saxicola* on limestone, Wales (Caernarvon) but doubtless under-recorded.

Indistinguishable in the field from species of *Verrucula*.

WAHLENBERGIELLA Gueidan & Thüs (2009)

Thallus crustose, epilithic, smooth and continuous or cracked, subgelatinous, dark green to greyish yellow green when dry, transparent green when wet (at least at the margins of young and thin thalli), sometimes interrupted by black carbonaceous ridges, rarely reduced to isodiametric punctae. **Photobiont** *Dilabifilum* or (in one non-British species) the brown alga *Petroderma maculiforme*. **Upper cortex** often absent, the algal layer reaching the surface. **Algal layer** formed by vertically oriented hyphae, with algal cells arranged in columns or not. **Medulla** absent or similar in structure to the algal layer. **Perithecia** immersed to superficial, small, with a reduced to dimidiate involucrellum, exciple pale to entirely black. **Hymenium** colourless, K/I+ blue. **Hamathecium** consisting of periphyses and short periphysoids. **Asci** clavate, 8-spored, *Verrucaria*-type. **Ascospores** aseptate, colourless, subglobose to ellipsoidal, with a median length usually shorter than 12 µm. **Conidiomata** pycnidia with a single cavity (although nearby cavities can sometimes be connected laterally), a dark-pigmented ostiole, and elongated conidiogenous cells lining a rudimentary wall. **Conidia** aseptate, bacilliform.

Marine saxicolous lichens growing in the intertidal zone, periodically immersed. A small monophyletic group, basal to other Verrucariaceae except for *Verrucula* and *Placocarpus*. Sequences from Heiðmarsson *et al*. (2017) indicate that *Verrucaria ceuthocarpa* and *V. degelii* may belong in this genus, but that was not the focus of their paper and further molecular data are needed to confirm their position. *Verrucaria halizoa* may well belong here also. All are included in the key below.

Similar to *Hydropunctaria*, but differing by the following combination of characters: small ascospores (median length generally shorter than 12 µm), subgelatinous thallus, smooth surface of the involucrellum, greenish thallus colour, and the general absence of an upper cortex or a differentiated medulla.

Literature
Gueidan *et al*. (2009, 2011), Heiðmarsson *et al*. (2017), Orange *et al*. (2009b), Pérez-Ortega *et al*. (2010).

1 Thallus in section with more or less discrete, densely pigmented areas, these either free or extending upwards from a dark basal layer; in surface view dark dots or ridges often visible on the thallus 2
Thallus in section without such areas; a blackish basal layer may be present, but without distinct upward projections; in surface view without dots or ridges (except dark pycnidia in some species) 3

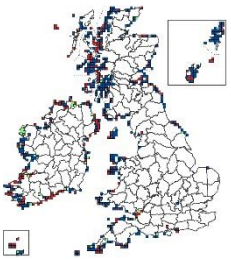
2(1) Thallus cracked into areolae, these bordered by dark ridges ..... ***Verrucaria degelii***
Thallus not cracked (but new cracks can appear after collection) ..... ***striatula***

3(1) Thallus cracked, the cracks with dark sides ..... ***Verrucaria ceuthocarpa***
Thallus usually uncracked, and cracks not dark-sided 4

4(3) Perithecia completely immersed in the thallus ..... ***mucosa***
Perithecia forming projections ..... ***Verrucaria halizoa***

Wahlenbergiella mucosa (Wahlenb.) Gueidan & Thüs (2009) **LC**

Verrucaria mucosa Wahlenb. (1803)



Thallus superficial, to 1 mm thick, subgelatinous, smooth, shiny, uncracked, olive-green (shade) to dark green or black (full sun), weakly translucent when fresh and wet, prothallus white. Perithecia immersed. Involucrellum small, surrounding the apex of the perithecium; perithecia to 150 µm diam., pale except at the apex. Ascospores 7–10 × 4–7 µm, relatively thick-walled. **BLS 1506**.

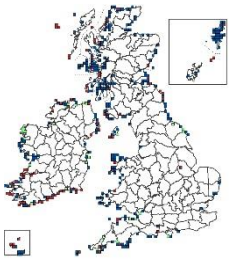
On rocky seashores in the mid-littoral zone, in sun or shade, among barnacles and macroalgae, rarer on sheltered shores and intolerant of silt, forming more or less extensive patches; very common. Throughout Britain and Ireland except S.E. England.

The thallus can resemble the freshwater *Verrucaria elaeomelaena*. *V. ceuthocarpa* is dull brown to ± black, with numerous deep cracks, the perithecia can be more prominent and it is known only from two sites in Scotland.

The probably lichenicolous *Stigmidium marinum* (Deakin) Swinscow (1965) is sometimes associated with this species.

Wahlenbergiella striatula (Wahlenb.) Gueidan & Thüs (2009) **LC**

Verrucaria striatula Wahlenb. (1803)



Thallus superficial, bright green to dark dull green, subgelatinous, translucent when wet, very thin, to *ca* 60 µm; not cracked, but cracks often develop in the dried collections; usually densely covered with shiny, black spots and simple or branched shiny ridges 40–60 × 40–120 µm in size; these ridges become sparse to absent in shade, but obscure the basal green thallus in full sun when the thallus takes on a black appearance. Perithecia forming moderate to prominent conical projections 180–360 µm diam., these often become irregular or lop-sided in shape, often ± angular in surface view, the apex rounded or often flattened, slightly depressed, or lobed; not covered by thallus; involucrellum thick, appressed to the exciple and broadened at the base. Ascospores ellipsoidal, 8–10 (–12) × (5–) 5.5–6 µm, length/width ratio (1.3–) 1.4–1.8 (–2.1). Conidiomata occasional, often abundant when present, visible as black dots to 70 µm diam. with a paler centre; conidia straight or slightly curved, 2.9–4.1 × 1.2–1.6 µm. **BLS 1517**.

On siliceous or calcareous rocks, in the mid-littoral zone on rocky seashores, between zones of *Hydropunctaria amphibia* and *W. mucosa*, often amongst the red alga *Hildenbrandia*; very common. Throughout Britain and Ireland except parts of S.E. & E. England.

The thallus is very variable. *Hydropunctaria amphibia* differs in the longer ascospores, perithecium shape and thinner black ridges. Morphs with no punctae or ridges differ from *Verrucaria halizoa* in the irregularly shaped perithecia. *V. ditmarsica* differs in the smaller perithecia, smaller ridges and brown thallus. *Collemopsidium elegans* recalls this species in its ridged thallus, but has 1-septate ascospores and interascal filaments.

The probably lichenicolous *Stigmidium marinum* is sometimes associated with this species.

Nomenclature

Parabagliettoa impressa (Stizenb.) Orange, **comb. nov.** **IF 900281**

Basionym: *Sagedia impressa* Müll. Arg., *Flora* Regensburg **55**: 504 (1872)
Typification: [France] "ad saxa calcarea ad pedem montis Salève, locis siccis".

Parabagliettoa pinguicula (A. Massal.) Orange, **comb. nov.** **IF 900282**
Basionym: *Verrucaria pinguicula* A. Massal., *Lotos* **6**: 80 (1856).
Typification: [Germany] "ad saxa in Franconia superiori prope Muggendorf' legit Arnold".

Literature

Amtoft, A., Lutzoni, F. & Miądlikowska, J. (2008). *Dermatocarpon* (Verrucariaceae) in the Ozark Highlands, North America. *Bryologist* **111**: 1-40.

Aptroot, A. (2016). The first European *Willeya* (Verrucariaceae) on limestone brought from China. *Herzogia* **29**: 688-691.

Breuss, O. (1990). Die Flechtengattung *Catapyrenium* (Verrucariaceae) in Europa. *Stapfia* **23**: 1-153.

Breuss, O. (1994). Über einige wenig bekannte *Verrucaria*-Arten (Lichenes, Verrucariaceae). *Österreichische Zeitschrift für Pilzkunde* **3:** 15–20.

Breuss, O. (1996). Eine verfeinertes Gliederungskonzept für *Catapyrenium* (lichenisierte Ascomyceten, Verrucariaceae) mit einem Schlüssel für die bisher bekannten Arten. *Annalen des Naturhistorisches Museum Wien* **98B** Suppl.: 35-50.

Breuss, O. (2009a). *Catapyrenium*. In *Lichens of Great Britain and Ireland* (Smith, C.W., Aptroot, A., Coppins, B.J., Fletcher, A., Gilbert, O.L., James, P.W. & Wolselsey, P.A. eds): 281-282. London: British Lichen Society.

Breuss, O. (2009b). *Involucropyrenium*. In *Lichens of Great Britain and Ireland* (Smith, C.W., Aptroot, A., Coppins, B.J., Fletcher, A., Gilbert, O.L., James, P.W. & Wolselsey, P.A. eds): 444-445. London: British Lichen Society.

Breuss, O. (2009c). *Placidiopsis*. In *Lichens of Great Britain and Ireland* (Smith, C.W., Aptroot, A., Coppins, B.J., Fletcher, A., Gilbert, O.L., James, P.W. & Wolselsey, P.A. eds): 707-708. London: British Lichen Society.

Breuss, O. (2009d). *Placidium*. In *Lichens of Great Britain and Ireland* (Smith, C.W., Aptroot, A., Coppins, B.J., Fletcher, A., Gilbert, O.L., James, P.W. & Wolselsey, P.A. eds): 708-710. London: British Lichen Society.

Breuss, O. (2009). A synopsis of the lichen genus *Placopyrenium* (Verrucariaceae), with descriptions of new taxa and a key to all species. *Bibliotheca Lichenologica* **99**: 93–112.

Breuss, O. (2010). An updated world-wide key to the catapyrenioid lichens (Verrucariaceae). *Herzogia* **23:** 205-216.

Breuss, O. (2016). *Involucropyrenium romeanum* is the correct name for *I. squamulosum* (lichenised Ascomycota, Verrucariaceae). *Herzogia* **29**: 196-197.

Breuss, O. & Hansen E.S. (1988). The lichen genera *Catapyrenium* and *Placidiopsis* in Greenland. *Plant Systematics and Evolution* **159:** 95-105.

Breuss, O. & Türk, R. (2004). *Involucropyrenium pusillum* (Verrucariaceae) eine neue Flechtenart aus Oberösterreich. *Beitrage Naturkunde Oberösterreichs* **13**: 213-216.

Bungartz, F., Garvie, L.A.J. & Nash, T.H. (2004). Anatomy of the endolithic Sonoran Desert lichen *Verrucaria rubrocincta* Breuss: implications for biodeterioration and biomineralization. *Lichenologist* **36**: 55-73.

Clauzade, G., Diederich, P. & Roux, C. (1989). Nelikenigintaj fungoj likenlogaj. Ilustrita determinlibro. *Bulletin de la Societe Linneenne de Provence, Numero Special* **1:** 1-142.

Coppins, B.J. (2009). *Trimmatothele*. In *Lichens of Great Britain and Ireland* (Smith, C.W., Aptroot, A., Coppins, B.J., Fletcher, A., Gilbert, O.L., James, P.W. & Wolselsey, P.A. eds): 911. London: British Lichen Society.

Coppins, B.J., Kondratyuk, S.Y., Etayo, S. & Cannon, P.F. (2021). Notes on lichenicolous species of *Opegrapha* s. lat. (Arthoniales) on Arthoniaceae and Verrucariaceae, with a key to British and Irish lichenicolous Opegraphaceae. *Lichenologist* **53**: 159–169.

Czarnota, P. & Coppins, B.J. (2000). A new species of *Agonimia* and some interesting lichens from Gorce Mts (Western Biskidy Mts) new to Poland. *Graphis Scripta* **11(2)**: 56-60.

Diederich, P., Lawrey, J.D. & Ertz, D. (2018). The 2018 classification and checklist of lichenicolous fungi, with 2000 nonlichenized, obligately lichenicolous taxa. *Bryologist* **121**: 340-425.

Dymytrova, L.V., Breuss, O. & Kondratyuk, S.Y. (2011). *Agonimia borysthenica*, a new lichen species (Verrucariales) from Ukraine. *Österreichische Zeitschrift für Pilzkunde* **20**: 25-28.

Ertz, D. & Diederich, P. (2004). Revision of *Trimmatothele* (Verrucariaceae), and a description of *Oevstedalia* for *Trimmatotheliopsis antarctica*, a new lichen genus with true ascoconidia. *Mycological Progress* **3**: 229-236.

Fontaine, K.M., Beck, A., Stocker-Wörgötter, E. & Piercey-Normore, M.D. (2012). Photobiont relationships and phylogenetic history of *Dermatocarpon luridum* var. *luridum* and related *Dermatocarpon* species. *Plants* **2012**(1): 39-60.

Frisch, A. & Ohmura, Y. (2015). The phylogenetic position of *Normandina simodensis* (Verrucariaceae, lichenized Ascomycota). *Bulletin of the National Science Museum* Tokyo, ser. B, **41**: 1-7.

Giavarini, V. & Fox, B.W. (2009). *Endocarpon*. In *Lichens of Great Britain and Ireland* (Smith, C.W., Aptroot, A., Coppins, B.J., Fletcher, A., Gilbert, O.L., James, P.W. & Wolselsey, P.A. eds): 385-386. London: British Lichen Society.

Gueidan, C., Monnat, J.-Y. & Roux, C. (2022). *Verrucariopsis* Gueidan, Monnat et Cl. Roux gen. nov., genre nouveau de lichens (Ascomycota, Verrucariaceae). *Bulletin de la Société Linnéenne de Provence* **73**: 61–77.

Gueidan, C., Roux, C. & Lutzoni, F. (2007). Using a multigene phylogenetic analysis to assess generic delineation and character evolution in Verrucariaceae (Verrucariales, Ascomycota). *Mycological Research* **111**: 1145-1168.

Gueidan, C., Savić, S., Thüs, H., Roux, C., Keller, C., Tibell, L., Prieto, M., Heiðmarsson, S., Breuss, O., Orange, A., Fröberg, L., Wynns, A.A., Navarro-Rosinés, P., Krzewicka, B., Pykälä, J., Grube, M. & Lutzoni, F. (2009). Generic classification of the Verrucariaceae (Ascomycota) based on molecular and morphological evidence: recent progress and remaining challenges. *Taxon* **58**: 184-208.

Gueidan, C., Thüs, H. & Pérez-Ortega, S. (2011). Phylogenetic position of the brown algae-associated lichenized fungus *Verrucaria tavaresiae* (Verrucariaceae). *Bryologist* **114**: 563-569.

Gueidan, C., Van Do, T. & Lu, N.T. (2014). Phylogeny and taxonomy of *Staurothele* (Verrucariaceae, lichenized ascomycetes) from the karst of northern Vietnam. *Lichenologist* **46**: 515-533.

Guzow-Krzemińska, B., Halda, J.P. & Czarnota, P. (2012). A new *Agonimia* from Europe with a flabelliform thallus. *Lichenologist* **44**: 55-66.

Hafellner, J. (2010). Contributions to a revision of lichenized, phaeospored species of *Polyblastia* coll., mainly in the Central European mountains. *Bibliotheca Lichenologica* **104:** 117-141.

Hafellner, J. (2011). *Halospora* resurrected and segregated from *Merismatium*. *Bibliotheca Lichenologica* **106**: 75-93.

Halda, J. (2003). A taxonomic study of the calcicolous endolithic species of the genus *Verrucaria* (Ascomycotina, Verrucariales) with the lid-like and radiately opening involucrellum. *Acta Musei Richnoviensis, Sect. natur*. **10**: 1-148.

Hawksworth, D.L. (1989). Notes on aquatic species of *Verrucaria* in the British Isles. *Lichenologist* **21**: 23–28.

Heiðmarsson, S. (1998). Species delimitation in the long-spored species of *Dermatocarpon* in the Nordic countries. *Annales Botanici Fennici* **35**: 59-70.

Heiðmarsson, S. (2000). The genus *Dermatocarpon* (Verrucariales, lichenized Ascomycotina) in the Nordic countries. *Nordic Journal of Botany* **20**: 605-639.

Heiðmarsson, S., Gueidan, C., Miadlikowska, J. & Lutzoni, F. (2017). Multi-locus phylogeny supports the placement of *Endocarpon pulvinatum* within *Staurothele* s. str. (lichenised ascomycetes, Eurotiomycetes, Verrucariaceae). *Phytotaxa* **306**: 37-48.

Krzewicka, B. (2012). A revision of *Verrucaria* s.l. (Verrucariaceae) in Poland. *Polish Botanical Studies* **27**: 3-143.

Hafellner, J. (2014). Distributional and other data for some *Agonimia* species (Verrucariales, lichenized Ascomycota). *Fritschiana* **78**: 25-46.

Lee, B.G. & Hur, J-S. (2022). A new lichenized fungus, *Psoroglaena humidosilvae*, from a forested wetland of Korea, with a taxonomic key to the species of *Psoroglaena*. *Journal of Fungi* **8**: 392.

Lücking, R. (2008). Foliicolous lichenized fungi. *Flora Neotropica Monograph* **103**: 866 pp.

Lücking, R., Hodkinson, B.P. & Leavitt, S.D. (2016). The 2016 classification of lichenized fungi in the Ascomycota and Basidiomycota – approaching one thousand genera. *Bryologist* **119**: 361-416.

Lücking, R. & Moncada, B. (2017). Dismantling *Marchandiomphalina* into *Agonimia* (Verrucariaceae) and *Lawreymyces* gen. nov. (Corticiaceae): setting a precedent to the formal recognition of thousands of voucherless fungi based on type sequences. *Fungal Diversity* **84**: 119-138.

McCarthy, P.M. (1991). The lichen genus *Endocarpon* Hedwig in Australia. *Lichenologist* **23:** 27–52.

Moberg, M., Tibell, S. & Tibell, L. (eds) (2017). Verrucariaceae I. *Nordica Lichen Flora* **6**: 85 pp.

Morse, C.A. & Ladd, D. (2019). *Staurothele nemorum* sp. nov. (Ascomycota: Verrucariaceae), with a revised key to North American *Staurothele* s. lat. *Lichenologist* **51**: 495-506.

Muggia, L., Gueidan, C. & Grube, M. (2010). Phylogenetic placement of some morphologically unusual members of Verrucariales. *Mycologia* **102**: 835-846.

Navarro-Rosinés, P., Roux, C. & Gueidan, C. (2007). La genroj *Verrucula* kaj *Verruculopsis* (Verrucariaceae, Verrucariales). *Bulletin de la Société Linnéene de Provence* **58**: 133-180.

Nyati, S., Beck, A. & Honegger, R. (2007). Fine structure and phylogeny of green algal photobionts in the microfilamentous genus *Psoroglaena* (Verrucariaceae, lichen-forming Ascomycetes). *Plant Biology* **9**: 390-399.

Orange, A. (1998). *Dermatocarpon leptophyllodes* and related species in the British Isles. *Lichenologist* **30**: 1-20.

Orange, A. (2004a). The *Verrucaria fuscella* group in Great Britain and Ireland. *Lichenologist* **36**: 173-182.

Orange, A. (2004b). A remarkable new freshwater *Verrucaria* from Europe. *Lichenologist* **36**: 349-354.

Orange, A. (2009a). *Atla*. In *Lichens of Great Britain and Ireland* (Smith, C.W., Aptroot, A., Coppins, B.J., Fletcher, A., Gilbert, O.L., James, P.W. & Wolselsey, P.A. eds): 188-189. London: British Lichen Society.

Orange, A. (2009b). *Psoroglaena*. In *Lichens of Great Britain and Ireland* (Smith, C.W., Aptroot, A., Coppins, B.J., Fletcher, A., Gilbert, O.L., James, P.W. & Wolselsey, P.A. eds): 765. London: British Lichen Society.

Orange, A. (2009c). *Merismatium*. In *Lichens of Great Britain and Ireland* (Smith, C.W., Aptroot, A., Coppins, B.J., Fletcher, A., Gilbert, O.L., James, P.W. & Wolselsey, P.A. eds): 581-582. London: British Lichen Society.

Orange, A. (2009d). Two parasitic species of *Placopyrenium* (Verrucariaceae) from freshwater habitats in north-west Europe. *Lichenologist* **41**: 131-139.

Orange, A. (2009e). *Thelidium*. In *Lichens of Great Britain and Ireland* (Smith, C.W., Aptroot, A., Coppins, B.J., Fletcher, A., Gilbert, O.L., James, P.W. & Wolselsey, P.A. eds): 879-883. London: British Lichen Society.

Orange, A. (2012). Semi-cryptic marine species of *Hydropunctaria* (Verrucariaceae, lichenized Ascomycota) from north-west Europe. *Lichenologist* **44**: 299-320.

Orange, A. (2013a). *British and Other Pyrenocarpous Lichens.* 250 pp. Cardiff: National Museum of Wales, https://amgueddfa.cymru/media/13849/Orange-A-2013-British-and-other-pyrenocarpous-lichens.pdf.

Orange, A. (2013b). Four new species of *Verrucaria* (Verrucariaceae, lichenized Ascomycota) from freshwater habitats in Europe. *Lichenologist* **45**: 305-322.

Orange, A. (2014). Two new or misunderstood species related to *Verrucaria praetermissa* (Verrucariaceae, lichenized Ascomycota). *Lichenologist* **46**: 605-615.

Orange, A. (2020) The *Verrucaria aethiobola* group (lichenised Ascomycota, *Verrucariaceae*) in North-west Europe. *Phytotaxa* **459**: 1-15.

Orange, A. (2022). The crustose species of *Normandina* (*Verrucariaceae*). *Lichenologist* **54**: 371–378.

Orange, A. & Aptroot, A. (2009). *Normandina*. In *Lichens of Great Britain and Ireland* (Smith, C.W., Aptroot, A., Coppins, B.J., Fletcher, A., Gilbert, O.L., James, P.W. & Wolselsey, P.A. eds): 625-626. London: British Lichen Society.

Orange, A. & Chhetri, S.G. (2022). Verrucariaceae from Nepal. *Lichenologist* **54**: 139–174.

Orange, A. & Coppins, B.J. (2009). *Dermatocarpon*. In *Lichens of Great Britain and Ireland* (Smith, C.W., Aptroot, A., Coppins, B.J., Fletcher, A., Gilbert, O.L., James, P.W. & Wolselsey, P.A. eds): 371-374. London: British Lichen Society.

Orange, A., Hawksworth, D.L., McCarthy, P.M. & Fletcher, A. (2009b). *Verrucaria*. In *Lichens of Great Britain and Ireland* (Smith, C.W., Aptroot, A., Coppins, B.J., Fletcher, A., Gilbert, O.L., James, P.W. & Wolselsey, P.A. eds): 931-957. London: British Lichen Society.

Orange, A., Purvis, O.W. & James, P.W. (2009a). *Polyblastia*. In *Lichens of Great Britain and Ireland* (Smith, C.W., Aptroot, A., Coppins, B.J., Fletcher, A., Gilbert, O.L., James, P.W. & Wolselsey, P.A. eds): 722-727. London: British Lichen Society.

Orange, A., Purvis, O.W., & James, P.W. (2009c). *Staurothele*. In *Lichens of Great Britain and Ireland* (Smith, C.W., Aptroot, A., Coppins, B.J., Fletcher, A., Gilbert, O.L., James, P.W. & Wolselsey, P.A. eds): 852-856. London: British Lichen Society.

Orange, A. & Purvis, O.W. (2009). *Agonimia*. In *Lichens of Great Britain and Ireland* (Smith, C.W., Aptroot, A., Coppins, B.J., Fletcher, A., Gilbert, O.L., James, P.W. & Wolselsey, P.A. eds): 136-138. London: British Lichen Society.

Pérez-Ortega, S., De Los Ríos, A., Crespo, A. & Sancho, L.G. (2010). Symbiotic lifestyle and phylogenetic relationships of the bionts of *Mastodia tesselata* (Ascomycota, incertae sedis). *American Journal of Botany* **97**: 738-752.

Pérez-Ortega, S., Miller, K.A. & De los Rios, A. (2018). Challenging the lichen concept: *Turgidosculum ulvae* (Verrucariaceae) represents an independent photobiont shift to a multicellular blade-like alga. *Lichenologist* **50**: 341-356.

Pinna, D., Salvadori, O. & Tretiach, M. (1998). An anatomical investigation of calcicolous endolithic lichens from the Triest karst (NE Italy). *Plant Biosystems* **132**: 183–195.

Powell, M. (2015). Two overlooked but widespread crusts: *Verrucaria obfuscans* and *V. ochrostoma*. *Bulletin of the British Lichen Society* **117**: 2-6.

Prieto, M., Aragón, G. & Martínez, I. (2010a). The genus *Catapyrenium* s. lat. (Verrucariaceae) in the Iberian Peninsula and the Balearic Islands. *Lichenologist* **42**: 637-684.

Prieto, M., Martínez, I. & Aragón, G. (2011). The genus *Placidiopsis* in the Iberian Peninsula. *Mycotaxon* **114**: 463-472.

Prieto, M., Martínez, I., Aragón, G., Otálora, M.A.G. & Lutzoni, F. (2010b). Phylogenetic study of *Catapyrenium* s. str. (Verrucariaceae, lichen-forming Ascomycota) and related genus *Placidiopsis*. *Mycologia* **102**: 291-304.

Prieto, M., Martínez, I., Aragón, G., Gueidan, C. & Lutzoni, F. (2012). Molecular phylogeny of *Heteroplacidium*, *Placidium* and related catapyrenioid genera (Verrucariaceae, lichen-forming Ascomycota). *American Journal of Botany* **99**: 23-35.

Prieto, M. & Westberg, M. (2017). *Heteroplacidium* Breuss. In Moberg, R., Tibell, S. & Tibell, L. (eds.), *Nordic Lichen Flora* **6**: 27-28.

Pykälä, J. & Myllys, L. (2016). Three new species of *Atla* from calcareous rocks (Verrucariaceae, lichenized Ascomycota). *Lichenologist* **48:** 111-120.

Pykälä, J., Launis, A. & Myllys, L. (2017a). Four new species of *Verrucaria* from calcareous rocks in Finland. *Lichenologist* **49**: 27-37.

Pykälä, J., Launis, A. & Myllys, L. (2017b). *Verrucaria ahtii*, *V. oulankaensis* and *V. vitikainenii*, three new species from the *Endocarpon* group (Verrucariaceae, lichenized Ascomycota). *Lichenologist* **49**: 107-116.

Pykälä, J., Launis, A. & Myllys, L. (2018). *Verrucaria tenebrosa* (Verrucariaceae), a new lichen species from Finland and Norway, and notes on the taxonomy of epiphytic taxa belonging to the *V. hydrophila* complex. *Phytotaxa* **361**: 211-221.

Pykälä, J., Launis, A. & Myllys, L. (2019). Taxonomy of the *Verrucaria kalenskyi – V. xyloxena* species complex in Finland. *Nova Hedwigia* **109**: 489-511.

Roux, C. and collaborators (2020). *Catalogue des Lichens et Champignons Lichénicoles de France Métropolitaine*. Edn 3: 1769 pp. Fontainebleau: Association Française de Lichénologie.

Roux, C., Gueidan, C. & Navarro-Rosines, P. (2002). La position systematique de *Polyblastia deminuta*. *Mycotaxon* **84**: 1-20.

Savić, S. & Tibell, L. (2008a). *Atla*, a new genus in the Verrucariaceae (Verrucariales). *Lichenologist* **40:** 269-282.

Savić, S. & Tibell, L. (2008b). The lichen genus *Henrica* (Verrucariaceae, Eurotiomycetes) in northern Europe. *Nordic Journal of Botany* **26**: 237-247.

Savić, S. & Tibell, L. (2009). Taxonomy and species delimitation in *Sporodictyon* (Verrucariaceae) in Northern Europe and the adjacent Arctic—reconciling molecular and morphological data. *Taxon* **58**: 585-605.

Savić, S., Tibell, L., Gueidan, C. & Lutzoni, F. (2008). Molecular phylogeny and systematics of *Polyblastia* (Verrucariaceae, Eurotiomycetes) and allied genera. *Mycological Research* **112**: 1307-1318.

Schmitt, I., del Prado, R., Grube, M. & Lumbsch, H.T. (2009). Repeated evolution of closed fruiting bodies is linked to ascoma development in the largest group of lichenized fungi (Lecanoromycetes, Ascomycota). *Molecular Phylogenetics and Evolution* **52**: 34-44.

Sérusiaux, E., Diederich, P., Brand & van den Boom, P. (1999). New or interesting lichens and lichenicolous fungi from Belgium and Luxembourg. VIII. *Lejeunia* **162**: 1-95.

Swinscow, T.D.V. (1971). Pyrenocarpous lichens: 15. Key to *Polyblastia* in the British Isles. *Lichenologist* **5**: 92-113.

Thüs, H., Muggia, L., Pérez-Ortega, S., Favero-Longo, S.E., Joneson, S., O'Brien, H., Nelsen, M.P., Duque-Thüs, R., Grube, M., Friedl, T., Brodie, J., Andrew, C.J., Lücking, R., Lutzoni, F. & Gueidan, C. (2011). Revisiting photobiont diversity in the lichen family Verrucariaceae (Ascomycota). *European Journal of Phycology* **46**: 399-415.

Thüs, H. & Nascimbene, J. (2008). Contributions toward a new taxonomy of Central European freshwater species of the lichen genus *Thelidium* (Verrucariales, Ascomycota). *Lichenologist* **40**: 499–521.

Thüs, H., Orange, A., Gueidan, C., Pykälä, J., Ruberti, C., Lo Schiavo, F. & Nascimbene, J. (2015). Revision of the *Verrucaria elaeomelaena* species complex and morphologically similar freshwater lichens (Verrucariaceae, Ascomycota). *Phytotaxa* **197**: 161-185.

Thüs, H. & Schultz, M. (2009). *Fungi: Lichens Pt. 1* (Süßwasserflora von Mitteleuropa / Freshwater Flora of Central Europe). Spektrum Akademischer Verlag, Heidelberg, Germany. 223 pp.

Tibell, S. & Tibell, L. (2015). Two new species of *Atla* (Verrucariaceae). *Lichenologist* **47:** 93-98.

Tibell, S. & Tibell, L. (2017). *Polyblastia*. In Moberg, R., Tibell, S. & Tibell, L. (eds), *Nordic Lichen Flora* **6**: 35-52.

Triebel, D. (1989). Lecideicole Ascomyceten. Eine Revision der obligat lichenicolen Ascomyceten auf lecideoiden Flechten. *Bibliotheca Lichenologica* **35**: 1-278.

Van den Boom, P. & Brand, M. (2003). *Verrucaria squamulosa*, a new species from Belgium, Luxemburg and the Netherlands (lichenized ascomycetes, Verrucariales). *Linzer Biologisches Beiträge* **35**: 547-553.

Yuzon, J., Roux, C., Lendemer, J.C. & Gueidan, C. (2014). Molecular phylogeny and taxonomy of the endolithic lichen genus *Bagliettoa* (Ascomycota: Verrucariaceae). *Taxon* **63**: 1177-1192.

Index