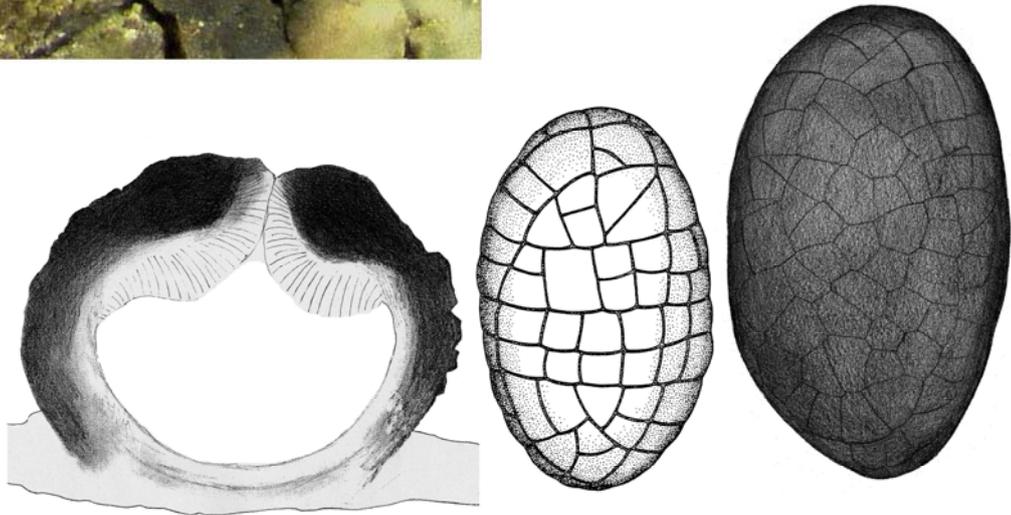
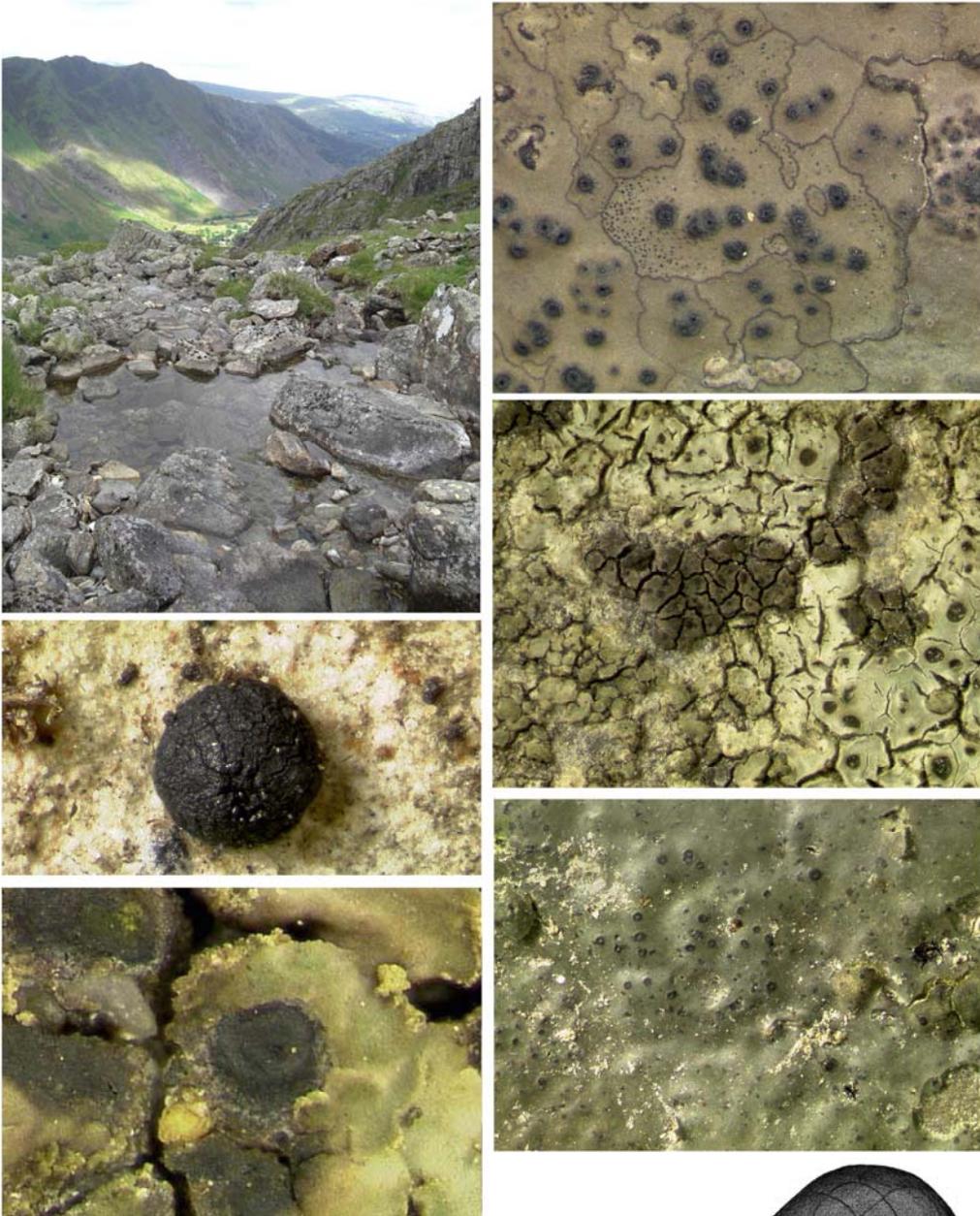
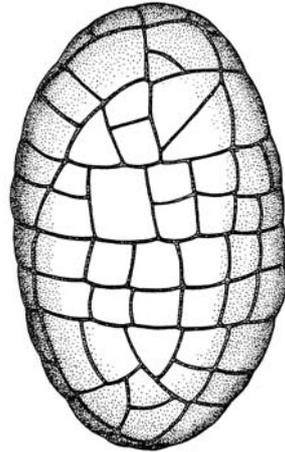


British and Other Pyrenocarpous Lichens



Alan Orange
August 2013

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Note:

This informal identification guide was originally prepared for the British Lichen Society Workshop 'Pyrenocarps on Rock', held at the Blencathra Field Study Centre, Keswick, Cumbria, on 26 August to 2 September 2006. Although much of the material is original, most of the accounts were originally prepared for the second edition of the *The Lichen Flora of the Great Britain and Ireland*, and the authorship is complex. Some accounts are almost completely the work of other authors.

This version updates some taxonomy and nomenclature, and includes some colour images, but is still only a preliminary account, especially for Verrucariaceae.

1 Introduction

1.1 What is a pyrenocarp?

According to the Dictionary of Fungi, the term 'pyrenocarp' is synonymous with the term perithecium, but is colloquially used to mean a fungus with perithecia.

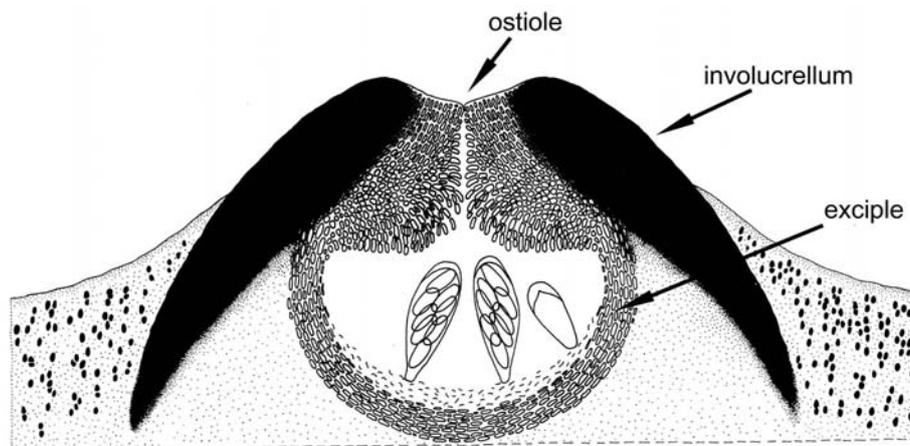
A perithecium is a fruiting body which is rounded or flask-shaped, and which opens by a narrow pore at the apex, as opposed to an apothecium, where the hymenium is exposed as a narrow or broad disc.

As it is usually used now, the term perithecium is purely descriptive of the shape and does not imply any particular mode of development. Despite this, it is possible to see in the literature phrases like 'ascomata apothecia, but perithecia-like'. In some of these cases the taxon in question has ascomata which open by a narrow pore, whereas its close relatives have ascomata which are similar in structure but have at least a narrow disc. Thus the perithecioid ascomata in these taxa can be seen as an extreme development of 'apothecia'. In other cases, although the ascoma appears to open by a narrow pore in dry material, when the ascoma is wet the pore may gape open to some extent so that the hymenium is more or less exposed, and the ascoma is functionally an apothecium.

In the keys below, all British lichenized fungi with perithecioid ascomata are included, at least to genus.

1.2 Taxonomic characters

1.2.1 Exciple and involucrellum

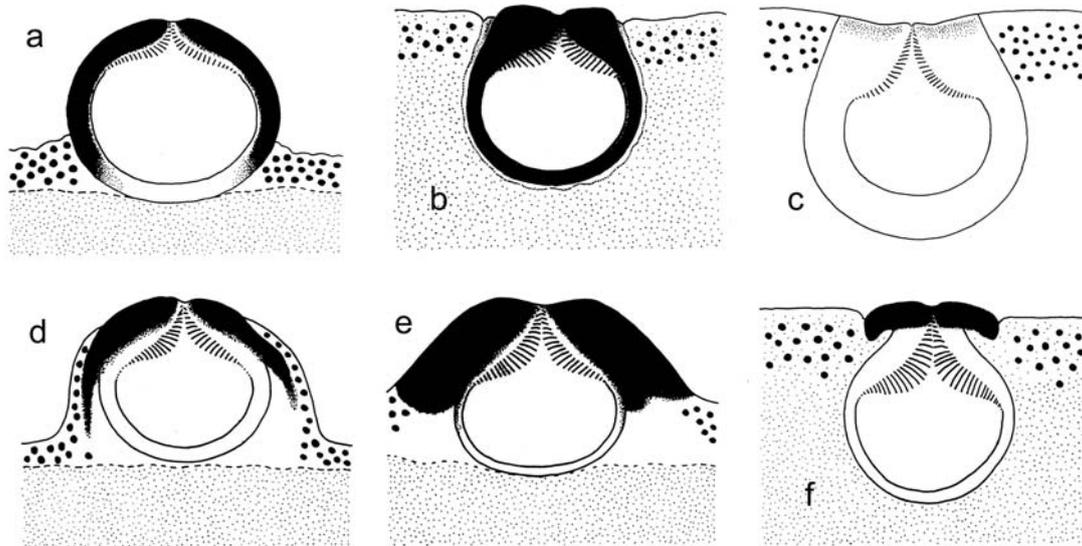


The hymenium is usually delimited by a layer of cells, the exciple (or excipulum). This may be colorless or pigmented, thin or thick. The hyphal structure of the exciple can be a useful taxonomic character, mainly at generic level or above, varying from a pseudoparenchyma to tissues where the filamentous nature of the hyphae is apparent.

Outside the exciple, there is sometimes a pigmented zone, presumably of protective function, known as the involucrellum (the term clypeus is often used more or less synonymously, although that term sometimes implies that host tissue is incorporated into it). The involucrellum appears to be formed as a result of different developmental pathways in different taxa: in some species it develops from part of the ascoma primordium, but in others it develops by darkening of thallus cells adjacent to the ascoma. For this reason it seems unnecessary to be too pedantic about whether an involucrellum is present or absent; it is better to describe each individual situation. An involucrellum is usually

regarded as present when it can be distinguished as a separate structure from the exciple. When the exciple itself is darkly pigmented this is not regarded as an involucrellum.

In species including *Belonia russula* and *Porina lectissima*, the perithecium is often said to be covered by a layer of thallus. Although this layer contains photobiont cells, the hyphae are thicker-walled than in the thallus, and the layer is also thicker than the normal thallus. This layer covering the perithecium can reasonably be regarded as an involucrellum.



The figure shows examples of perithecia:

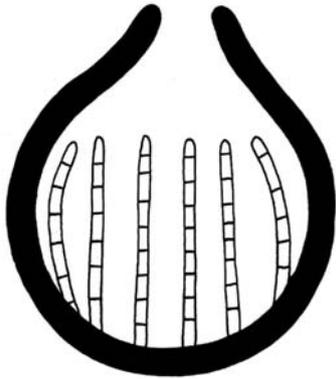
- a. involucrellum absent, exciple pigmented except at base.
- b. involucrellum absent, exciple pigmented throughout; ascoma in pit in limestone.
- c. involucrellum absent, exciple unpigmented or almost; ascoma immersed in thallus.
- d. involucrellum present, exciple unpigmented except at ostiole; ascoma partly covered by layer of thallus.
- e. involucrellum present, exciple unpigmented except at ostiole.
- f. involucrellum present, disc-shaped; exciple unpigmented except at ostiole; ascoma in pit in limestone.

1.2.2 Hamathecium

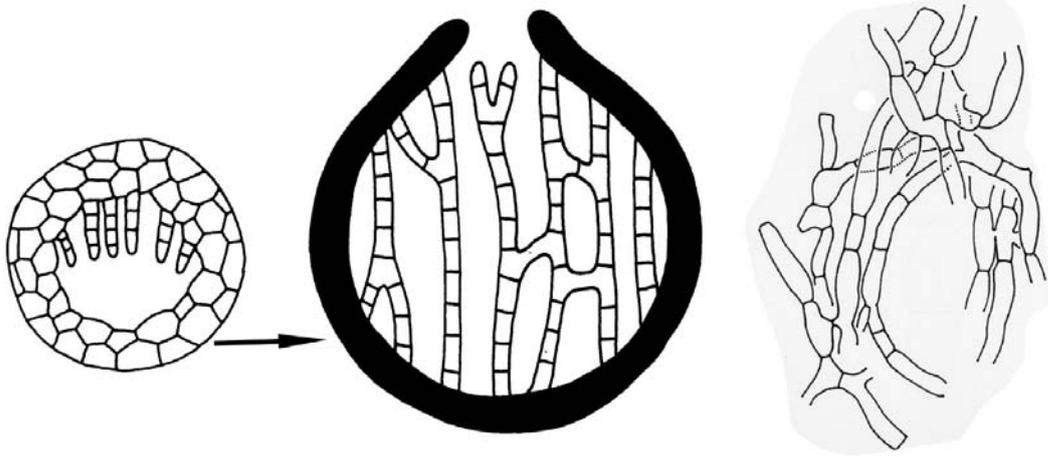
The term ‘hamathecium’ is a neutral term for all tissues (usually filamentous) occurring between the asci or projecting into the cavity of the ascoma. Several types are recognized (sometimes more than one can occur together); these are defined by the origin of the tissue during development of the ascoma.

Although the types often differ in their appearance in the mature ascoma, only careful developmental studies of the young stages of the ascoma can provide conclusive proof of the type present, and such studies are beyond the scope of the average lichenologist. For this reason, the neutral term ‘interascal filaments’ is useful to specify any hyphal tissues penetrating between the asci (either paraphyses, pseudoparaphyses or paraphysoids in the list below). The types of hamathecium are:

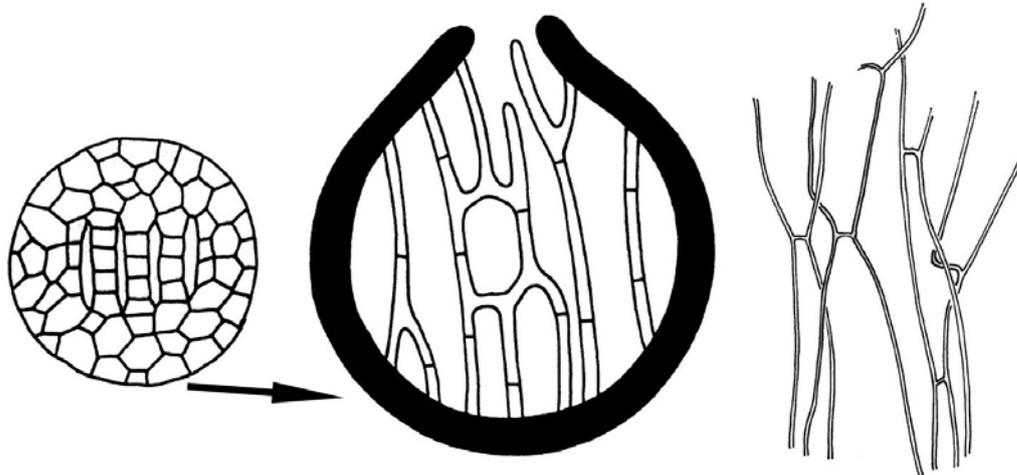
Paraphyses – filaments which grow upwards from the base of the ascomal cavity; these are often unbranched, or only sparingly branched and anastomosed:



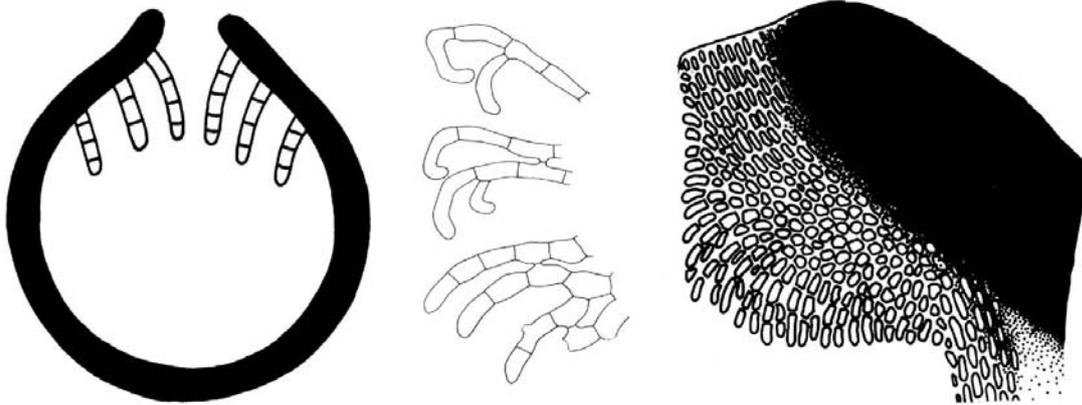
Pseudoparaphyses – filaments which grow down from the roof of the ascomal cavity, becoming attached to the base and often free above; they are often regularly septate, branched and anastomosing, relatively broad, and with an irregular 'lumpy' outline:



Paraphysoids – interascal tissue which stretches as the ascoma increases in size; they are often branched and anastomosing, but slender and with distant (often inconspicuous) septa:



Periphysoids: filaments which grow down from the roof of the ascomal cavity, but do not reach the base. Often grade into periphyses, as in right-hand diagram:



Periphyses: unbranched short hyphae lining the ostiolar canal, and directed upwards:

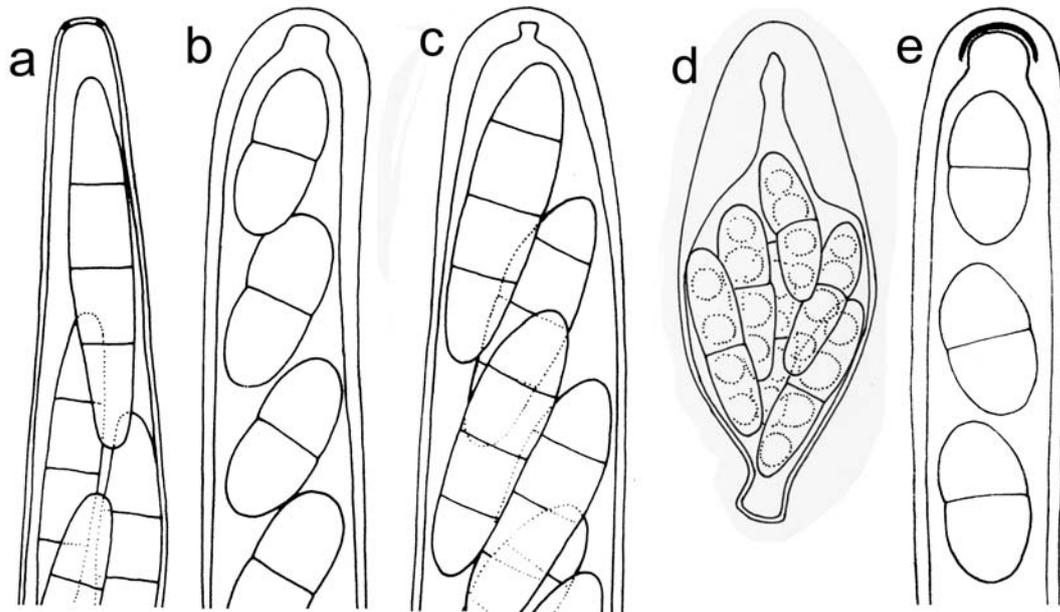


1.2.3 Asci

The ascus wall may be uniformly thin, or variously thickened, especially towards the apex. These thickenings, or lack of them, are related to the type of dehiscence. Asci are best observed first in water, and then in K. A number of asci, both mature and immature, should be examined.

Uniformly thin-walled asci, such as those in *Porina*, show no thickening of the wall in water or K. The asci of the superficially similar genus *Strigula* show a distinct thickening of the wall near the apex. If thickenings are not easy to see in water, the inner wall layers of asci often swell in K, making the thickening conspicuous. Thickenings, and structures in the apex, are often easier to see in immature asci. The thickened apex of an ascus often has a cavity in the underside, the ocular chamber. In K this can become closed by swelling of the adjacent wall, so that it appears as a line rather than a cavity. The shape of the ocular chamber has some taxonomic significance, and it is the shape in water that is usually referred to.

The ascus wall, or structures in the ascus apex, may show a reaction with iodine solution (see below).



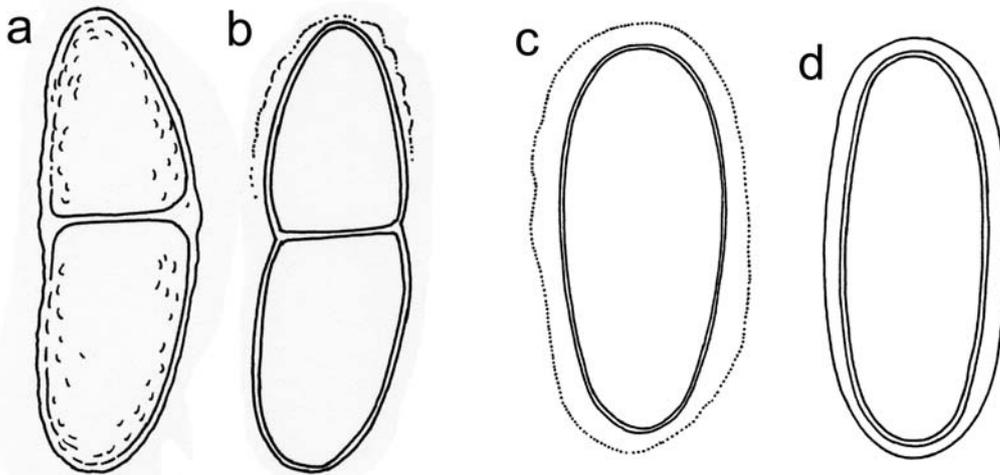
The figure shows apices of asci:

- a. wall uniformly thin-walled (apex also has a refractive ring) (*Porina lectissima*).
- b. wall thickened above, apex with broad ocular chamber (*Anisomeridium*).
- c. wall thickened above, with narrow ocular chamber (*Strigula*).
- d. wall thickened above (*Arthopyrenia*).
- e. wall thickened at apex, containing a thin dome (shown here staining with Congo Red) (*Acrocordia*).

1.2.4 Ascospores

Ascospore septation is an important character at species-level, but the presence of only immature spores can be misleading. Conversely, over-mature spores, or spores in material in poor condition, may show additional septa to the usual number. Mature, healthy spores can often be distinguished by their 'plump' appearance and smooth, well-defined outlines, especially in fresh material. One way to ensure that only healthy spores are seen is to place a coverslip on the surface of freshly collected material placed in a damp chamber, for a few hours, but this is rarely necessary. In *Verrucaria* and related genera, immature spores are usually narrower in shape than mature spores.

The perispore is a gelatinous layer that surrounds the main spore wall in some taxa. In some species it is conspicuous, but in others it may be less easy to decide if one is present. Sometimes it can be seen surrounding each spore within the ascus. The perispore can be seen in water, but observing spores in Congo Red stain in K can be helpful. The perispore can be compact and difficult to distinguish from the spore wall. In *Acrocordia* the warty appearance of the spores is apparently due to the perispore, which becomes indistinct in K.



The figure shows examples of perispores:

- a. warty perispore not distinguishable from wall, in water (*Acrocordia*).
- b. same spore in K, perispore becoming indistinct.
- c. gelatinous perispore easily distinguishable from the spore wall (*Verrucaria aethiobola*).
- d. compact perispore easily overlooked as part of a 'layered' spore wall (*Verrucaria aethiobola*).

Ascospores may be colourless, or the walls may turn brown at maturity in some taxa. In these, healthy, mature spores are brown. In a few taxa, the mature spores are colourless, but over-mature spores may be brownish, often with a granular perispore.

1.2.5 Iodine reactions

Various parts of the hymenium give a constant and valuable reaction with iodine. For most purposes a solution with a concentration of 0.5 % iodine is adequate (see below). For more critical work (when describing a species, for instance) it is necessary to record the concentration of iodine used, and sometimes to use more than one concentration.

Lugol's solution is adequate for general use:

iodine	0.5 g
potassium iodide	1.5 g
distilled water	100 ml

For more precise work it is useful to use a range of iodine-potassium iodide (IKI) solutions with different concentrations of iodine, where there is twice as much potassium iodide as iodine. Thus 0.5 % IKI is made up as:

iodine	0.5 g
potassium iodide	1 g
make up to 100 ml with distilled water (dissolve the iodine and potassium iodide first in a small volume of water, then make up to full volume when dissolved).	

Procedure for routine work:

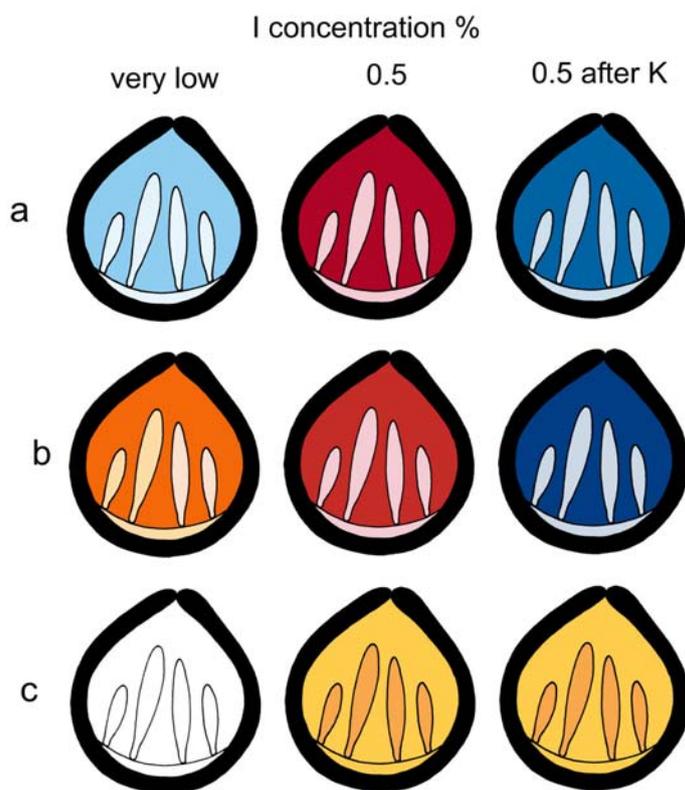
1. Mount a section of the hymenium in water.
2. Add a drop of iodine to the side of the coverslip and draw it through using a piece of tissue.

3. Observe colour changes (reddish or blue, colours sometimes dull and inconspicuous); under high power note whether they are associated with gel surrounding the asci and hamathecium, or whether they are localized in the ascus wall.
4. Treat another (or the same) section with 5–10% KOH, and add iodine (excess KOH prevents colour reactions, so it is useful to wash the section in water before adding iodine). Observe colour changes as before. This reaction is often written as 'K/I'.

Colour reactions, if they occur, depend on the concentration of iodine and whether the hymenium has been pre-treated with KOH. Statements in the literature that the hymenium 'changes from blue to red' with iodine are misleading, as the initial blue reaction is merely due to the initial very low concentration of iodine as it is drawn under the coverslip.

Note that simple absorption of iodine, resulting in a yellow-brown or reddish brown colour of tissues, is a negative reaction.

All Verrucariaceae, and some others, show a 'hemiamyloid' reaction of the hymenial gel. This reaction is I + red, but I + blue after treatment with K. Some species of *Thelocarpon* are similar, but are I + orange or orange-red. Iodine reactions of the hymenium in lichens are usually reddish or blue (not shades of lilac or violet as often seen in thalline tissues), but some species of *Mycomicrothelia* show an I + violet reaction.



The figure shows examples of iodine reactions of the hymenial gel (diagrammatic):

- a. I + red, K/I + blue (hemiamyloid), but briefly I + blue at very low concentrations as iodine is introduced (Verrucariaceae).
- b. I + orange-red, K/I + strong blue; no blue reaction at very low concentrations (*Thelocarpon opertum*).
- c. no reaction: yellow-brown or reddish brown tints are due to simple absorption of iodine.

1.2.6 Pigments

Most pyrenocarps have dark, acetone-insoluble pigments in the ascoma wall. These have not been chemically characterized, but the colours in water and in K and strong acids can be helpful.

Mount a thin section in water and observe the colour. Run in K (10% KOH) and observe any changes in colour, and whether the pigment goes into solution. It is sometimes useful to look at the colour in N (concentrated nitric acid: water 1: 1); this reagent produces corrosive fumes, so it is best to mount a

section directly into N (use a small drop so there is not excess N outside the coverslip) and observe quickly, without leaving the slide on the microscope stage longer than necessary.

To describe a pigment more fully, follow the procedure in Meyer & Printzen (2000), summarized in Orange *et al.* (2001).

2. Classification

Ascomycete classification above the rank of family has long been in a state of flux, and molecular methods are currently the most important means by which relationships are being worked out. Character states previously considered to be of prime importance in pyrenocarp classification, such as the ascolocular versus ascohymenial development of the ascoma, and unitunicate versus bitunicate asci, are now regarded as having arisen more than once in the evolution of the fungi, and to be in any case oversimplifications of a greater diversity of character states. Taxa with perithecioid ascomata occur widely amongst the lichenized ascomycetes. An important new outline of the classification fungi, down to the level of order, was produced by Hibbett *et al.* (2007). The position of the lichenized ascomycetes is indicated in Fig. 1. Ostropales, Pyrenulales and Verrucariales contain significant numbers of distinctly pyrenocarpous taxa; some families of uncertain position in Dothideomycetidae contain pyrenocarpous lichens, but most members of this group are non-lichenized. Capnodiales, Lichinales and Pertusariales contain small numbers of species with perithecioid ascomata. The position of all genera of fungi is listed in Lumbsch & Huhndorf (2007).

3. Nomenclature

The binomial system of names established by Linnaeus has two functions: to act as a universally agreed label for a species, and to indicate its relationship with other, closely related species. Unfortunately these two functions are in conflict. Changing knowledge of relationships between species means that species can be transferred to other genera, thus changing the species' name and undermining its use as a label. In the present work, a conservative approach is taken to new generic names. This is purely for practical reasons, and does not imply any criticism of the use of new genera. We must be thankful that Linnaeus did not introduce a trinomial system, whereby the species name carried information on its placement in a family, as well as a genus.

Name changes also occur because of changes in circumscription of a species (species may be split or merged as a result of taxonomic studies), or because an examination of the type specimen shows that names have been misapplied.

References

- Hibbett, D.S., Binder, M., Bischoff, J.F., Blackwell, M., Cannon, P.F., Eriksson, O.E., Huhndorf, S., James, T., Kirk, P.M., Lücking, R., Lumbsch, H.T., Lutzoni, F., Matheny, P.B., McLaughlin, D.J., Powell, M.J., Redhead, S., Schoch, C.L., Spatafora, J.W., Stalpers, J.A., Vilgalys, R., Aime, M.C., Aptroot, A., Bauer, R., Begerow, D., Benny, G.L., Castlebury, L.A., Crous, P.W., Dai, Y.-C., Gams, W., Geiser, D.M., Griffith, G.W., Gueidan, C., Hawksworth, D.L., Hestmark, G., Hosaka, K., Humber, R.A., Hyde, K.D., Ironside, J.E., Kõljalg, U., Kurtzman, C.P., Larsson, K.-H., Lichtwardt, R., Longcore, J., Miądlikowska, J., Miller, A., Moncalvo, J.-M., Mozley-Standridge, S., Oberwinkler, F., Parmasto, E., Reeb, V., Rogers, J.D., Roux, C., Ryvarden, L., Sampaio, J.P., Schüßler, A., Sugiyama, J., Thorn, R.G., Tibell, L., Untereiner, W.A., Walker, C., Wang, Z., Weir, A., Weiss, M., White, M.M., Winka,

K., Yao, Y.-J. and Zhang, N. (2007) A higher-level phylogenetic classification of the Fungi. *Mycological Research* **111**: 509-547.

Lumbsch, H.T. & Huhndorf, S.M. (eds) (2007) Outline of Ascomycota – 2007. *Myconet* **13**: 1-58. [online at <http://www.fieldmuseum.org/myconet>].

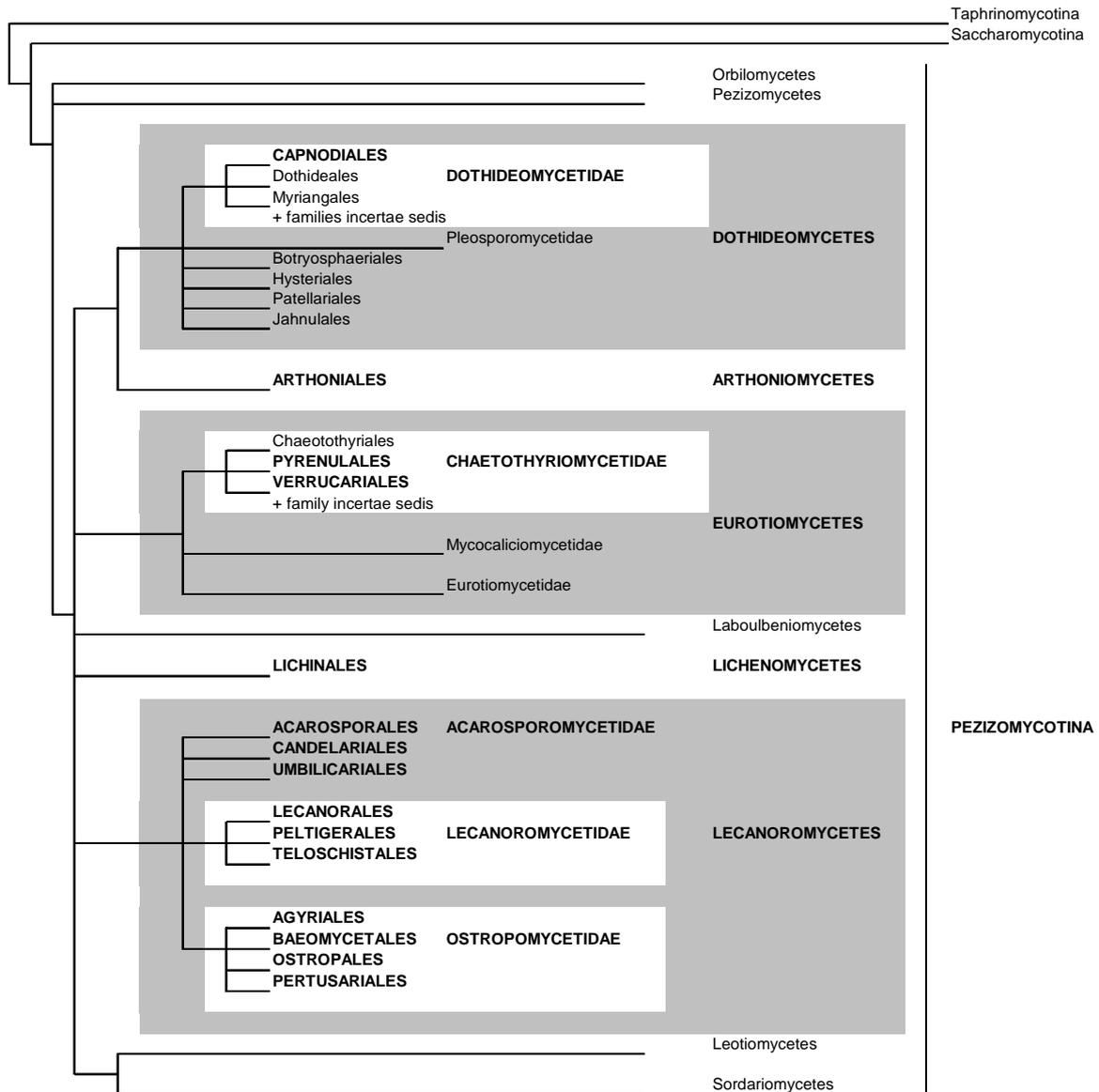


Fig. 1. The position of lichenized taxa in the Ascomycota (adapted from figure in Hibbett et al. 2007). Taxa in upper case contain at least some lichenized species.

3. Keys to genera of British lichens with perithecioid ascomata (all substrata)

The key includes some non-lichenized, non-lichenicolous fungi, but non-lichenized, lichenicolous genera are excluded.

Key A. Thallus fruticose, foliose or squamulose

- | | | |
|---|--|--------------------------|
| 1 | Photobiont a cyanobacterium | 2 |
| | Photobiont a green alga | 4 |
| 2 | Thallus squamulose, comprising umbilicate clusters or rosettes of lobes or lobules
..... <i>Phylliscum (damangeonii)</i> | |
| | Thallus fruticose | 3 |
| 3 | Thallus form determined by the growth form of the photobiont (<i>Stigonema</i>), the cells of
which form transverse tiers easily visible in whole mounts of thallus branches, the mycobiont
hyphae mainly running through the sheaths of the photobiont, near the surface of the branches
..... <i>Ephebe</i> | |
| | Thallus form not determined by the growth form of the photobiont (<i>Calothrix</i> or <i>Dichothrix</i>),
the cells of which occur in clusters but do not form tiers; mycobiont hyphae abundant, also
forming a photobiont-free central strand to the thallus branches
..... <i>Lichina</i> | |
| 4 | Thallus minutely squamulose or minutely fruticose, without special attachment organs, lower
cortex absent or scarcely differentiated | 5 |
| | Thallus squamulose or foliose, attached to substratum by rhizohyphae, rhizines or holdfasts,
lower cortex often present | 6 |
| 5 | Ascomata pale, exciple without dark pigments; ascospores septate to muriform, 8 per ascus
..... <i>Psoroglaena</i> | |
| | Ascomata dark, exciple with dark pigments; ascospores muriform, 2–8 per ascus
..... <i>Agonimia</i> | |
| 6 | Hymenium containing photobiont cells; ascospores muriform, 1–2 per ascus | <i>Endocarpon</i> |
| | Hymenium not containing photobiont cells; ascospores various | 7 |
| 7 | Thallus squamulose to distinctly foliose, attached by one or more holdfasts, rhizohyphae
absent; lower cortex of anticlinal rows of thick-walled cells, the inner cells larger than the
outer, with brown pigment at surface; ascospores simple; growing tightly attached to rock
..... <i>Dermatocarpon</i> | |
| | Thallus squamulose, attached by rhizohyphae, holdfasts absent; lower cortex absent or
present; ascospores simple or 1-septate; growing on soil or in rock crevices, rarely tightly
attached to rock | 8 |
| 8 | Ascospores simple | <i>Catapyrenium s.l.</i> |
| | Ascospores 1-septate | <i>Placidiopsis</i> |

Key B. Thallus crustose

- | | | |
|------|--|---|
| 1 | Photobiont a cyanobacterium | 2 |
| | Photobiont a green alga, or absent | 5 |
| 2(1) | Ascospores 1-septate; all parts of hymenium I-, hamathecium of branched and anastomosing
interascal filaments | 3 |

- Ascospores simple; thallus and hymenium various 4
- 3(2) Thallus of small globose or flattened squamules up to 0.5 mm diam., connected to the base of the ascoma by thick-walled, dark hyphae; on dead bryophytes or plant debris in montane habitats *Frigidopyrenia (bryospila)*
Thallus a continuous, patchy, or cracked crust, not connected to base of ascoma by dark hyphae; on wet or calcareous rock or sand, or in marine habitats *Collemopsidium*
- 4(2) Hamathecium of simple to branched and anastomosing interascal filaments, periphysoids absent; asci various *Pyrenopsis*
Hamathecium comprising a zone of periphysoids near to the ostiole; interascal filaments either absent or inconspicuous and much shorter than the asci; asci thin-walled *Cryptothele*
- 5(1) Asci with >8 spores 6
Asci with (1-)2-8 spores 8
- 6(5) Photobiont trentepohlioid; hamathecium of mostly unbranched interascal filaments and of periphyses; hymenial gel I- or almost; asci thin-walled, ascospores 0-3(-5)-septate, size in the range 10-20 µm long *Thelopsis*
Photobiont not trentepohlioid, or absent 7
- 7(62) Exciple with dark pigments, vulpinic acid derivatives absent (hamathecium of periphyses; hymenial gel I+ red, K/I+ blue; photobiont green) *Trimmatothele*
Exciple without dark pigments, yellow-green vulpinic acid derivatives sometimes present, as a pruina on thallus or ascoma, or within the exciple (hamathecium and hymenial gel reactions various; photobiont green or absent) *Thelocarpon*
- 8(5) 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 (hymenial gel I + red, interascal filaments absent, ascospores 3-septate) *Phylloblastia*
Thallus various; if the hyphal nature is clearly apparent, then hyphae immersed in the substratum, colourless, or narrower 9
- 9(8) Hamathecium of periphyses and periphysoids only (lining the ostiolar canal and upper part of centrum), interascal filaments absent; hymenial gel I+ red (blue at very low concentrations of iodine), K/I+ blue; ascus wall thickened above, I-; photobiont green (not trentepohlioid); ascospores various (*Verrucariaceae*) 10
Hamathecium at least partly comprising interascal filaments, these rarely absent, and then hymenial gel I- or I+ faint blue 17
(*Verrucariaceae* is a natural group which can be easily recognised with a little practice. Periphyses and periphysoids are always present, but interascal filaments are absent; take care not to confuse the indistinct outlines of dehisced asci for these filaments. When introducing iodine into a preparation, the hymenium often shows a fleeting blue reaction, due to the initially very low concentration of iodine.)
- 10(9) Ascospores simple (spores colourless, very rarely brown) *Verrucaria s.l.*
Ascospores septate or muriform 11
- 11(10) Ascomata pale, exciple at most pale brown, without dark pigments; involucrellum absent; ascospores septate or muriform; thallus cells often 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) 12
- 12(11) Ascospores transversely septate, occasionally with a proportion of spores submuriform; ascospores colourless 13
Ascospores consistently submuriform or muriform, colourless or brown 14
- 13(12) Ascospores predominantly *c.* 7-septate, narrowly ellipsoid, 3.5-6.5 times as long as wide; involucrellum absent, exciple dark more or less throughout *Normandina*
Ascospores predominantly 1- or 3(-5)-septate, mostly 2-3 times as long as wide; involucrellum present or absent *Thelidium*
- 14(12) Hymenium containing photobiont cells *Staurothele*
Hymenium not containing photobiont cells 15
- 15(14) 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 16
- 16(15) Ascospores brown, with a distinct perispore (ascospores (18-)22.5-27.5(-31) μm long, with 6-15 cells visible in optical section) *Merismatium (deminutum)*
Ascospores colourless or brown, but if brown then without a distinct perispore
..... *Polyblastia, Henrica, Atla and Sporodictyon*
- 17(9) Ascospores simple, colourless, ellipsoid (hamathecium of simple or anastomosing interascal filaments) 18
Ascospores septate or muriform, rarely simple and then narrowly fusiform 19
- 18(17) Ascomata enclosed within thalline warts on a superficial thallus; thallus on rock, K + bright yellow *Coccotrema* (not treated below)
Ascomata immersed in soil; thallus K- (lichen substances absent)
..... *Thrombium*
- 19(17) Asci thin-walled throughout, without apical thickenings (but sometimes slightly truncate and with a refractive ring in the apical wall), unitunicate; on rock or soil (sometimes over bryophytes) (interascal filaments simple, with smooth outline; photobiont consistently present, usually *Trentepohlia*, rarely trebouxoid) 20
Asci with the wall thickened above, if unthickened then growing on bark (interascal filaments various; photobiont present or absent) 22
- 20(19) Photobiont trebouxoid (hymenial gel I -, K/I -; ascospores multiseptate, long and narrow; on soil) *Belonia (incarnata)*
Photobiont *Trentepohlia* 21
- 21(20) Ascomata pale, colourless or red-brown in section; hymenial gel I + dull red, K/I + blue; asci without a refractive ring in the apex; on rock, soil or bryophytes
..... *Belonia p.p.*
Ascomata pale to dark, with yellow, brown or blue-grey pigments in section; hymenial gel always K/I-; asci sometimes with a chitinous ring in the apex; on rock, bark, or bryophytes
..... *Porina*
- 22(19) Ascospores very narrowly ellipsoid to filiform, 5-85 times as long as wide, 1.5-4.5 μm wide, simple or 1- to multiseptate; always on bark 23

- Ascospores broadly to narrowly ellipsoid, 2-5 times as long as wide, 1- to multiseptate or muriform 26
- 23(22)** Hymenial gel K/I+ deep blue; hamathecium of smooth, branched and anastomosing interascal filaments 1.5-2 μm wide (paraphysoids); periphyses present in ostiolar canal; ascospores filiform, 7- or more septate; ascomata solitary, not united under a common involucrellum *Rhaphidicyrtis (trichosporella)*
Hymenial gel K/I- or K/I+ blue-green 24
- 24(23)** Ascus functionally unitunicate, thin or slightly thickened at apex; periphyses sometimes present in the ostiolar canal; hamathecium of smooth, sometimes branching and anastomosing interascal filaments 1.5-2 μm wide (paraphyses) *Cresporhaphis*
Ascus with two functional wall layers, fissitunicate; hamathecium of pseudoparaphyses or paraphysoids; periphyses absent 25
- 25(24)** Hamathecium of branched, anastomosing, frequently septate interascal filaments, constricted at the septa (pseudoparaphyses); ascospores 1-5-septate, *c.* 5-30 times as long as wide *Leptorhaphis*
Hamathecium of anastomosing, narrow interascal filaments, not constricted at the septa (paraphysoids); ascospores 5-14-septate, *c.* 30-80 times as long as wide *Celothelium*
- 26(22)** Ascomatal wall bright green, K-, N+ red (photobiont absent; ascospores colourless, septate to muriform; always on bark) *Mycoglaena*
Ascomatal wall shades of brown or green-brown, but not bright green 27
- 27(26)** Ascospores 1-3-septate 28
Ascospores >3-septate, or submuriform or muriform 39
- 28(27)** Ascospores 3-septate, walls strongly and unequally thickened, so that the lumina appear angular or lenticular in optical section; hamathecium of more or less unbranched interascal filaments (paraphyses) and periphyses; always on bark (ascospores brown in the British species) *Pyrenula*
Ascospores with walls more or less equally and not strongly thickened 29
- 29(28)** Ascomata united below a common involucrellum; ascospores 1-3-septate, colourless or brown; hamathecium of pseudoparaphyses with lumpy outline; photobiont absent; always on bark 30
Ascomata not united under a common involucrellum (exceptionally a few ascomata clustered) 32
- 30(29)** Ascomata regularly circular or broadly ellipsoid in outline in surface view; ascospores 3-septate when mature, colourless (a few old spores may be brownish) *Tomasellia (gelatinosa)*
Ascomata elliptical or irregular in outline in surface view 31
- 31(30)** Ascospores 1-septate and dark brown when mature; on *Alnus* *Tomasellia (diffusa)*
Ascospores 1-septate and colourless when mature (a few old spores may be 3-septate and/or lightly browned); on *Ilex* *Mycoporum (lacteum)*
- 32(29)** Ascospore wall brown at maturity (exclusively on bark) 33
Ascospore wall colourless at maturity, only brown when overmature 35
- 33(32)** Ascospores 3- or more septate, the central cells often darker than the end cells; microconidia colourless, bacilliform to filiform, macroconidia brown, 1- or more septate *Eopyrenula*

- Ascospores 1-septate; conidia simple or 1-septate, colourless or brown 34
- 34(33)** Ascospores in the range 13-21(-25) μm long, distinctly brown at maturity; hymenial gel I- or I+ violet *Mycomicrothelia*
Ascospores in the range 27-40 μm long, at most pale brown at maturity; hymenial gel always I- *Mycoporum (antecellens)*
- 35(32)** Ascus with a convex structure in the apical wall (easily seen in Congo Red); ascospores with a warty perispore which disintegrates in K *Acrocordia*
Ascus variously thickened at apex, but without such a structure 36
- 36(35)** Hamathecium of interascal filaments (paraphysoids) which are mostly unbranched except adjacent to the exciple; ascospores 1- to many septate (or muriform), 1-septate spores sometimes disarticulating into part-spores within the ascus; ascus with a narrow ocular chamber; macroconidia subapically inserted on the conidiogenous cell, 0- to several septate, sometimes with gelatinous appendages *Strigula p.p.*
Hamathecium of interascal filaments which are usually branched and anastomosing (rarely absent, and then periphyses present); ascospores 1-3-septate, never disarticulating; ascus various; macroconidia when present apically inserted, 0(-3)-septate, without appendages 37
- 37(36)** Involucrellum more or less cellular, not containing bark cells; hamathecium of slender, branched and anastomosing pseudoparaphyses; periphyses absent; hymenial gel always I-; ascospores 1-3-septate, the first-formed septum often below the middle of the spore; perispore absent; lichenized *Anisomeridium*
Involucrellum of compacted hyphae and often with layers of bark cells; hamathecium of slender or lumpy, branched and anastomosing pseudoparaphyses, or (rarely) interascal filaments absent and then periphyses present; ascospores 1-3-septate, the first-formed septum generally at or above the middle of the spore; perispore absent or present; lichenized or not 38
- 38(37)** Ascospores 27-40 \times 8-13 μm , often becoming brown and verruculose (ascospores 1-septate; involucrellum brown in K) *Mycoporum (antecellens)*
Ascospores <27 μm long or <8 μm wide, colourless *Arthopyrenia*
- 39(27)** Ascospores brown when mature, large, (57-)70-135(-140) μm long, muriform; hamathecium of more or less unbranched interascal filaments (paraphyses) and periphyses; ascomata large, 1-1.2 mm diam., ostioles lateral, often joined in groups; on bark *Pyrenula (hibernica)*
Ascospores colourless (sometimes faintly brown when old) 40
- 40(39)** Photobiont green, not trentepohlioid 41
Photobiont trentepohlioid, or absent 42
- 41(40)** Ascus wall K/I+ blue, apex with a darker staining internal structure; hymenial gel I+ red, K/I+ blue (hemiamyloid) *Protothelenella*
Ascus wall and hymenial gel I- *Thelenella*
- 42(40)** Photobiont trentepohlioid; forming a distinct thallus; interascal filaments not or sparsely branched except adjacent to the exciple *Strigula p.p.*
Photobiont absent, or at most with an indistinct thallus weakly lichenized with a trentepohlioid alga; interascal filaments branched and anastomosing (exclusively on bark) 43
- 43(42)** Interascal filaments slender; ascospores with a perispore *Julella*
Interascal filaments lumpy in outline; ascospores without a perispore *Cyrtidula*

4 Accounts of genera

Accounts of most pyrenocarp genera in Britain follow; nearly all saxicolous species are covered, and many corticolous. The following genera are treated below:

1. Acrocordia
2. Agonimia
3. Anisomeridium
4. Arthopyrenia
5. Atla
6. Belonia
7. Catapyrenium s.l.
8. Collemopsidium
9. Cryptothele
10. Dermatocarpon
11. Endocarpon
12. Eopyrenula
13. Henrica
14. Heteroplacidium
15. Hydropunctaria
16. Julella
17. Merismatium
18. Mycomicrothelia
19. Normandina
20. Phylliscum
21. Phylloblastia
22. Polyblastia
23. Porina
24. Protothelenella
25. Psoroglaena
26. Pyrenula
27. Sporodictyon
28. Staurothele
29. Strigula
30. Thelenella
31. Thelidium
32. Thelocarpon
33. Thelopsis
34. Thrombium
35. Trimmatothele
36. Verrucaria

ACROCORDIA A. Massal. (1854)

Thallus crustose, effuse, whitish or pale, thin or immersed in the substratum, ecorticate. **Photobiont** *Trentepohlia*. **Ascomata** perithecia, almost entirely immersed to \pm sessile, black (rarely pink or whitish), compound, with a hemispherical to globose, brown-black involucrellum surrounding a \pm globose, colourless or pale brownish exciple. **Hymenial gel** I –, K/I –. **Hamathecium** of persistent, slender, sparingly branched or anastomosing, long-celled pseudoparaphyses; paraphyses absent. **Asci** (4–)8-spored, cylindrical, K/I–, fissitunicate; apical dome with a broad ocular chamber surmounted by a hemispherical meniscus-like structure. **Ascospores** uniseriate, colourless, ellipsoid to oblong-ellipsoid, the ends usually rounded, 1(–3)-septate, the median septum thick and cells \pm equal, not or slightly constricted at the septum, additional septa (if present) thin; perispore verrucose in water, becoming smooth in K. **Conidiomata** pycnidia; conidiogenous cells cylindrical, elongate; conidia acrogenous, ellipsoid to narrowly ellipsoid, simple, colourless. **Chemistry**: lichen products not detected by t.l.c. **Ecology**: \pm basiphilous, on bark of broad-leaved trees or on mostly vertical surfaces of calcareous or basic rocks in humid situations.

Classification: Chaetothyriomycetidae, Pyrenulales?, Monoblastiaceae.

Characterized by the cylindrical asci, with an apparently unique apical structure, and uniseriate, 1-septate, ellipsoid ascospores, with a warted perispore. The hamathecium in the British species comprises an anastomosing network of narrow, parallel-sided hyphae 1.2–1.5 μ m wide, with inconspicuous septa. The presence of a rough perispore causes the ascospores to appear finely to strongly verrucose in water, and often with a slightly projecting septum; in K the perispore apparently swells or becomes diffuse, so that the warted surface disappears or is represented only by a slightly lumpy diffuse layer.

- | | | |
|------|--|-------------------|
| 1 | On rocks, rarely on soil | 2 |
| | On bark, rarely on wood | 4 |
| 2(1) | Involucrellum spreading laterally away from exciple, never continuous below | 3 |
| | Involucrellum incurved under exciple, often more or less continuous below | salweyi |
| 3(2) | Ascospores 12–19 \times 6–9 μ m; perithecia with the ostiole often projecting as a papilla; thallus usually immersed | conoidea |
| | Ascospores 19–26(–28) \times 9.5–12 μ m; perithecia without a distinctly papillate ostiole | macrospora |
| 4(1) | Perithecia 0.5–1 mm diam., ascospores 15–27(–30) \times 9–12 μ m | gemma |
| | Perithecia 0.3–0.6 mm diam., ascospores 11–16.6 \times 5.5–9.5 μ m | cavata |

Acrocordia cavata (Ach.) R.C. Harris (1974)

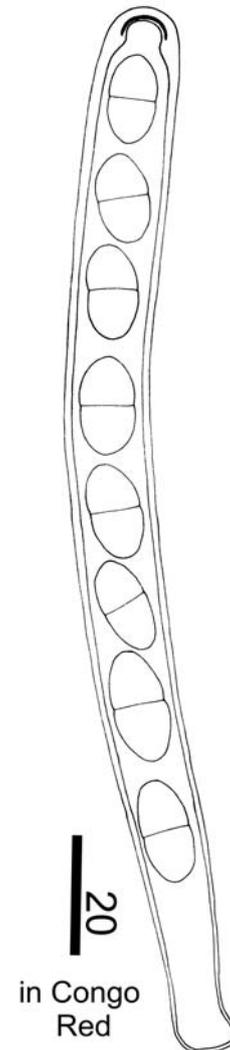
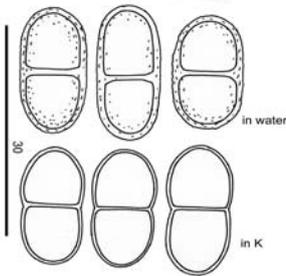
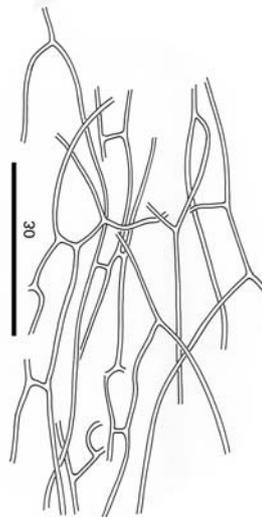
Thallus immersed, grey-white. Perithecia 0.3–0.6 mm diam., half-immersed; involucrellum hemispherical. Ascospores 11–16.5 \times 5.5–9.5 μ m. Pycnidia not known.

On wood of *Ilex* and on bark of *Corylus*. C.N. Scotland (Argyll, Perth). Europe, North America.

Similar to *A. gemmata* but with smaller perithecia and ascospores. *Anisomeridium bifforme* differs in the ascus structure and the smaller, smooth ascospores.

Acrocordia conoidea (Fr.) Körb. (1855)

Thallus immersed or superficial and cracked, smooth or finely granular, effuse, pale grey or brownish grey, often with pinkish tinge when fresh. Perithecia 0.5–1 mm diam., one quarter to half-immersed, conical-hemispherical, often flattened and with distinct papillose ostioles; involucrellum spreading outwards away from the exciple. Ascospores $12\text{--}19 \times 6\text{--}9 \mu\text{m}$, the ends mostly rounded but sometimes pointed, occasionally with a thin secondary septum



dividing each cell. Pycnidia 0.14–0.2 mm diam., frequent, often numerous. Conidia ellipsoid, *c.* $3.3 \times 1.5 \mu\text{m}$.

On hard limestones and calcareous walls in \pm shaded and moist situations. Abundant in areas with naturally occurring hard limestones (particularly Devonian and Carboniferous limestone). C., N., & W. Britain, N.W. Ireland. Europe, North America.

When well-developed, easily recognized by the shallowly conical shape of the rather evenly dispersed perithecia. Difficult specimens can be distinguished from *A. macrospora* and *A. salweyi* in sections by the more outwardly spreading base of the involucrellum and the smaller ascospores.

Acrocordia gemmata (Ach.) A. Massal. (1854)

Thallus immersed, white or pale grey. Perithecia 0.5–1 mm diam., black (rarely pink), one-quarter- to entirely immersed; ostiole often eccentric and sometimes papillate. Ascospores $15\text{--}30 \times 8\text{--}12 \mu\text{m}$. Pycnidia 0.1–0.25 mm diam., frequent but rarely numerous. Conidia $3\text{--}5 \times 0.8\text{--}1 \mu\text{m}$.

In woodlands or open situations on rough bark of mature trees, especially *Fraxinus*, *Quercus* and *Ulmus*, more rarely on smooth bark of *Corylus*; widespread and locally common but absent from areas due to air pollution. Throughout British Isles but absent from much of C. Britain. Europe, Macaronesia, ?North America.

Distinguished from the rare *A. cavata* by the larger perithecia and ascospores. The distinctive ascus and ascospore morphology of the genus distinguish *A. gemmata* from other superficially similar, bark-inhabiting taxa, e.g. *Anisomeridium* spp., *Pyrenula* spp. and the non-lichenized *Lophiostoma* spp. Occasionally found with pycnidia only.



Acrocordia gemmata

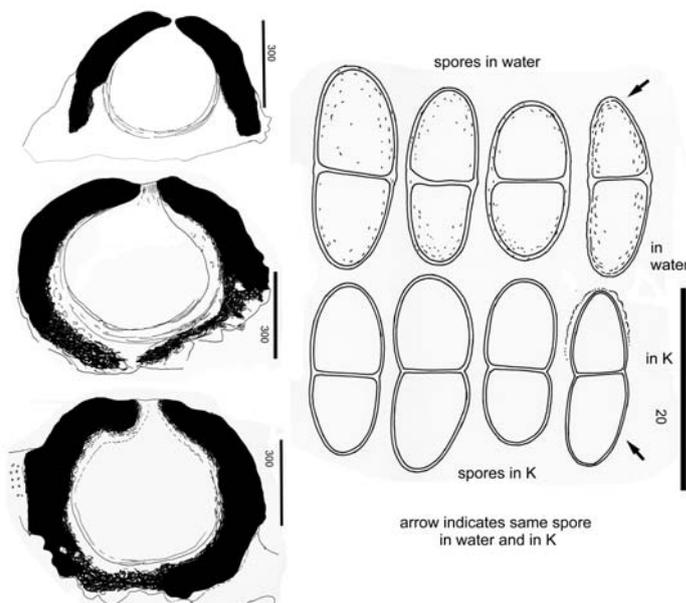
***Acrocordia macrospora* A. Massal. (1855)**

Thallus superficial, grey to grey-brown, smooth or \pm rimose. Perithecia 0.8–1 mm diam., rather prominent, ostiole not papillose; involucrellum \pm spreading laterally, never continuous below the exciple. Ascospores $19\text{--}26\text{--}(28) \times 9.5\text{--}12 \mu\text{m}$. Pycnidia 0.2–0.3 mm diam., usually few.

On sheltered, often shaded siliceous or weakly calcareous rocks in coastal areas. W. British Isles. France, Spain, Netherlands, Italy, Norway, Canary Islands.

Resembles *A. conoidea* but the perithecia are not flattened, lack papillate ostioles and the ascospores are larger. *A. salweyi* is distinguished in section by the tightly incurved involucrellum which is often continuous below the true exciple; it occurs on strongly calcareous substrata.

***Acrocordia salweyi* (Leight. ex Nyl.) A.L. Sm. (1911)**



Thallus \pm immersed, whitish to pale brownish grey, thin, granular or smooth to rimose. Perithecia 0.7–1.5 mm diam., one-quarter- to half-immersed; involucrellum usually tightly incurved around the exciple and often continuous below. Ascospores $20\text{--}35 \times 10\text{--}15 \mu\text{m}$. Pycnidia 0.2–0.3 mm diam., usually few.

On soft, \pm sheltered, often damp, highly calcareous rocks and especially old mortar, rarely terricolous. Throughout British Is., common in S. and W. England. Widespread in Europe.

AGONIMIA Zahlbr. (1909)

Thallus crustose and composed of goniocysts, to minutely squamulose; cortical cells often with small papillae. **Ascomata** perithecia, black, surface smooth or roughened. **Involucrellum** absent. **Exciple** thick, more or less layered, outer part of more or less rounded cells which are densely pigmented, middle layer of similarly shaped but unpigmented cells, innermost layer of exciple of compressed, colourless cells; pigments dark brown, K + grey-brown, to brown, K – 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, 2–8-spored, I –, K/I –. **Ascospores** colourless, muriform. **Conidiomata** pycnidia, rare; conidia colourless, bacilliform. **Chemistry:** no lichen substances detected. **Ecology:** on soil, bark, or associated with mosses over bark, soil and rock.

Classification: Chaetothyriomycetidae, Verrucariales, Verrucariaceae.

Distinguished from *Polyblastia sensu lato* by the somewhat layered exciple, lack of an involucrellum, and by the presence of papillae on the cortical cells of most species. *Protothelenella* and *Thelenella* differ in the presence of abundant interascal filaments.

LITERATURE: Coppins & James (1978), Czarnota & Coppins (2000), Sérusiaux *et al.* (1999).

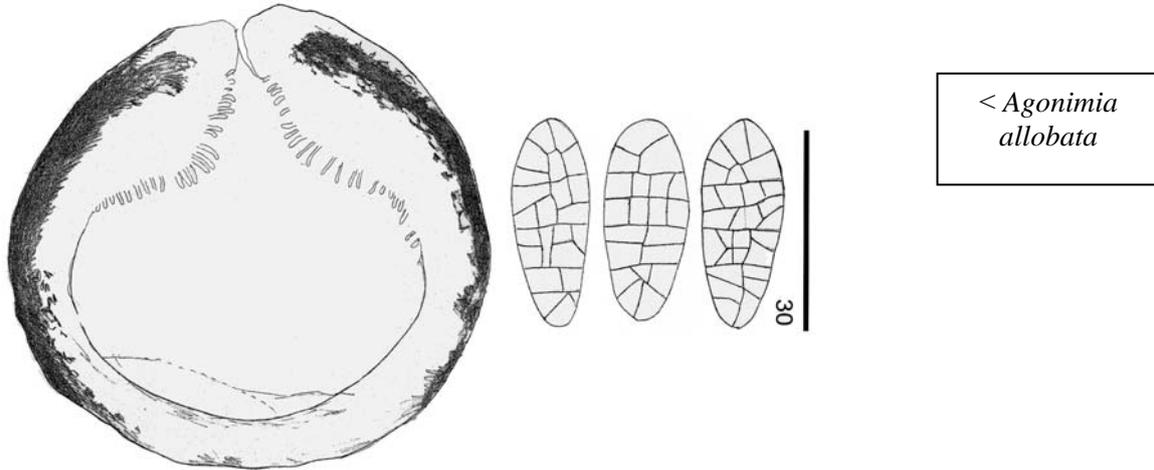
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|------|--|-----------------------|
| 1 | Ascospores (25–)29–55 µm long; thallus finely verrucose or with minute coralloid or finger-like squamules at most 240 × 100 µm; asci 8-spored | 2 |
| | Ascospores (42–)57–120 µm long (or perithecia absent), thallus distinctly squamulose, squamules 50–1000 × 50–300(–500) µm; asci (1–)2-spored or 8-spored | 6 |
| 2(1) | Perithecia smooth | 3 |
| | Perithecia rough, upper part with vertical cracks or furrows | repleta |
| 3(2) | Perithecia 0.12–0.25 mm diam.; ascospores 23–44 µm long; usually on bark | 4 |
| | Perithecia 0.25–0.6 mm diam., ascospores 31–55 µm long; on soil or on mosses over soil and rock | 5 |
| 4(3) | Thallus thin, roughened | allobata |
| | Thallus coralloid | flabelliformis |
| 5(4) | Sterile black globules 70–240 µm long usually present on thallus; thallus grey-green, cortical cells without pigment | globulifera |
| | Sterile black globules absent; thallus brown, cortical cells pigmented | gelatinosa |
| 6(1) | Squamules pruinose, with minute projecting hyaline hairs (perithecia unknown) | opuntiella |
| | Squamules without projecting hairs, at most cells with minute papillae | 7 |
| 7(6) | Asci 8-spored; squamules often elongate, branched, terete or slightly flattened, 50–250 × 50–120 µm, grey-green | octospora |
| | Asci (1–)2-spored; squamules sometimes elongate and terete, but often distinctly flattened, 100–1000 × 100–300(–500) µm, green-fawn to brown | tristicula |

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

Thallus grey-green to brown, continuous and minutely roughened. Perithecia 0.12–0.22 mm diam., more or less globose or taller than wide, occasionally collapsed when dry, two-thirds immersed to almost superficial; grey-brown when young, later often black, surface smooth, matt; ostiolar region

visible as a pale dot 40–100 µm diam. Asci 8-spored. Ascospores (25–)29–35(–44) × 10–15(–16.5) µm, ellipsoid.

On bark, amongst mosses, on sheltered trunks of old trees, particularly *Quercus*, *Ulmus* and *Fraxinus*, in long-established woodlands, sheltered gullies, rarely on wayside trees; local. S. and W. England, Wales, W. Scotland, Ireland. Widespread in Europe from Fennoscandia to Italy, and Spain to Estonia and Slovakia. N. America.

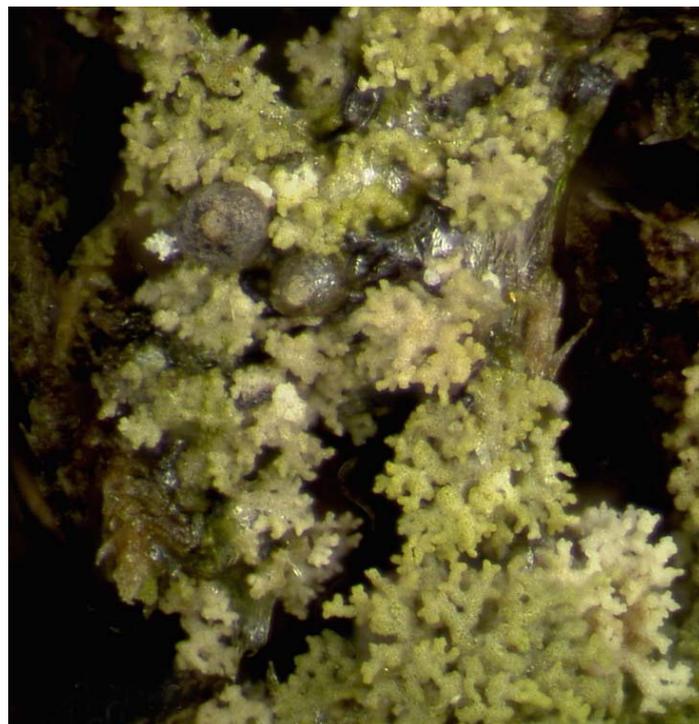


***Agonimia flabelliformis* Halda, Czarnota & Guzow-Krzemińska (2012)**

Thallus minutely flabelliform-squamulose to coralloid, composed of goniocyst-like units, pale brown-green. Perithecia globose, rarely ovoid to pyriform, 0.15–0.25 mm diameter, smooth. Ascospores oblong to ellipsoid, (23–)30(–35) × (11–)14(–15) µm, hyaline, muriform, fewer than 20 cells visible in optical section.

On bark; Wales, Czech Republic, Germany.

Differs from *A. allobata* in the coralloid thallus.



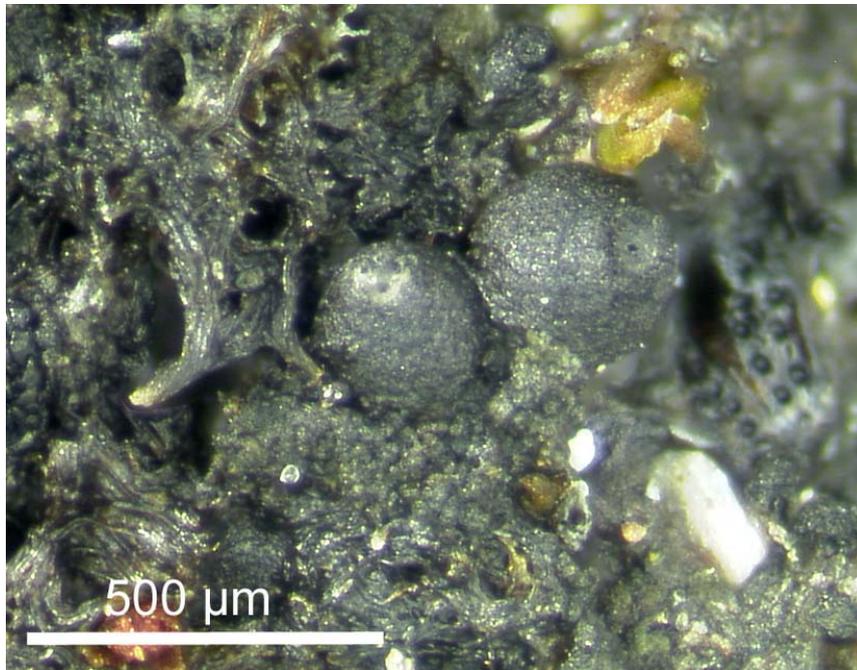
Agonimia flabelliformis (13909).

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

Prothallus conspicuous, of dark hyphae. Thallus dark brown, composed of rounded or lobed goniocysts 18–35 μm diam. or 70–120 μm long; surface cells brown, papillae absent. Sterile globules absent. Perithecia almost superficial, 0.3–0.5 mm diam., surface smooth, black, matt. Exciple 40–70 μm thick, of more or less rounded cells, pigmented near surface of exciple, with innermost layer of compressed colourless cells. Asci 8-spored. Ascospores ellipsoid, 31–55 \times 15–20 μm , muriform, with 16–30 cells visible in optical section. Pycnidia rare, small, ovoid, 70 \times 40 μm , black; conidia bacilliform, 2.3–3 \times 0.7–0.8 μm .

Over mosses or on soil in calcareous habitats, over limestone, mortar, mica-schist and on dunes, from sea-level to at least 700 m altitude, throughout Britain and Ireland. Widespread in Europe, but more frequent in arctic-alpine situations.

This species has been confused with *A. globulifera*, and probably with terricolous species of *Polyblastia*, the distribution needs revision. *A. globulifera* differs in the unpigmented thallus, the presence of sterile globules, and the more strongly muriform ascospores. *P. philaea* differs in the perithecia immersed in soil, the densely pigmented, unlayered exciple, and the thallus not composed of goniocysts.



Agonimia gelatinosa (20538).

Agonimia globulifera M. Brand & Diederich (1999)

Prothallus indistinct. Thallus grey-green to greenish, of minute granules or finger-like lobes 20–50 μm wide, often aggregated into larger, lobed squamules; surface cells without pigment, often with papillae 1–2.5 μm high. Sterile globules frequent: subspherical to oblong, 70–240 μm long, black, glossy, superficial, or lower third immersed in thallus; composed of thin-walled colourless to pigmented cells each containing a large oil drop. Perithecia rare, superficial or partly immersed, 0.25–0.6 mm diam., black, matt. Ascospores ellipsoid, (32–)37–50 \times (15–)16–26 μm , with (22–)35–60 cells visible in optical section. Pycnidia unknown.

Overgrowing mosses, lichens, sand, or rarely rocks, in calcareous habitats, possibly locally frequent but overlooked. Scattered records in England, Wales and Scotland. Europe (Sweden, Spain, France, Belgium, Luxembourg, The Netherlands, Germany).

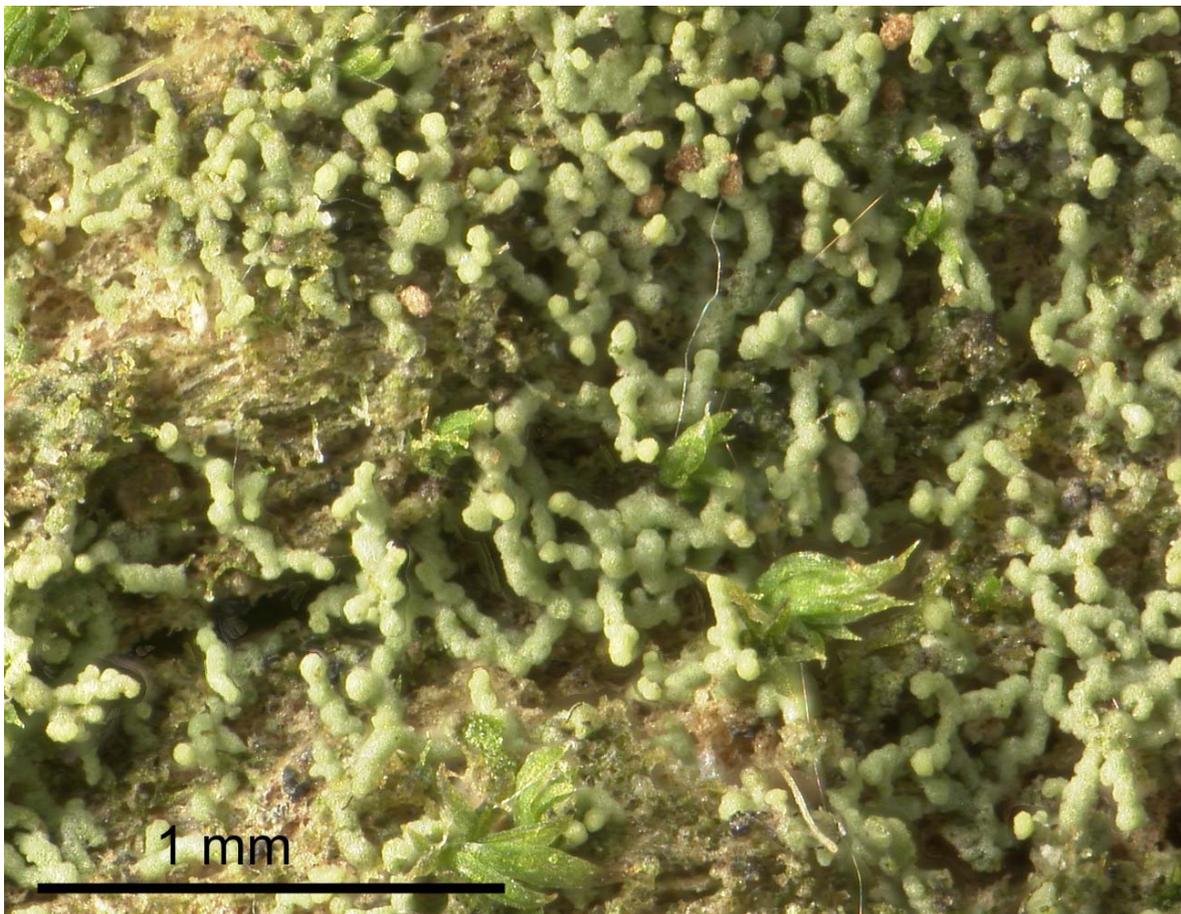
Distinguished by the conspicuous, glossy, black sterile globules scattered over the thallus.

Agonimia octospora Coppins & P. James (1978)

Thallus minutely squamulose, squamules 50–250 × 50–120 μm, more or less elongate, sometimes branched, terete or slightly flattened, the margin entire or notched; scattered and dispersed or in more or less contiguous groups and becoming imbricate; upper surface even, matt or slightly glossy, pale grey-green, blue-grey when wet. Perithecia occasional, scattered amongst squamules, 0.46–0.8 mm diam., one-quarter- to half-immersed, globose or more or less pyriform, black, matt or more or less glossy, 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 60–75(–85) × 20–26(–30) μm, ellipsoid.

On bark of trunks of aged *Quercus* and *Fagus*, often amongst mosses, in somewhat sheltered situations in old woodlands. S. and W. England and the Lake District, Wales, S.W. Ireland, rare. France (Brittany), Italy (Tuscany); Macaronesia. S. America (Brazil).

The perithecia are sometimes isolated from the squamules. Sterile specimens can be confused with *A. tristicula*, which has larger, usually more distinctly flattened squamules which are darker olivaceous or brownish when dry and bright green when wet, and with *Rinodina isidioides*, which has K + yellow coralloid lobes with larger photobiont cells and no papillae.



Agonimia octospora (21497).

Agonimia opuntiella (Buschardt & Poelt) Vězda (1997)

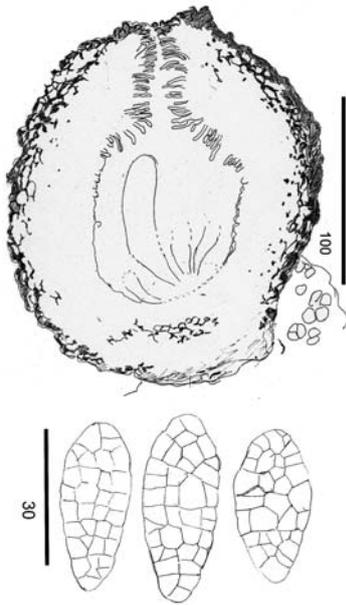
Squamules to 400 µm wide, greenish-grey to brownish, surface rough, often with minute hyaline hairs c. 17-21 × 5 µm. Perithecia unknown.

Amongst mosses on *Quercus*, and on rocks. Scotland, Wales. Europe, Macaronesia.



Agonimia opuntiella (20445)

Agonimia repleta Czarnota & Coppins (2000)



Thallus dull green, rarely brownish, granular to granular-verrucose or minutely squamulose; granules (30–)40–120 μm in diam., often coalescing; squamules sometimes present, elongate, to $240 \times 100 \mu\text{m}$; cortex often with papillae to 1.7 μm high on a few cells. Perithecia mostly half- to three-quarters immersed in the thallus, 0.14–0.2 mm diam., globose when young, later pyriform, upper part roughened with vertical cracks or grooves. Asci 8-spored. Ascospores $20\text{--}46 \times 12\text{--}20 \mu\text{m}$, mainly ellipsoid, sometimes globose.

On bark, often where mossy, and on mossy rock in upper flood zone of river, S.W. England (W. Cornwall, S. Devon), Wales (Radnorshire). Europe (Poland, Slovakia, Ukraine).

Agonimia tristicula (Nyl.) Zahlbr. (1909)

Thallus minutely squamulose, squamules to $100\text{--}1000 \times 100\text{--}300\text{--}(500) \mu\text{m}$, crowded, more or less contiguous and erect, sometimes nodulose and subgranular or rarely dispersed and elongate-digitiform, dull pale green-fawn to brown when dry, bright green when wet and fresh; upper cortex with irregular, low abraded projections, rarely with small papillae in shade. Perithecia 0.24–0.5 mm diam., rather frequent, often in between and overgrown by squamules, barrel-shaped, surface black, matt, plicate-rugose. Exciple thick. Asci (1–)2-spored. Ascospores $(42\text{--})57\text{--}120\text{--}(150) \times 26\text{--}50 \mu\text{m}$, elongate-ellipsoid.

On calcareous soil and dunes, or on mosses and lichens in crevices of more or less calcareous rocks and walls, including limestone, mortar, basalts and serpentine; frequent; more rarely on bark of base-rich trees, especially *Acer*, *Ulmus* and *Fraxinus*; also occasional amongst bryophytes on periodically inundated siliceous rocks by rivers and lakes. Throughout British Isles. Europe, Azores, N. America, Japan, Australia.

Sterile corticolous morphs are distinguished from *A. octospora* by their larger, more distinctly flattened squamules which are darker olivaceous or brownish when dry and bright green when wet and fresh. *A. vouauxii* (de Lesd.) Brand & Diederich is not reported from Britain but could occur here; like *A. tristicula* it has 2-spored asci, but the perithecia are smaller, 0.13–0.23 mm diam.

Literature:

- Coppins, B.J. & James, P.W. (1978) New or interesting British lichens II. *Lichenologist* **10**: 179-207.
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- Guzow-Krzemińska, B., Halda, J.P. & Czarnota, P. (201) A new *Agonimia* from Europe with a flabelliform thallus. *Lichenologist* **44**: 55-66.
- Sérusiaux, E., Diederich, P., Brand, A.M. & Van Den Boom, P. (1999) New or interesting lichens and lichenicolous fungi from Belgium and Luxembourg. VIII. *Lejeunia* **162**: 1-95.

ANISOMERIDIUM (Müll. Arg.) M. Choisy (1928)

Thallus crustose, immersed, whitish or pale grey. **Photobiont** *Trentepohlia*. **Ascomata** perithecia, hemispherical to globose, simple to compound; wall composed of \pm cellular hyphae, usually without bark cells, thicker in upper part, often with a well-differentiated involucrellum, brown-black above, pale brown to \pm colourless below; pigment K + greenish. **Hamathecium** of slender, branched and anastomosed, long-celled pseudoparaphyses, *c.* 1 μ m thick; paraphyses absent; hymenial gel I-. **Asci** cylindrical-clavate, K/I-, fissitunicate, the apical dome with indistinct or short and broad ocular chamber, 8-spored (sometimes a few spores aborting), the spores uniseriate to biseriate. **Ascospores** 1- to 3-septate, ovoid to clavate-fusiform, the first-formed septum often towards lower end of ascospore; colourless, smooth, without a distinct perispore. **Conidiomata** pycnidia, immersed to sessile, \pm globose or conical, black. **Conidiogenous cells** cylindrical, enteroblastic, with collarettes, often percurrently proliferating. **Macro- and microconidia** (produced in separate pycnidia) subglobose, ellipsoid, ovoid or rod-shaped, 0(-1) septate; rarely extruded as a cirrus of conidia bound by mucilage. **Chemistry**: no lichen products detected in European species. **Ecology**: mainly on bark, also on rock.

Classification: Chaetothyriomycetidae, Pyrenulales?, Monoblastiaceae.

A widely occurring subtropical to temperate genus of at least 15 species. Differs from *Arthopyrenia* in a combination of features, especially the \pm cellular structure of the involucrellum. *Strigula* differs in having a narrow ocular chamber in the ascus apex and septate macroconidia, which are obliquely attached to the conidiogenous cells. *Acrocordia* has a different ascus structure, the ascospores are ellipsoid to oblong-ellipsoid and have a median septum and a warted perispore.

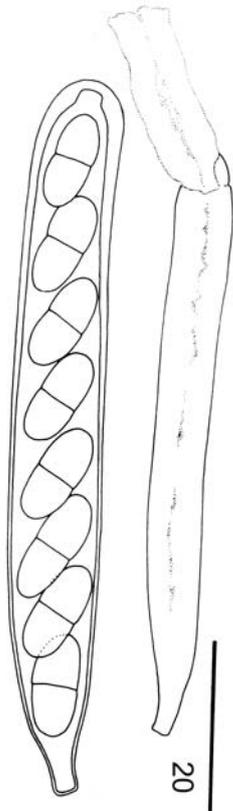
LITERATURE: Aptroot (1999), Coppins & Aptroot (2008).

- | | | |
|------|---|------------------------|
| 1 | Conical pycnidia present (globose base tapering into a short or long ostiolar neck), perithecia present or absent | 2 |
| | Conical pycnidia absent, perithecia or \pm globose pycnidia present | 3 |
| 2(1) | Conical pycnidia 80–150 μ m diam., containing conidia 3.5–4.5 μ m long | polypori |
| | Conical pycnidia 200–580 μ m diam., containing conidia 5.5–6.5 μ m long | robustum |
| 3(1) | Ascospores 1-septate, with lower cell much longer than the upper cell, and with a slight median constriction when mature | ranunculosporum |
| | Ascospores 1-septate, the lower cell equal to or shorter than the upper cell, or 3-septate | 4 |
| 4(3) | Ascomata 0.3–0.4(-0.5) mm diam.; ascospores 1-septate, (9-)12–16 \times 4.5–6(-7) μ m, cells equal or the lower shorter than upper | biforme |
| | Ascomata 0.14–0.25 mm diam. | 5 |
| 5(4) | Ascospores 1–3-septate, (3-)4.5–5(-6) μ m wide, the part above the primary septum wider and <i>c.</i> twice as long as the part below | polypori |
| | Ascospores 1-septate, 3.5–4.7 μ m wide, the cells \pm equal in length | viridescens |

Anisomeridium biforme (Borrer) R.C. Harris (1978)

Thallus usually conspicuous, whitish or pale greyish, effuse or delimited by a thin blackish prothallus. Perithecia 0.3–0.4(-0.5) mm diam., quarter- to almost totally immersed, usually numerous; upper wall with usually well-differentiated involucrellum, 50–100 μ m thick; lower wall pale or colourless. Asci

65–90 × 9–12 μm, cylindrical, the spores ± uniseriate. Ascospores (9–)12–16 × 4.5–6(–7) μm, 1-septate, ovoid- to fusiform-ellipsoid, the septum half- to two-thirds from upper end. Pycnidia of two types: (a) 100–200 μm diam., with subglobose to ellipsoid macroconidia 2.3–4 × 1.8–2.7 μm, extruded as a white blob; or (b) 40–100 μm diam., ± immersed, hemispherical to globose, with globose microconidia 1–1.5 μm diam.



< *Anisomeridium bifforme*: mature and dehisced asci

Anisomeridium polypori (Ellis & Everh.) M.E. Barr (1996)

Thallus often inconspicuous, effuse, whitish grey or pale grey-green. Perithecia 0.15–0.25 mm diam., rarely numerous, subconical to ± globose, initially immersed, becoming ± superficial; upper wall with a scarcely differentiated involucrellum, 30–50 μm thick; lower wall thinner and paler. Asci 55–75(–90) × 12–15 μm, cylindrical-clavate. Ascospores (12–)14–20(–23) × (3–)4.5–5(–6) μm, 1- to 3-septate, clavate-fusiform, the part above the primary septum wider and about twice as long as the lower. Pycnidia black, of two types: (a) 80–150 μm diam., 100–560(–760) μm high, ± sessile, conical with an ostiolar neck comprising vertically arranged, brown-walled hyphae, which at the apex of the neck have free, colourless, pointed ends, with ellipsoid or ovoid macroconidia with truncate base, 3.5–4.5 × 1.8–3 μm, extruded as a white cirrus, 10–20 μm wide, in which the conidia are bound by a gelatinous matrix; or (b) 50–100 μm diam., ± immersed, globose, with rod-shaped to narrowly ellipsoid microconidia, 2–3 × 1–1.3 μm.

On rough bark of broad-leaved trees, especially *Sambucus* and *Ulmus*, sometimes overgrowing bryophytes; also on shaded rock, especially damp pebbles, and bone; in humid woodland and tall scrub, tolerant of deep shade; common even in moderately polluted areas. Throughout British Isles. Europe, North America, Africa (Algeria), Asia (Hong Kong, Sumatra), Australia.

Illustrations: Dobson (2000) p. 63, Puntillo (1996) Tav. II.

Most often found only with abundant conical macropycnidia; the ostiolar neck is variable in length. When fertile it differs from *A. bifforme* in its less conspicuous thallus, the smaller perithecia with a thinner upper wall, and longer and narrower ascospores, which are often 2- or 3-septate. *A. polypori* has become more abundant in recent decades, but there is no evidence that it is a new arrival from outside Europe.

Anisomeridium ranunculosporum (Coppins & P. James) Coppins (2002)

Thallus immersed, white to fawn, often pinkish when fresh. Ascomata 0.22–0.36 × 0.2–0.3 mm, circular or ellipsoid, often matt or ± pruinose due to thin covering of bark cells; involucrellum brown, K+ greenish. Pseudoparaphyses 0.5–1.5 μm wide, persistent, much branched, cells 4–10 μm long. Asci 35–42 × 12–17 μm, obpyriform. Ascospores 14–16 × 4.5–5.7 μm, 1-septate, constricted at septum, with short uniguttulate upper cell and an elongate, biguttulate lower cell with a median constriction. Pycnidia frequent, of two types: (a) 80–120 μm diam., with macroconidia 7.6–10(–12) ×

3.5–4.3 μm , oblong-ellipsoid, 0(–1)-septate; (b) 30–60 μm diam., with microconidia 3.5–4 \times 0.5–0.8 μm , bacilliform.

Usually on smooth areas of fissured bark of tree trunks, especially *Fraxinus* and *Quercus*, sometimes on smooth bark of trunks or main stems of e.g. *Corylus*, *Ilex* and *Sorbus*, also *Calluna*; widely distributed in sheltered, old woodlands. W. British Isles. S.W. Norway, Spain, Denmark, Germany.

Easily identified by its ‘tadpole-shaped’ ascospores. It is occasionally found only with macroconidia.

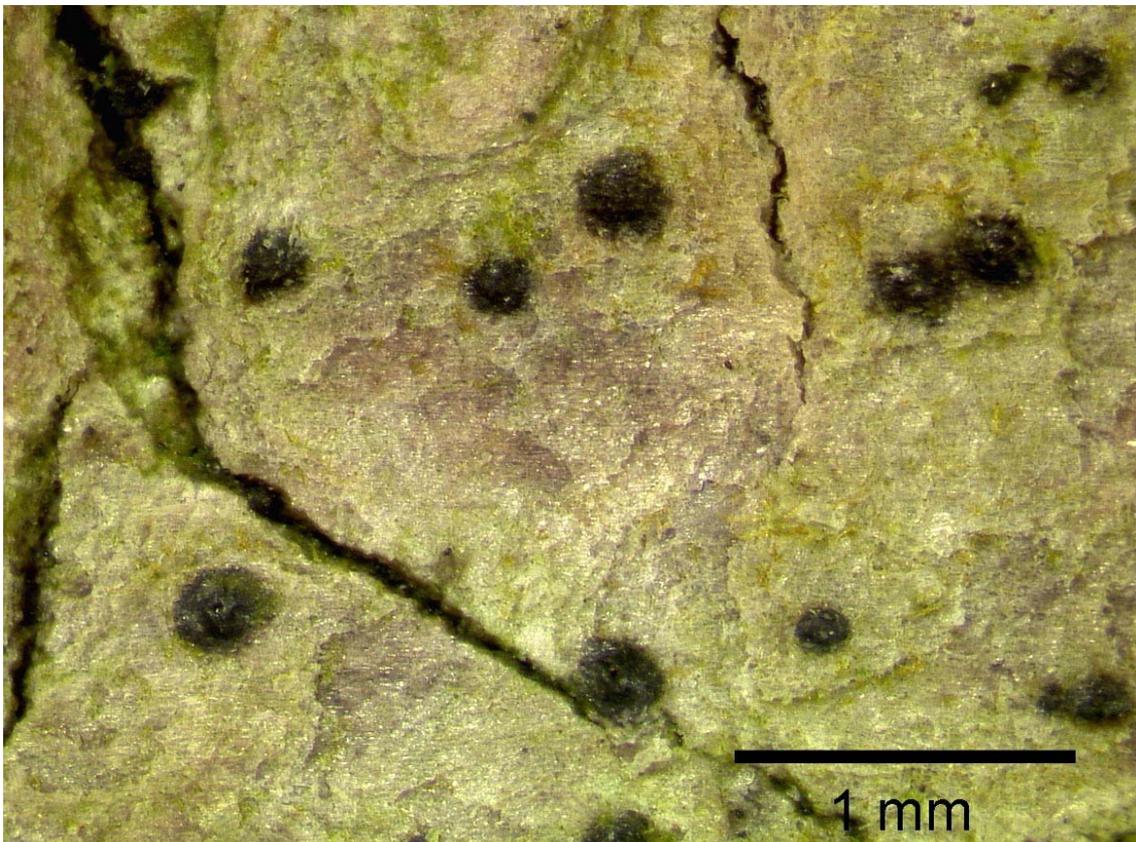
Anisomeridium viridescens (Coppins) R.C. Harris (1995)

Thallus a whitish or a pale fawn stain on bark, sometimes pinkish when fresh. Ascomata 0.14–0.2 \times 0.1–0.15 mm, circular to ellipsoid, mostly scattered; involucrellum brown, K+ green.

Pseudoparaphyses 0.8–1 μm thick, persistent, much-branched; cells 4–10 μm long. Asci 31–49 \times 11–17 μm , obclavate to short-cylindrical. Ascospores 12–17(–19) \times 3.5–4.7 μm , 1-septate, usually constricted at the septum; upper cell usually distinctly wider than lower, the cells usually biguttulate, without a median constriction; colourless or sometimes brownish and faintly warted when old; perispore indistinct. Pycnidia 40–50 μm diam., with either: (a) macroconidia 9–10.5 \times 2–2.5 μm , oblong, 2- to 3-guttulate; or (b) microconidia c. 4–5 \times 1–1.3 μm , ovoid-oblong to bacilliform, eguttulate.

On smooth bark of *Corylus* in old woodlands. Western Britain, Ireland. Azores, Spain, Austria.

Occurs in similar communities to *Arthopyrenia carneobrunneola*. Differs from species of *Arthopyrenia* which have very small ascomata in having a K+ green involucrellum and thin, slender paraphyses.



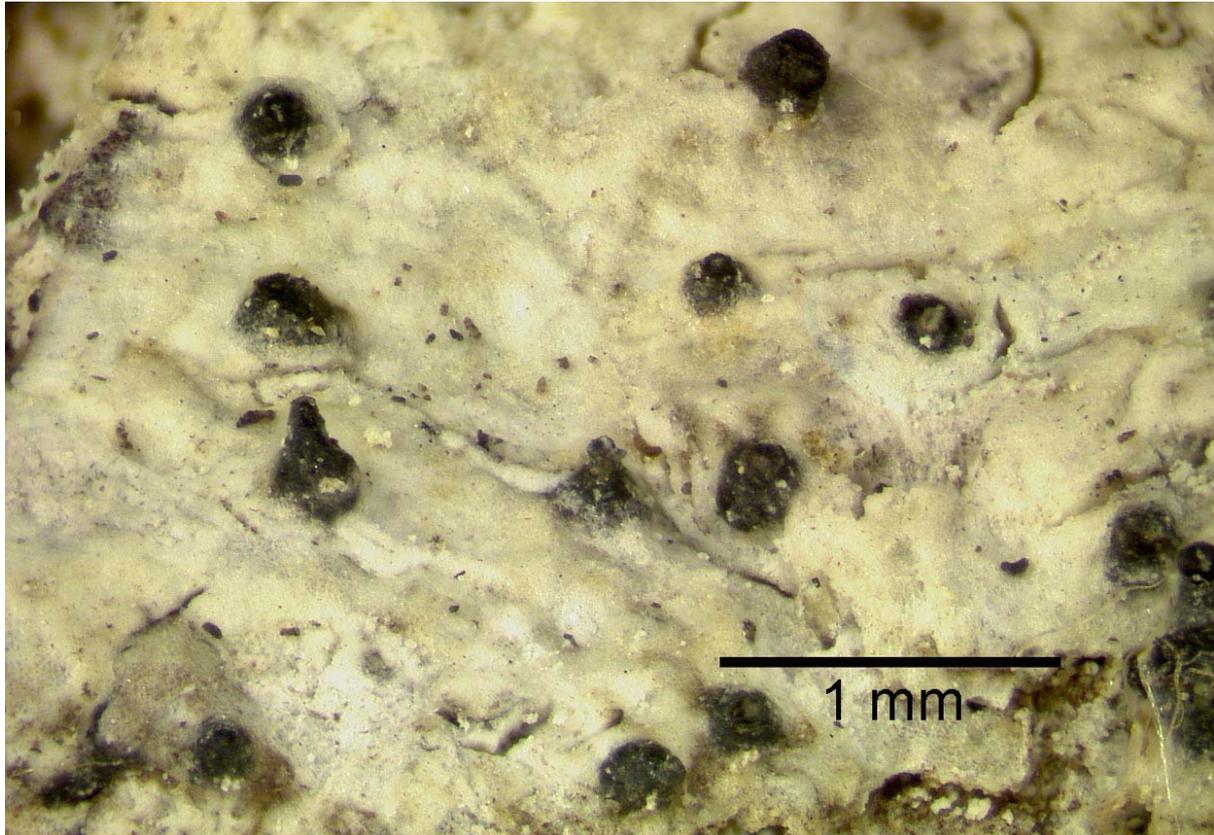
Anisomeridium viridescens (18450).

Anisomeridium robustum Orange, Coppins & Aptroot (2008)

Thallus white or pale greyish, often cracked. Ascomata unknown. Pycnidia 200-580 µm diam. and 200-500 µm high, with globose base tapering into narrow neck. Conidia pyriform-ellipsoid, with truncate base, 5.5-6.5 × 2.5-3 µm, sometimes extruded as a cirrus. Microconidia not detected.

On bark of mature *Quercus* and *Acer pseudoplatanus* in old woodland and parkland, and from *Salix*; very local. Western Britain from Cornwall to West Ross; Ireland.

Macropycnidia and conidia similar to *A. polypori*, but much larger. So far recorded mainly from sites rich in old-forest lichens.



Anisomeridium robustum (13876).

References:

Aptroot, A. (1999) Notes on taxonomy, distribution and ecology of *Anisomeridium polypori*.
Lichenologist **31**: 641-642.

Coppins, B.J. & Aptroot, A. (2008) New species and combinations in *The Lichens of the British Isles*.
Lichenologist **40**: 363-374.

ARTHOPYRENIA A. Massal. (1852)

Thallus immersed in bark or rock, inconspicuous or causing discoloration, sometimes blackish due to copious development of brown hyphae; lichenized thalli usually whitish to pale brown, often pinkish when fresh, effuse or occasionally delimited in lichenized species. **Photobiont** absent or *Trentepohlia*. **Ascomata** perithecia, circular to ellipsoid in surface view, in section comprising a dark, often laterally spreading, clypeate involucrellum composed of compacted hyphae and bark cells, and a thin, usually colourless true exciple that surrounds the centrum; hyphae dark brown, K- (or darkening) or K+ greenish. **Hamathacium** usually of branched and anastomosed, ± moniliform or slender pseudoparaphyses, gel I-, rarely without interascal filaments and then gel often I+ bluish; downwardly projecting periphysoids also present. **Asci** fissitunicate, with two functional wall layers, obpyriform, obclavate or ± cylindrical, 8-spored, I-; ocular chamber present to ± absent, variously shaped, often conical. **Ascospores** clavate, oblong or fusiform, 1- or 3-septate (rarely to 5-septate), usually medianly constricted, sole-shaped, colourless, smooth, but occasionally brownish and finely warted when old; perispore (in K) inconspicuous to distinct. **Conidiomata** pycnidia; blackish, wall with same pigment as involucrellum of ascomata. **Conidiogenous cells** unbranched, enteroblastic, often percurrently proliferating, ± cylindric, lageniform or ± globose. **Conidia** either bacilliform, oblong, ovoid or thread-like, 0(-1-3)-septate; some species have two anamorphs. **Chemistry**: no substances detected by TLC. **Ecology**: on (usually smooth) bark, rarely on limestone.

Classification: Dothideomycetidae, Arthopyreniaceae.

Anisomeridium differs in the ± cellular (not hyphal) involucrellum which typically does not contain bark cells (non-clypeate); the ascospores in that genus are always hyaline and lack a perispore. *Mycomicrothelia* has dark-coloured and usually ornamented ascospores. *Collemopsisidium* species usually have a cyanobacterial photobiont, and grow on soil and rocks. Other superficially similar genera on bark, but with different ascoma, ascus, ascospore, or hamathecium structure include *Acrocordia*, *Leptorhaphis*, *Mycoporum*, *Porina* and *Strigula*.

Arthopyrenia rhyponia is incorrectly recorded from the British Isles.

LITERATURE: Coppins (1988), Foucard (1992).

1	Ascospores 1-septate (a few old spores sometimes 3-septate)	2
	Ascospores soon 3-septate or up to 5(-7)-septate	13
2(1)	On limestone; ascospores (19-)20-25 × 4.5-7 µm	saxicola
	On bark	3
3	Involucrellum K + green	4
	Involucrellum brown in K	7
4(3)	Ascospores with a distinct gelatinous perispore, c. 2 µm wide in K	5
	Ascospore without, or with a very thin perispore, <1 µm wide in K	6
5(4)	Cells of mature ascospores both with a distinct median constriction; ascomata 0.2-0.45 mm wide	cinereopruinosa
	Cells of mature ascospores without a median constriction, except sometimes the lower cell; ascomata (0.3-)0.4-0.6 mm wide	analepta
6(4)	Ascospores with a short upper cell and an elongated lower cell	<i>Anisomeridium ranunculosporum</i>
	Ascospores with cells of ± equal length	<i>Anisomeridium viridescens</i>
7(3)	Ascospores 27-40 × 8-13 µm, often becoming brownish	<i>Mycoporum antecellens</i>
	Ascospores <27 µm long or 8 µm wide, colourless	8

- 8(7) Pseudoparaphyses absent, but periphysoids arising from upper wall of ascoma (section) **salicis**
Pseudoparaphyses present, slender to moniliform 9
- 9(8) Ascomata 0.25-0.5 mm diam.; asci 60–100 μm long **fraxini**
Ascomata <0.25 mm diam., asci 30–70 μm long 10
- 10(9) Thallus not lichenized (*Trentepohlia* absent); ascospores usually with distinct perispore *c.* 1 μm thick in K **punctiformis**
Thallus lichenized (*Trentepohlia* present); perispore absent 11
- 11(10) Ascospores 4.5–5(–6) μm wide; thallus whitish to pale buff **nitescens**
Ascospores 3–4.5 μm wide; thallus pale fawn to darkish brown 12
- 12(11) Ascospores (14–)15–19(–21) \times 3–4.5 μm , asci 31–45 μm long; usually on smooth bark **carneobrunneola**
Ascospores 17–21(–26) \times 3–4 μm , asci 55–70 μm long; usually on rough bark **atractospora**
- 13(1) Involucrellum K + green; ascomata 0.3–0.5 mm wide **cerasi**
Involucrellum brown in K; ascomata 0.1–0.3 mm wide 14
- 14(13) Ascospores 3-septate, 22–31 \times 7–9 μm **subcerasi**
Ascospores 3–5(–7)-septate, 24–30 \times 8–10 μm **platypyrenia**

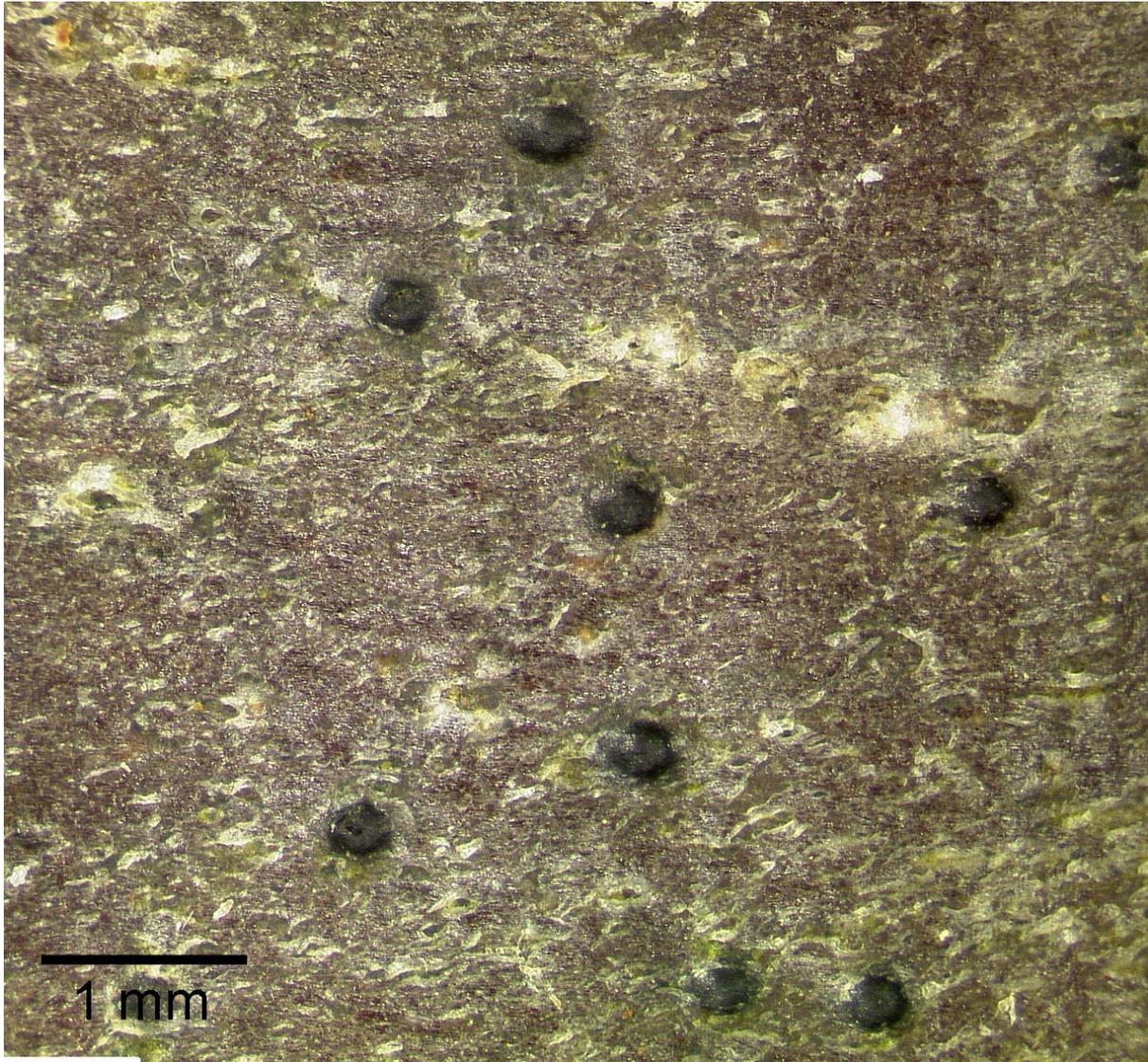
Arthopyrenia analepta (Ach.) A. Massal. (1852)

Thallus inconspicuous, not discolouring bark, non-lichenized. Ascomata (0.28–)0.4–0.6 \times 0.22 \times 0.55 mm, usually ellipsoid and with flat border formed by the spreading involucrellum; involucrellum brown, K+ greenish. Pseudoparaphyses slender, distantly branched, 1.5–2 μm wide, cells 8–15(–18) μm long. Asci 65–100 \times 12–16(–20) μm , \pm cylindrical. Ascospores 15–23 \times 5.5–8(–9) μm , 1-septate (a few old spores occasionally 3-septate), clavate with rounded apices, markedly constricted at septum, each cell often biguttulate but without a median constriction (except sometimes faintly so in the lower cell); perispore distinct and *c.* 2 μm thick in K. Pycnidia, when present, 60–100 μm diam.; conidia 7–11 \times 0.8–1 μm , thread-like, \pm straight.

On smooth bark of many trees, often as an early colonizer on thin branches; common. Throughout British Isles, but rare in Central and Eastern England. Europe, North America.

Illustrations: Dobson (2000) p. 63.

Usually recognized by the rather large, \pm ellipsoid ascomata in an inapparent thallus (without *Trentepohlia*), but several less common species have a similar appearance: *A. cerasi*, *A. cinereopruinosa*, *A. fraxini*, *Julella sericea* and *Pyrenula coryli*.



Arthopyrenia analepta (17900).

***Arthopyrenia atractospora* Zahlbr. (1935)**

Thallus lichenized. Ascomata globose, 0.14-0.2 mm diam., involucrellum brown, K –. Asci 55-70 μ m. Ascospores 1-septate, 17-21(-26) \times 3-4 μ m.

On rough bark of *Quercus*. England (Somerset), Wales, Scotland. N. America (Alabama, Florida).

A. carneobrunneola differs in the shorter asci and ascospores, and usually occurs on smooth bark.

***Arthopyrenia carneobrunneola* Coppins (1988)**

Thallus pale fawn to darkish brown, often pinkish when fresh, lichenized. Ascomata 0.1-0.2 \times 0.1-1.6 mm, sometimes a few confluent; involucrellum brown in water and K. Pseudoparaphyses \pm moniliform, 1.5-3 μ m wide. Asci 31-45 \times 14-17(-21) μ m; ascospores 1-septate, (14-)15-19(-21) \times 3-4.5 μ m, not or only slightly constricted at septum, without perispore.

On smooth bark, mainly *Corylus* (often with *A. nitescens*), distribution hyperoceanic. N. England (rare), W. Scotland, W. Ireland. France (Pyrenees).

A. nitescens is similar, but differs in the paler thallus, and smaller asci and ascospores.

Arthopyrenia cerasi (Schrad.) A. Massal. (1852)

Thallus inapparent or slightly bleaching the bark, non-lichenized. Ascomata 0.3–0.5 × 0.25 × 0.4 mm, often ellipsoid; involucrellum brown, K+ greenish. Pseudoparaphyses slender, 1.5–2 µm wide, cells *c.* 8–14 µm long. Asci 60–75 × 14–18 µm, cylindrical-clavate. Ascospores 17–22 × 5–7 µm, clavate with rounded apices, 3-septate, constricted at septa, especially the median one; perispore distinct, *c.* 2 µm thick in K. Pycnidia 80–120 µm, with either macro- or microconidia; macroconidia 11–13 × 2–2.5 µm, oblong, 3-septate; microconidia 9–14 × 0.8 µm.

On smooth bark, especially *Corylus*. N. & W. British Isles.

Close to *A. analepta* but differing in the smaller ascomata, 3-septate ascospores, and in conidial characters.

Arthopyrenia cinereopruinosa (Schaer.) A. Massal. (1855)

Thallus inconspicuous or slightly bleaching the bark, non-lichenized. Ascomata (0.2–)0.3–0.45 × 0.2–0.3 mm, circular or ellipsoid, often covered by a thin layer of bark cells giving a whitish pruinose appearance; involucrellum brown, K + greenish. Pseudoparaphyses slender, 1–1.5 µm wide, cells 8–16 µm long. Asci 55–77 × 12–19 µm, cylindrical-clavate. Ascospores 14.5–22 × 5–8 µm, clavate, with rounded apices, 1-septate, much constricted at the septum and each cell with a median constriction; perispore distinct, *c.* 2 µm thick in K. Pycnidia 60–100 µm diam., with either macro- or microconidia; macroconidia 8–11 × 1.8–2.2 µm, bacilliform; microconidia 4.7–6 × 1 µm, bacilliform.

On smooth bark, especially young *Fraxinus*. N. & W. British Isles. Europe, North America, E. Asia.

Close to *A. analepta*, but ascomata somewhat smaller, ascospores with a distinct median constriction in both cells, pseudoparaphyses slightly narrower, and conidia different.

Arthopyrenia fraxini A. Massal. (1852)

Thallus inconspicuous, or visible as a pale fawn or pale brown stain, non-lichenized. Ascomata 0.25–0.5 × 0.2–0.4 mm, circular or ellipsoid; involucrellum brown in water and K. Pseudoparaphyses 1–1.5 µm wide, richly branched, cells 6–12 µm long. Asci 60–90(–100) × 16–25 µm, narrowly obpyriform. Ascospores (17–)19–26 × (4.5–)5–7 µm, 1(–3)-septate, ± constricted at the septum, the apices ± rounded; perispore distinct, 1–1.5 µm thick in K. Pycnidia *c.* 100 µm diam.; conidia 4–6 × 0.8 µm, bacilliform.

On smooth bark, usually on branches, of *Fraxinus*, also on *Alnus*, *Betula*, *Corylus*, *Ilex* and *Quercus*. Scotland, Wales, S.W. England, Ireland. Europe, North America.

Superficially, easily mistaken for *A. analepta*, but distinguished by its K– involucrellum, more richly branched pseudoparaphyses, ± obpyriform asci and shorter conidia. The internal features of *A. fraxini* more closely resemble *A. punctiformis*, which has smaller ascomata, asci and ascospores and ± moniliform pseudoparaphyses.

Arthopyrenia nitescens (Salwey) Mudd (1861)

Thallus whitish to pale buff, usually pinkish when fresh, lichenized. Ascomata 0.15–0.2 × 0.12–0.17 mm, circular to ellipsoid, mostly scattered; involucrellum brown in water and K. Pseudoparaphyses 1.5–3 µm wide, persistent, much branched, ± moniliform, the cells 3–8 µm long. Asci 40–60 × (16–)19–23 µm, obpyriform or obclavate. Ascospores (18–)19–26(–29) × 4.5–5(–6) µm, 1-septate, scarcely constricted at septum; cells ± equal, each usually biguttulate; perispore indistinct. Pycnidia 30–40 µm diam., frequent; conidia 2.8–3.8 × 0.8 µm, bacilliform.

On smooth bark, mainly *Corylus*, in old woodlands. W. Scotland, rare in Wales and S.W. England, W. Ireland. Spain.

May be confused with *A. punctiformis*, but the ascospores never have a distinct perispore, and the species grows in mature, species-rich communities (i.e. with *Arthonia*, *Pyrenula*, *Thelotrema* species etc.). Closely related to *A. carneobrunneola*.

Arthopyrenia platypyrenia (Nyl.) Arnold (1870)

Thallus inconspicuous, non-lichenized. Ascomata hemisphaerical, depressed, circular in outline, 0.25–0.3 mm diam. Asci clavate, c. $60 \times 12\text{--}18 \mu\text{m}$. Pseudoparaphyses thin, c. 2μ wide, branched and anastomosing. Ascospores 3–5(–7)-septate, $24\text{--}30 \times 8\text{--}10 \mu\text{m}$. Conidia rod-shaped, $3\text{--}5 \times 1\text{--}1.5 \mu\text{m}$.

On bark, especially of *Hedera*. Ireland.

A non-lichenized species of uncertain affinity.

Arthopyrenia punctiformis A. Massal. (1852)

Thallus inconspicuous, or bark darkened (due to abundant brown hyphae), non-lichenized. Ascomata 0.1–0.23 mm diam., \pm circular, scattered, or clustered; involucrellum brown in water and K. Pseudoparaphyses (1–)1.5–2.5(–3) μm wide with cells 3–8 μm long, much branched, \pm moniliform. Asci 40–55 \times 15–22 μm , obpyriform. Ascospores 16–20(–22) \times 4.5–5 μm , 1-septate and colourless, (sometimes yellowish brown and 3-septate when old), slightly constricted at the septum, cells often biguttulate but without median constrictions; perispore usually distinct, c. 1 μm thick in K. Pycnidia not detected.

On smooth bark of many trees and shrubs, usually as an early colonizer of twigs and thin branches and often accompanied by *Arthonia punctiformis*; common (except in very polluted areas). Throughout British Isles, but rare in C. England. Europe, North America, Asia (Israel), New Zealand.

Illustrations: Dobson (2000) p. 63, Puntillo (1996) Tav. IV.

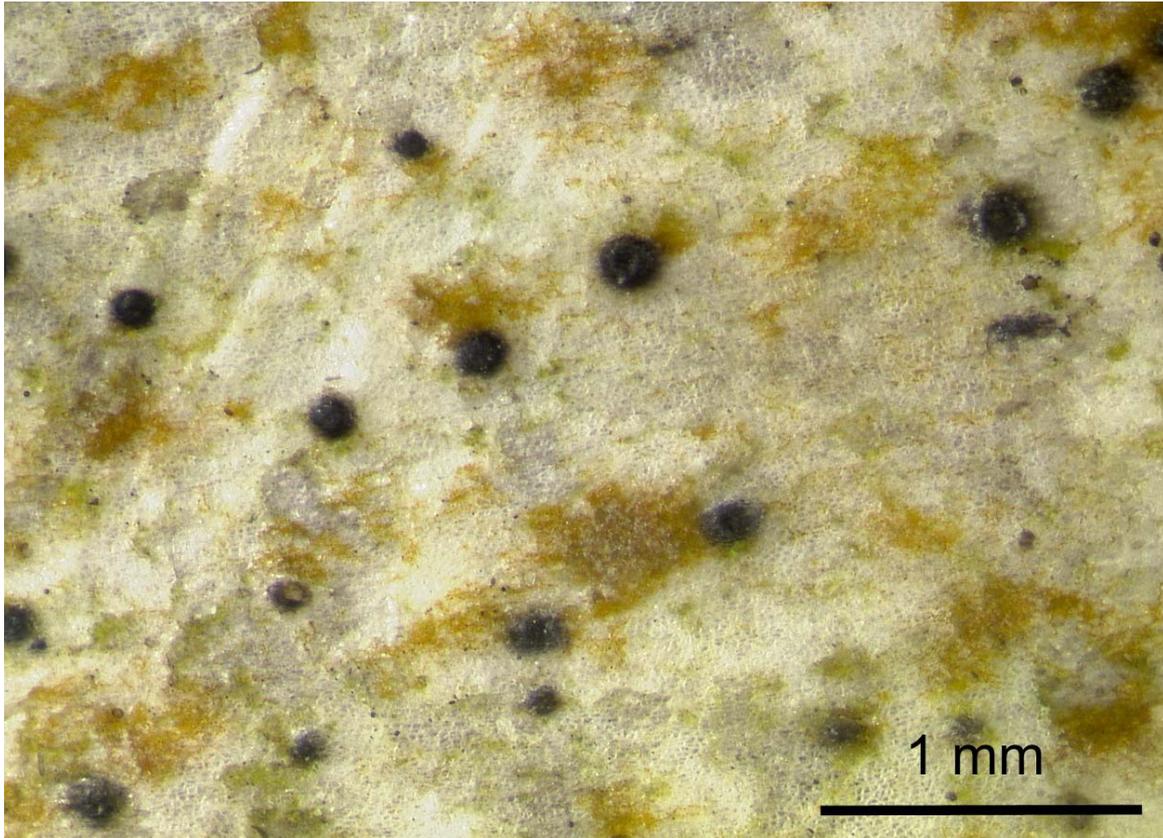
A rather broad concept of the species is used here to include extreme morphs with a blackish thallus (i.e. *A. laburni*) or with irregularly clustered ascomata (i.e. *A. cembrina*); further critical studies on this complex are needed. Usually easily recognized in the field by the small ascomata and habitat ecology, but can be confused with *A. salicis*, which has slightly larger ascomata and no pseudoparaphyses. Other species with small ascomata and 1-septate ascospores include *A. carneobrunneola*, *A. nitescens* and *Anisomeridium viridescens*, but these all have a clearly lichenized thallus containing *Trentepohlia*.

Arthopyrenia salicis A. Massal. (1852)

Thallus often inconspicuous, pale fawn brown, sometimes pinkish when fresh, more rarely dark brown (due to abundant brown hyphae), apparently either lichenized or not. Ascomata 0.15–0.3 \times 0.15–0.2 mm, often with depressed ostiole, circular or ellipsoid; involucrellum brown in water and K. Pseudoparaphyses absent at maturity; periphysoids present, 7–15 \times 1–1.5 μm , unbranched, 0- to 2-septate; hymenial gel sometimes I+ pale blue. Asci 33–45 \times 14–20 μm , obpyriform. Ascospores (12–)14–17(–21) \times 4–5.5 μm , 1-septate, constricted at the septum, each cell biguttulate, the lower cell often with a median constriction, the apices rather blunt; perispore indistinct. Pycnidia c. 60 μm diam.; conidia c. 3–3.7 \times 1 μm , \pm bacilliform.

On smooth bark, especially of *Corylus*; rather common. Throughout British Is., especially frequent in the north and west. Europe, North America, Asia (New Guinea).

Thalli vary from having no detectable to abundant *Trentepohlia* cells. Differs from *A. punctiformis* and all other small perithecioid species in lacking pseudoparaphyses and possessing periphysoids.



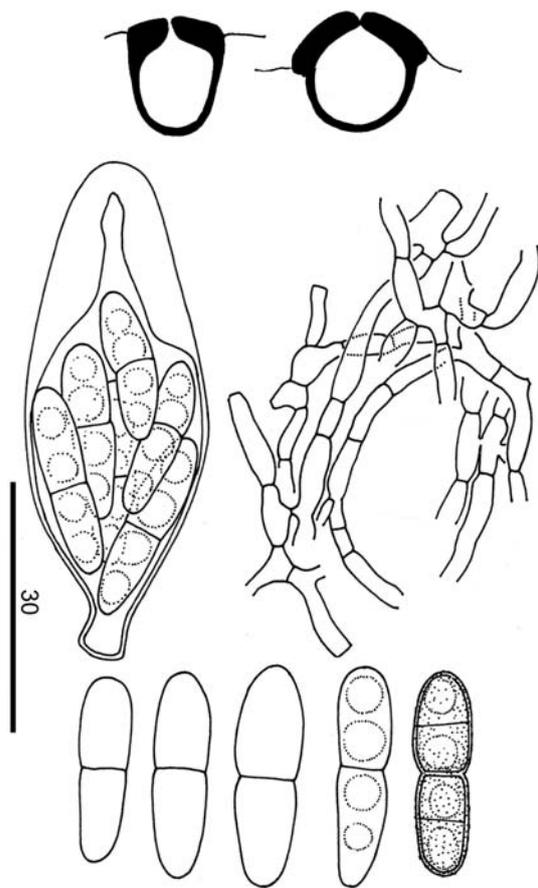
Arthopyrenia salicis (20877).

***Arthopyrenia saxicola* A. Massal. (1855)**

Thallus immersed (rarely superficial?), grey (often discoloured blackish by cyanobacteria), sometimes clearly delimited, lichenized. Ascomata 0.1–0.2 mm diam., globose, half- to almost completely immersed in pits in rock, apex black, convex or disc-like. Involucrellum appressed to upper half of exciple, or indistinguishable from thickened apex of exciple, pigment brown, K + slightly darkening. Exciple brown. Pseudoparaphyses richly branched, 2–2.5 μm wide. Asci 65–85 \times 17–23 μm , clavate, obclavate to subcylindrical. Ascospores (19–)20–26.5 \times 4.5–8 μm , 1-septate, \pm oblong, the upper cell only slightly broader than the lower; overmature spores brown, finely rugulose, sometimes thinly 3-septate. Pycnidia frequent, 60–80 μm diam.; conidia 4–5 \times 0.5–1.2 μm .

On hard limestones; local. Throughout Britain, Ireland. Europe, E. Asia (Hong Kong).

Easily confused in the field with *Porina linearis*, which differs in the 3-septate ascospores, \pm simple paraphyses, and different pigment in the involucrellum.



< *Arthopyrenia saxicola*: outlines of ascomata; asci, part of hamathecium, and ascospores, including one overmature spore.

***Arthopyrenia subcerasi* (Vain.) Zahlbr. (1921)**

Thallus inconspicuous, non-lichenized. Ascomata 0.2–0.26 × 0.14–0.2 mm, ± ellipsoid; involucrellum brown in water and K. Pseudoparaphyses 1.5–2.5 µm wide, persistent, much branched; cells c. 4–10 µm long. Asci 55–80 × 19–30 µm, obpyriform. Ascospores 3-septate, 22–31 × 7–9 µm, colourless, sometimes brownish and warty when old; perispore very thin or indistinct. Pycnidia 40–60 µm diam; conidia 4–5 × 0.8–1 µm, ± bacilliform.

On smooth bark of *Betula* trunks in old woodlands; rare. Scotland. Scandinavia, Spain, Austria.

Most likely to be confused with *Mycoporum antecellens* but differs in the generally smaller ascomata and smaller ascospores, which become 3-septate very early and only rarely become brownish. *A. cerasi* differs in its larger ascomata, ± cylindric asci, shorter ascospores, K+ green involucrellum and different conidia. The species may belong in *Mycoporum*.

References

Coppins, B.J. (1988) Notes on the genus *Arthopyrenia* in the British Isles. *Lichenologist* **20**: 305-325.
 Foucard, T. (1992) Notes on the corticolous *Arthopyrenia*-species in Sweden. *Graphis Scripta* **4**: 49-60.

Thallus crustose, immersed, or superficial, granular to areolate. **Photobiont** Chlorophyceae, or possibly also cyanobacteria in part; hymenial algae absent. **Ascomata** perithecia, projecting, or immersed in the substratum. **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** 8 per ascus, 113–306 × 39–112 μm, ellipsoid, muriform, colourless to dark brown. **Conidiomata** unknown. **Chemistry**: lichen products absent. **Ecology**: on calcareous rocks and soil. **Distribution**: 4 species, Europe, Novaya Zemlya.

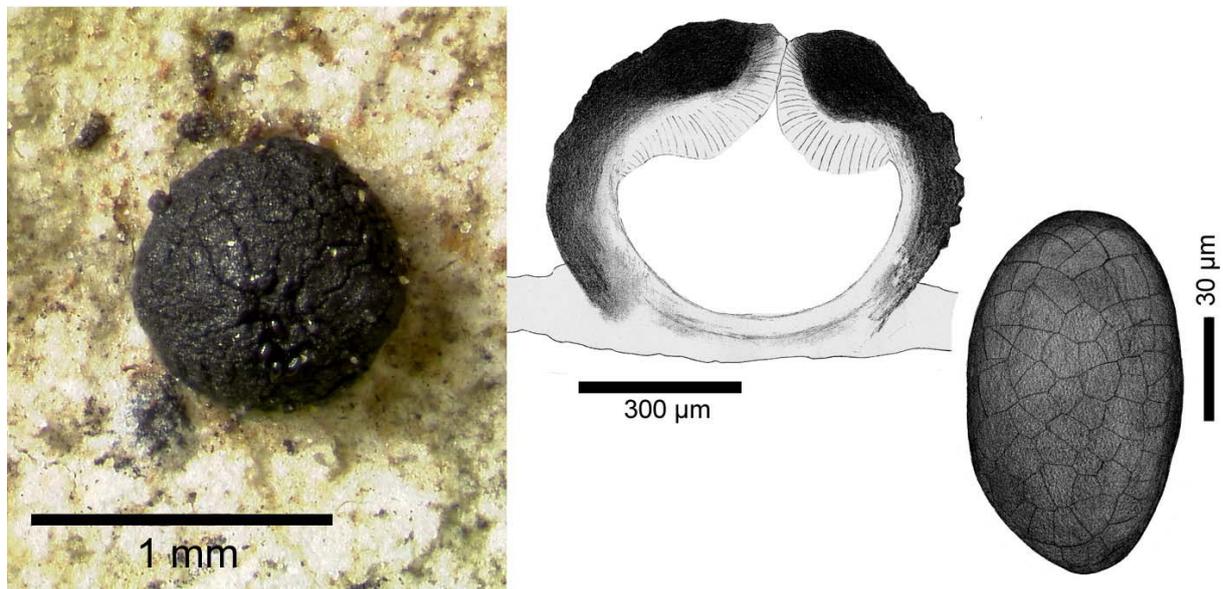
This genus is well-supported by molecular data, but is difficult to distinguish morphologically from some related genera. Recent authors have treated the species under the genus *Polyblastia*; see the key under that genus.

LITERATURE: Savić & Tibell (2008).

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

Atla alpina S. Savić & Tibell (2008)

Polyblastia theleodes auct. brit. p.p.



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, surface rough, without 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 cells outlines mostly obscured; (63–)72–87(–98) × (30–)35–47.5(–52) μm, length/width ratio (1.5–)1.7–2.3(–2.7).

On damp limestone and calcareous sandstone on cliff ledges and below overhangs, upland, 150–900 m. S. Wales, C. and W. Scotland. Scandinavia, Spitsbergen, Novaya Zemlya, C. Europe.

This species has been confused with *Sporodictyon schaeerianum*, 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)

Polyblastia wheldonii Travis (1947)



Scale = 300 μ m

Thallus superficial, granular, brown to dark brown, granules 0.02-0.1 mm diam., composed of distinct goniocysts, but cyanobacteria also often associated with 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 produced above into a short neck. Asci (3-)4-8-spored when mature. Ascospores muriform, brown to dark brown, opaque when mature, 80-160 \times 40-92 μ m (the larger spores are probably derived from asci with fewer than 8 spores)..

On base-rich soil and on dying mosses, over limestone, epidiorite, basic schist and calcareous sandstone; also on dunes and mine spoil-heaps; rare. Wales, N. England, Scotland. Spain (Pyrenees), Austria, Norway, Sweden.

Literature:

Savić, S. & Tibell, L. (2008) *Atla* – a new genus in the Verrucariaceae (Verrucariales). *Lichenologist* 40: 269-282.

BELONIA Körb. ex Nyl. (1852)

Thallus crustose, superficial, or immersed in the substratum; sometimes finely granular but without true soredia. **Cortex** absent. **Photobiont** usually *Trentepohlia*, rarely *Trebouxia*. **Ascomata** perithecioid, opening by an apical pore, or the pore opening somewhat at maturity; immersed in the thallus, in projecting thalline warts, or emergent. **Exciple** prosoplectenchymatous or of rounded to shortly elongated cells, sometimes two-layered; exciple without dark pigments, or partly brown-pigmented. **Involucrellum** absent. **Hymenium** sometimes containing small yellow-orange oil droplets; hymenial gel either I –, K/I –, or I + dull blue to dull red (but blue at low concentrations of I), K/I + blue. **Hamathecium** of paraphyses; these thin, to 3 µm wide, simple, septate, lax, not forming a distinct epithecium, but filling the cavity formed by the ascomatal walls; paraphyses and periphysoids absent. **Asci** (4–)8-spored, I – or K/I + blue, narrowly cylindrical to elongate-clavate, thin-walled, without apical thickening or apparatus. **Ascospores** colourless, mostly needle-shaped, septate or rarely muriform with attenuated apices. **Conidiomata** unknown. **Chemistry:** lichen products not detected by TLC. **Ecology:** on bark, calcareous rock and soil.

Classification: Ostropomycetidae, Ostropales, Gyalectaceae?

A genus of approximately 12 species, known from the Northern and Southern Hemispheres. The ascomata are perithecioid, but their ontogeny is similar to apothecioid ascomata in related genera; in some species the apical pore is said to open when wet. Paraphyses arise either mainly from the base of the centrum or from both the base and sides, but there is no distinct zone of paraphyses. *B. incarnata* appears to differ from all other species in its trebouxoid photobiont, I – hymenial gel, and habitat on soil.

LITERATURE: Jørgensen *et al.* (1983), Navarro-Rosinés & Llimona (1997).

- | | | | |
|------|--|----------------------|---|
| 1 | Ascospores muriform | nidarosiensis | |
| | Ascospores transversely septate | | 2 |
| 2(1) | On soil, bryophytes or algal mats; apothecia without thalline covering in upper part; photobiont <i>Trebouxia</i> | incarnata | |
| | On rock; photobiont <i>Trentepohlia</i> | | 3 |
| 3(2) | Thallus superficial; inconspicuous to thickly granular; ascomata in thalline warts 250–600 µm diam.; ascospores 50–100(–125) µm long | russula | |
| | Thallus semi-immersed, thin; ascomata in thalline warts 200–250 µm diam.; ascospores 50–75(–100) µm long | callicola | |

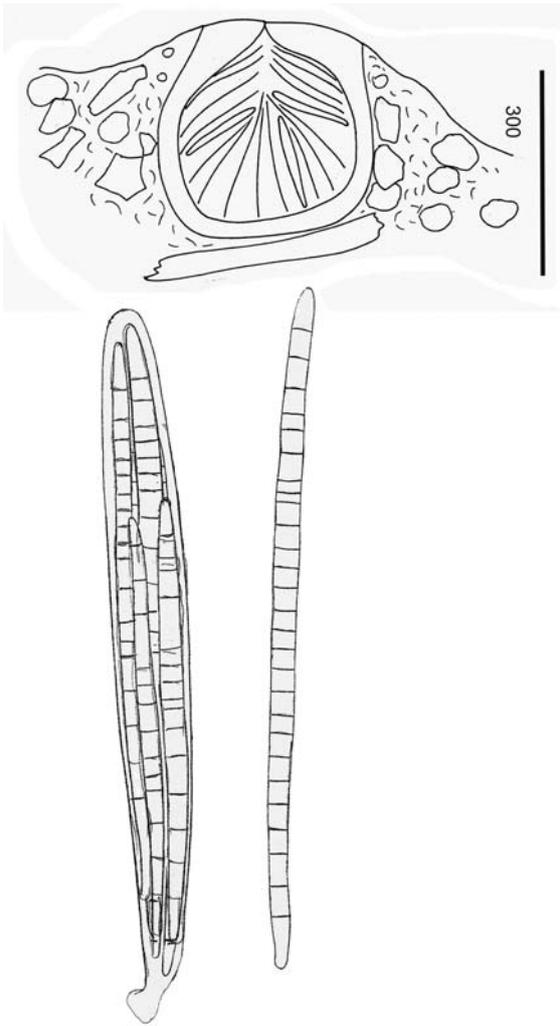
Belonia callicola Walt. Watson (1935)

Thallus semi-immersed, effuse, pink-white. Photobiont *Trentepohlia*. Ascomata discrete or in clusters of 1 to 3, one-quarter to half-immersed in thallus, in fertile warts 200–250 µm diam., apex free of thallus. Involucrellum absent. Exciple colourless to pale yellow-brown or pink. Asci (2–)4–8-spored. Ascospores 50–75(–100) × 3–7 µm, acicular, 10–20-septate.

On limestone; rare. S.W. England (N. Somerset: Goblin Combe) and N.W. England (Cumberland: Buttermere). Endemic.

Close to *B. russula* and possibly conspecific, differing in the partly immersed thallus, smaller size of ascomata and ascospores, and possibly the smaller number of ascospores in the ascus.

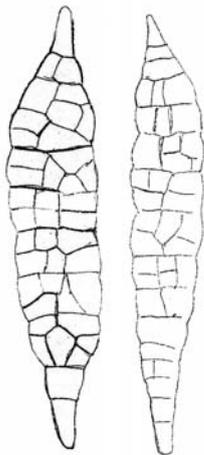
Belonia incarnata Th. Fr. & Graewe ex Th. Fr. (1865)



Thallus indistinct, effuse, thin, varnish-like, greyish white or greenish grey, more or less gelatinous when wet, comprising goniocyst-like clusters of trebouxioid algae in a matrix of narrow, filamentous hyphae. Ascumata one- to three-quarters immersed, irregularly scattered, single or clustered, pinkish or yellowish grey, 250–450 μm diam., not covered by a thalline layer; opening remaining pore-like; exciple pale pink to reddish brown, thin. Hymenial gel I –, K/I –. Asci 8-spored, I –, K/I –. Ascospores 120–160 \times 3–4 μm , acicular, multiseptate.

On mosses on more or less basic soils, and on algal films over peat on mine spoil heaps; rare, probably overlooked. S.W. England (Dartmoor), N.E. England (Teesdale), Wales (Ystwyth), Scotland (Highlands). Scandinavia, Czech Republic, Azores.

Belonia nidarosiensis (Kindt) P.M. Jørg. & Vězda (1983)



Thallus more or less superficial, effuse, rather thin, often wide-spreading, pink-orange, fading to whitish cream in the herbarium; uneven, irregularly cracked, finely powdery-granular, the granules 20–30 μm diam. Photobiont *Trentepohlia*. Ascumata uncommon, scattered, 240–420 μm diam., pale pink, globose, with an apical pore which is closed in healthy ascumata when dry, but is said to open somewhat when wet; exciple not covered by a thalline layer. Hymenial gel I + dull red (blue at low concentrations of I), K/I + blue. Asci (4–)6–8-spored. Ascospores (36–)50–60(–82) \times (8–)10–12(–14) μm , muriform, with (7–)12–15(–19) transverse septa; elongate, more or less constricted at the middle septum, and with attenuated apices.

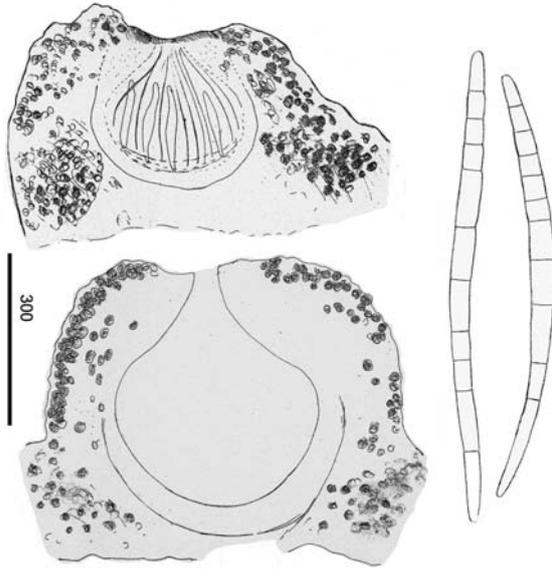
On dry, rain-sheltered vertical surfaces and overhangs on calcareous rocks, especially hard limestone, but also on calcareous mudstone, and common on cement-mortar-plaster-stone walls; widely distributed and locally frequent. W. British Isles from Devon to Shetland

Isles, also S.E. England in churchyards, W. Ireland. Scandinavia, Spain, France, C. Europe.

Often forming extensive sterile, sorediate, orange-pink sheets on vertical rock faces and north-facing church walls; some morphs resemble sorediate morphs of *Opegrapha gyrocarpa*, the thallus of which is C + red (gyrophoric and schizopeltic acids). Care should be taken to avoid

confusion with poorly developed sterile thalli of other *Trentepohlia*-containing species including *Porina linearis* and *Gyalecta jenensis*.

***Belonia russula* Körb. ex Nyl. (1857)**



Thallus mostly superficial, effuse, inconspicuous to thickly granular, dull pinkish orange to dark reddish grey to reddish brown. Photobiont *Trentepohlia*. Ascomata mostly discrete, rarely contiguous, immersed in prominent thalline warts (250–)400–600 μm diam., dull reddish brown, the apex pale grey or pink-grey, translucent when wet. Exciple more or less completely covered by thalline tissue. Hymenial gel I + dull red (blue at low concentrations of I), K/I + blue. Asci 8-spored, wall K/I + blue. Ascospores (50–)75–100(–125) \times 3–6 μm , acicular, 10–20-septate, sometimes faintly constricted at septa.

On epidiorite, calcareous schists and limestones in moist, shaded overhangs, usually above 600 m; local. Scotland (Highlands). Mountains of N. and C. Europe.

The thalline tissue surrounding the exciple has a denser structure than the rest of the thallus, forming a pale involucrellum-like structure. See under *B. calcicola* for differences from that species.

References:

- Jørgensen, P.M., Vězda, A. & Botnen, A. (1983) *Clathroporina calcarea*, a misunderstood lichen species, and a note on the genus *Clathroporina* in Europe. *Lichenologist* **15**: 45-55.
- Navarro-Rosinés, P. & Llimona, X. (1997) *Belonia mediterranea*, a new calcicolous lichen species from Catalonia (NE Spain). *Lichenologist* **29**: 15-27.

CATAPYRENIUM Flot. (1850) *sensu lato*

Thallus squamulose, lower surface attached by colourless or brownish rhizohyphae. **Upper cortex** paraplectenchymatous, medulla paraplectenchymatous or plectenchymatous, lower cortex absent or of rounded to angular cells. **Photobiont** chlorococcoid. **Ascomata** perithecia, immersed in the thallus or located between the squamules. **Involucrellum** present or absent. **Hamathecium** of periphyses and periphysoids. **Asci** 8-spored, clavate or cylindrical, wall thickened above. **Ascospores** biseriate or uniseriate in the ascus, colourless, simple, ellipsoid. **Conidiomata** pycnidia, immersed in the squamules or forming projection at the squamule margins. **Conidia** oblong to shortly bacilliform. **Chemistry:** no lichen substances detected by TLC. **Ecology:** mostly on soil or on decaying bryophytes and plant debris, rarely directly on rock or bark.

Classification: Chaetothiomycetidae, Verrucariales, Verrucariaceae.

The division of *Catapyrenium s.l.* into smaller genera, based on morphology, is supported by molecular studies, but the species are treated together here for convenience.

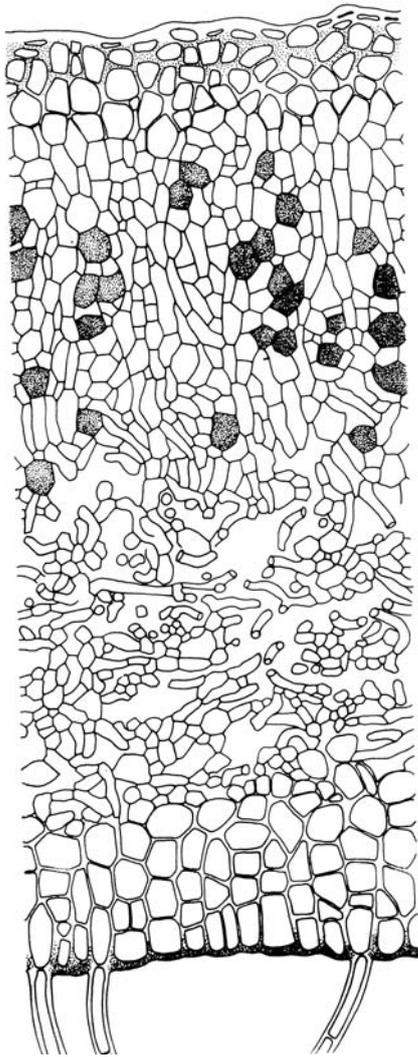
LITERATURE: Breuss (1990).

- | | |
|------|--|
| 1 | Perithecia situated between the squamules, with involucrellum. Squamules very small (scarcely over 1–1.5 mm) and thin (usually only 100–200 µm), ± united into a crust. Rhizohyphae narrow (only about 4 µm) (Rhizohyphae dark; squamules with black prosoplectenchymatous lower cortex; involucrellum entire; ascospores usually oblong-ovoid to clavate) Involucropyrenium waltheri (On soil and humus, very rare. N.C. Scotland (Westernness: Ben Alder). C. & N. Europe, arctic-alpine). Perithecia immersed in the squamules, without involucrellum (but blackened wall in part) 2 |
| 2(1) | Rhizohyphae dark; asci clavate, spores biseriate; upper cortex thin (rarely over 20 µm) and indistinctly delimited, paraplectenchymatous and small celled (cells 5–8 µm) 3
Rhizohyphae colourless (in part proximally delicately browned). (Thallus small- to large-squamuled or foliose-squamulose, medulla prosoplectenchymatous or at least with longer-hyphaed sections; squamules appressed to ascending, isolated or approximate or overlapping each other, not crowded in cushion-like complexes, attached by rhizohyphal tomentum, without rhizines. Asci cylindrical, spores uniseriate) 5 |
| 3(2) | Squamules finely crenate to deeply cleft crenate-lobed with narrowly contiguous lobules, ± appressed, usually whitish pruinose, often dark-bordered, with black paraplectenchymatous lower cortex. Spores narrow-ovoid to clavate. Principally arctic-alpine Catapyrenium cinereum (On soil, humus and mosses, especially on calcareous ground; upland areas and on or near the coast. Europe).
Squamules more coarsely lobed, not finely deeply crenate, without dark bordering, forming a foliose-lobed, ± effigurate thallus, without lower cortex, medullary hyphae by brown colouration grading into rhizohyphal tomentum 4 |
| 4(3) | Asci 55–65 × 13–15 µm; ascospores ellipsoid to almost fusiform, on average below 17 µm long, in part pseudodiblastic (rarely truly 2-celled). Squamules usually light brown to greyish or grey-greenish-tinged, squamule apices often patchily pruinose; thallus usually corticolous, but also on moss over rocks Catapyrenium psoromoides (On bark or on bryophytes on limestone; very rare. S. England, N. Wales, E.C. Scotland. Europe, E. Africa, N. America, New Zealand). |

- Asci 75–85 × 17–20 µm; ascospores elongate-ovoid to clavate, on average over 17 µm long, not pseudodiblastic; thallus usually mid-to dark-brown, often distinctly rosette-like; marginal lobes broadly rounded and thick, epruinose; pruina, when present, on the inner part of the thallus and finer, diffuse, not patchy; thallus on soil or over soil mosses **Catapyrenium daedaleum**
(On soil, humus, or decaying bryophytes; rare. E.C. Scotland. C. & N. Europe, arctic-alpine).
- 5(2) Perithecial wall dark, under 20 µm thick **Placidium michelii**
(On sandy soil, very rare and local. S.E. England. Alps, Sweden).
Perithecial wall colourless, more than 20 µm thick 6
- 6(5) Pycnidia marginal, ± projecting as nodules, usually numerous and striking, but sometimes rare or inapparent 7
Pycnidia laminal and completely immersed in the squamules, or absent. (Lower cortex not of anticlinal hyphae) 9
- 7(6) Lower cortex composed of anticlinally arranged hyphae, the cells in distinct vertical rows (see figure below); medulla prosoplectenchymatous; conidia *c.* 5–7 µm long, bacilliform. (Squamules mostly dark (red-) brown, rarely more than 7 mm wide, roundish to lobed, frequently with ± swollen upturned margin. Pycnidia usually 0.2–0.3 mm diameter).
..... **Placidium lachneum var. lachneum**
(On soil and humus, upland. Wales, Scotland. Fennoscandia, C. & N. Europe).
Lower cortex not of anticlinal hyphae, cells globose to polygonal, not in distinct vertical rows; conidia *c.* 3–5 µm long, bacilliform or oblong-ellipsoid 8
- 8(7) Ascospores *c.* 12–17 × 5.5–7.5 µm; squamules usually at least at the margin finely hairy, crowded to imbricate, to 6 mm wide, usually less than 350 µm thick; medulla weakly developed, of 'mixed' type; rhizohyphae thin (5 µm) and developed to the squamule margins **Placidium pilosellum**
(On soil or humus. S.W. England to Scotland. Europe, predominately (sub-)atlantic-(sub-)mediterranean; Morocco, Australia).
Ascospores broadly ellipsoid, *c.* 15–20 × 7.5–9.5 µm; squamules always without hairs, usually imbricate, undulate, large (to 11 mm), 350–700 µm thick, with strongly developed prosoplectenchymatous medulla (to 300 µm); rhizohyphae 5.5–7.5 µm diameter, absent in a broad marginal zone **Placidium rufescens**
(On calcareous rocks or soil, local. Widespread in Britain. Europe).
- 9(6) On limestone and mortar; squamules usually dark-bordered, underside black; periphyses thin (2–3 µm) **Placidium boccanum**
(Mortar and calcareous rocks; very rare. England (S. Devon). Mediterranean region).
On soil; squamules not distinctly dark-bordered, underside usually pale, but not uncommonly also blackened; periphyses 3–4 µm thick. (Widespread in Britain)
..... **Placidium squamulosum**
(On soil and humus. Widespread in Britain and Ireland. Europe).

Literature:

Breuss, O. (1990) Die Flechtengattung *Catapyrenium* (Verrucariaceae) in Europa. *Stapfia* **23**.



< *Placidium lachneum*: section of thallus showing distinctive lower cortex with cells in rows.

COLLEMOPSISIDIUM Nyl. (1881)

Pyrenocollema auct.

Thallus crustose, superficial to immersed, usually subgelatinous, the hyphae generally vertically orientated. **Photobiont** a cyanobacterium (*Hyella*, *Gloeocapsa* or *Nostoc*) with orange, blue-green or violet cells, rarely a green alga. **Ascomata** perithecioid, usually unilocular. **True exciple** dark brown; wall \pm cellular, normally densely pigmented. **Involucrellum** present or absent. **Hamathecium** of sparingly to richly branched and anastomosing pseudoparaphyses, with numerous but inconspicuous septa; hymenial gel I –. **Asci** ovoid to subcylindrical, usually stalked, I –, usually 8-spored; wall thickened above, with an ocular chamber; with two functional wall layers, dehiscence fissitunicate, dehisced asci with a distinct extruded rostrum. **Ascospores** colourless, oblong to ovoid-fusiform, 1-septate, the upper cell usually shorter and broader than the lower; a poorly defined gelatinous perispore sometimes present. **Conidiomata** pycnidia. **Conidiogenous cells** \pm cylindrical, phialidic. **Conidia** bacilliform or ellipsoid. **Chemistry:** lichen products not detected. **Ecology:** on calcareous substrata in moist situations, on wet sand, or on acid or calcareous rocks in freshwater or maritime habitats.

Classification: Lichinomycetes, Lichinales, Xanthopyreniaceae.

In studying littoral *Collemopsisidium* species, care should be taken to avoid confusion with the lichenicolous fungus *Stigmidium marinum* (Deakin) Swinscow (1965), which occurs on *Verrucaria* species, particularly *V. halizoa* and *V. mucosa*, which has perithecia 150-200 μm diam., lacks interascal filaments, and has 1-septate ascospores constricted at the septum, 10-15 \times 4-6 μm .

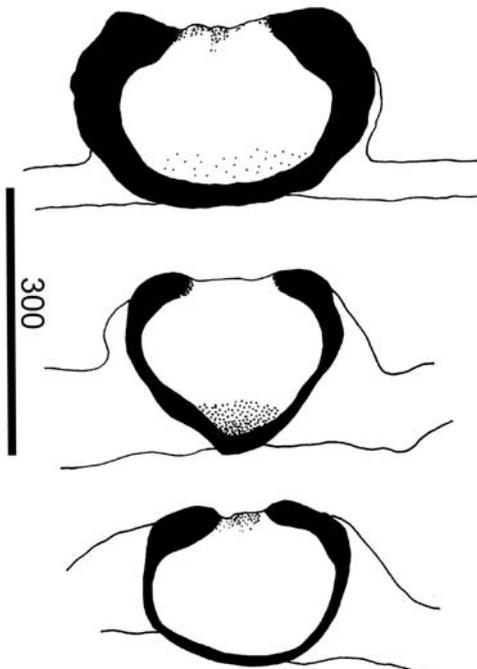
LITERATURE: Kohlmeyer *et al.* (2004), Mohr *et al.* (2004), Nordin (2002).

- | | | |
|------|--|----------------------------------|
| 1 | In terrestrial or freshwater habitats; involucrellum absent | 2 |
| | In marine habitats on rock, shells, barnacles or seaweeds; involucrellum often present | 9 |
| 2(1) | On turf, soil, or bryophytes | 3 |
| | On rocks or mortar | 6 |
| 3(2) | Ascospores > 25 μm long | 4 |
| | Ascospores < 25 μm long | 5 |
| 4(3) | Ascospores 26–37 μm long; in sand dune slacks | arenisedum |
| | Ascospores 27–44 μm long; in montane habitats | bryospilum |
| 5(3) | Ascospores 21–22 \times 8 μm , on inland sandy banks | argilospilum |
| | Ascospores 15–19(–21) \times 5–7 μm ; in calcareous dune slacks or machair | subarenisedum |
| 6(2) | Ascospores more or less oblong, the lower cell not markedly narrowed (photobiont <i>Trentepohlia</i>) | see <i>Arthopyrenia saxicola</i> |
| | Ascospores ovoid to ovoid-fusiform, the lower cell distinctly narrowed towards the apex | 7 |
| 7(6) | Thallus superficial, on siliceous rocks by rivers and lakes or on flushed outcrops | angermannicum |
| | Thallus immersed or superficial, on calcareous rocks | 8 |

- 8(7) Asci subcylindrical, pseudoparaphyses sparingly branched; on chalk stones or mortar **monense**
 Asci obclavate to obpyriform, pseudoparaphyses richly branched; on flushed limestone or calcareous schists **caesium**
- 9(1) Growing on the seaweed *Pelvetia* **pelvetiae**
 Growing on rocks or calcareous shells 10
- 10(9) Thallus superficial 11
 Thallus immersed in the (calcareous) substratum 12
- 11(10) Thallus with black ridges or warts **elegans**
 Thallus without black ridges or warts **halodytes**
- 12(10) Involucrellum intermixed with the substratum, wide-spreading, often covering more than one perithecium **ostrearum**
 Involucrellum not containing material from the substratum 13
- 13(12) Ascomata superficial or semi-immersed, 150–550 μm diam., involucrellum well-developed and either hemispherical or spreading laterally **sublitorale**
 Ascomata immersed in pits in the substratum, 100–240 μm diam., involucrellum lid-like, scarcely spreading laterally **foveolatum**

Collemopsidium angermannicum (Degel.) A. Nordin (2002)

Pyrenocollema strontianense (Swinscow) R.C. Harris (1987)



Thallus superficial, thin to moderately thick, 80–120 μm thick, smooth or cracked, mid green-brown to dark brown. Photobiont cells isodiametric to slightly elongate. Ascomata 120–300 μm diam., more or less immersed in thallus, partly immersed in a thalline wart, or almost sessile; globose or often slightly flattened, ostiole often in a depression and up to 90 μm wide in larger ascomata. Exciple pigmented throughout or slightly paler at base, thickened around ostiole. Involucrellum absent. Pseudoparaphyses densely branched and anastomosing. Asci obovate, 85–100 \times 19–25 μm . Ascospores 1-septate, 17–26 \times 6–12 μm , upper cell often wider than lower. Pycnidia sessile or partly immersed in thallus; conidia oblong-ellipsoid, 2.9–3.3 \times 1.2 μm .

On siliceous rocks beside rivers and lakes, rarely on flushed rock surfaces, often with *Verrucaria* species. N. and W. Britain. Norway, Sweden, France, Spain, N. America.

Distinguished from *C. caesium* by the superficial thallus.

Collemopsidium arenisedum (A.L. Sm.) ined.

Pyrenocollema arenisedum (A.L. Sm.) Coppins (1992)

Thallus whitish or grey, immersed. Photobiont cells yellowish orange (*Hyella*). Ascomata 160–200 μm diam., \pm globose with a conical apex, mostly half- to three-quarters immersed. Involucrellum absent. Pseudoparaphyses densely branched and anastomosed above. Asci 100–105 \times 19–20 μm , subcylindrical, 4- to 8-spored. Ascospores 26–37 \times (8–)9–10 μm , ovoid-fusiform.

On damp sand encrusted with calcareous deposits, in coastal dune slacks. S. and W. England (Devon, Dorset, Hampshire), N. England (Cheshire, Lancashire). Netherlands, Germany.

C. subarenisedum, which occurs in similar situations, has smaller ascospores.

Collemopsidium argilospilum (Nyl.) ined.

Pyrenocollema argilospilum (Nyl.) Coppins (1992)

Thallus dull olive-green, gelatinous when wet. Photobiont cells blue-green. Ascomata \pm globose, semi-immersed. Ascospores 21–22 \times 8 μm , oblong-ovoid.

On inland wet sand banks. W. England (Shropshire), not recorded since the 19th century. ?Endemic.

Collemopsidium bryospilum (Nyl.) Coppins (2004)

Pyrenocollema bryospilum (Nyl.) Coppins ex H.F. Fox (2000)

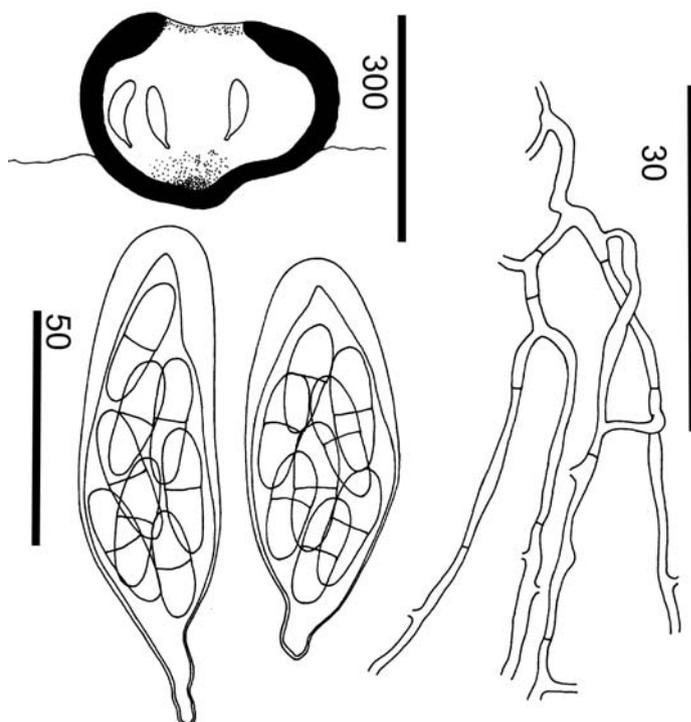
Thallus indistinct, bluish. Ascomata \pm conical. Asci 2–8-spored, oblong. Ascospores 27–44 \times 8–12 μm .

On mosses and schistose soil in montane localities. N.E. Scotland (E. Inverness, Ben Alder; Perth, Ben Lawers).

This species may belong to the primarily lichenicolous genus *Cercidospora*, but requires a more critical study.

Collemopsidium caesium (Nyl.) ined.

Pyrenocollema caesium (Nyl.) R.C. Harris (1987)



Thallus mostly immersed in substrate, but often reaching surface as small dark brown flecks. Photobiont cells yellowish or blue-green. Ascomata 150–400(–500) μm diam., subconical to globose, often flattened, and depressed in the centre when dry; more or less sessile, to half-immersed (often in soft deposits), rarely forming well-defined pits in limestone. Involucrellum absent. Pseudoparaphyses richly branched and anastomosed. Asci elongate-clavate to obpyriform. Ascospores 20–30(–33) \times (7.5–)8.5–12 μm ,

ovoid to ovoid-fusiform, sometimes with additional pseudosepta.

On damp base-rich siliceous rock and on limestone, often tufa-incrusted, in flushes, wet runnels and on dripping rocks; also on limestone rocks and walls. Wales, N. England, Scotland, W. Ireland. Norway, France, Switzerland, North America.

See notes under *C. monense*.

Collemopsidium elegans (R. Sant.) Grube & B.D. Ryan (2002)

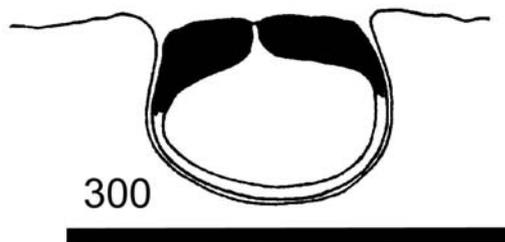
Pyrenocollema elegans R. Sant. (1992)

Thallus superficial, very thin, dark brown, but with irregular black warts 100–200(–300) μm wide, and black ridges up to 150×500 (–700) μm , the ridges radiating and flattened near the thallus margin, elsewhere irregular and usually flat, but sometimes raised and rather sharp, up to 35–50 μm high. Photobiont with yellowish brown cells. Ascomata usually rather sparse, sometimes abundant, prominent, 100–300(–500) μm diam., ostiole depressed. Involucrellum well-developed, spreading. Ascospores (4–)8 per ascus, not constricted at the septum, $11.5\text{--}18$ (–20) \times 3.5–7 μm . Pycnidia immersed in the ridges.

On siliceous rocks in the littoral zone of sea shores. S. England, Wales, N. and W. Scotland, S. and W. Ireland. Norway, N. and S. America.

In the field resembles a brown morph of *Verrucaria striatula*, which differs in the simple ascospores and absence of interascal filaments. *C. halodytes* is very similar, but differs in the absence of warts or ridges on the thallus; some specimens with very few ridges may be difficult to name.

Collemopsidium foveolatum (A.L. Sm.) F. Mohr (2004)



Thallus immersed. Photobiont in scattered groups or absent. Ascomata 100–240 μm diam., usually entirely immersed in pits in the substrate, occasionally emerging; involucrellum lid-like, flat to slightly convex, scarcely spreading, sometimes absent. Ascospores $14\text{--}21 \times 5\text{--}9 \mu\text{m}$. Pycnidia common to absent, black, immersed.

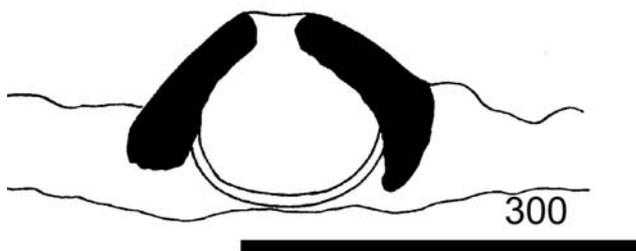
On calcareous rock and shells (of barnacles, limpets and mussels) in the littoral zone of sea shores, common. Coasts of Britain and Ireland.

Norway. Distribution elsewhere uncertain due to taxonomic confusion.

C. sublitorale differs in the usually sessile, generally larger ascomata, but some forms may be impossible to distinguish. *C. ostrearum* differs in the wide-spreading involucrellum mixed with particles of the substratum.

Collemopsidium halodytes (Nyl.) Grube & B.D. Ryan (2002)

Pyrenocollema halodytes (Nyl.) R.C. Harris (1987), *P. orustense* (Erichsen) A. Fletcher (1992)



Thallus superficial, light brown, thin, continuous or scattered, without dark ridges. Photobiont abundant. Ascomata 100–400 μm diam., sessile, flattened, involucrellum spreading laterally. Ascospores $13\text{--}22 \times 5\text{--}9 \mu\text{m}$. Pycnidia

common, resembling the ascomata but smaller and flatter.

On siliceous, less commonly calcareous, rock in the littoral zone of sea shores. Coasts of Britain and Ireland, common. Europe (Norway, Sweden, France, Germany); distribution elsewhere uncertain due to taxonomic confusion.

Distinguished from other maritime species on rock by the superficial thallus and sessile ascomata. *C. elegans* differs in the black ridges on the thallus, but very sparsely ridged forms may be difficult to distinguish. The species has sometimes been delimited broadly to include *C. elegans* (6), *C. foveolatum* (7) and *C. sublitorale* (13), but these species, and *C. ostrearum* (10), are morphologically distinct and are supported by molecular data.

Collemopsidium monense (Wheldon) Coppins & Aptroot (2008)

Pyrenocollema monense (Wheldon) Coppins (1992)

Thallus immersed to superficial, dull grey or green-grey, scurfy or filmy. Photobiont cells yellowish or blue-green. Ascomata 150–200 µm diam., 0.5–0.75-immersed, ± globose. Involucrellum absent. Pseudoparaphyses sparingly branched. Asci 80–115 × 16–19 µm, narrowly obpyriform to subcylindrical. Ascospores 17–30(–35) × 6–8 µm, ovoid to ovoid-fusiform.

On chalk stones in grassy banks and woodland clearings, or mortar of shaded walls, lowland. England, rare in Scotland. Netherlands.

C. caesium is said to differ in the broader asci and more densely branched pseudoparaphyses, and in the shape of the ascoma, but the relationship between the two species needs further study.

Collemopsidium ostrearum (Vain.) F. Mohr (2004)

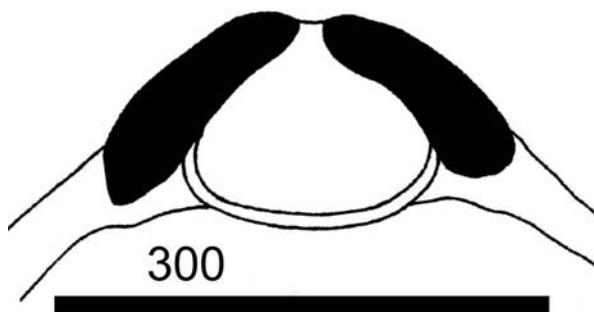
Thallus immersed, occasionally partly delimited by a black line. Ascomata 340–600 µm diam., usually densely clustered, immersed. Involucrellum very wide-spreading, intermixed with particles of the substratum; often more than one many perithecium united under one involucrellum. Ascospores 23–25 × 9–11 µm. Pycnidia similar in appearance to ascomata but smaller, though overlapping in size.

On calcareous rock and shell, in the littoral zone of sea shores, apparently rare. Ireland (Galway). West Africa (São Tomé and Príncipe), New Zealand.

A poorly known species, distinguished from the other maritime species by the clustered ascomata, the large involucrellum mixed with substratum particles, and the larger ascospores. Probably overlooked.

Collemopsidium pelvetiae (G.K. Sutherl.) Kohlm., D. Hawksw. & Volkm.-Kohlm. (2004)

Pyrenocollema pelvetiae (G.K. Sutherl.) D. Hawksw. (1988)



Spain.

Thallus superficial, dark brown. Ascomata 1.2–3.4 mm diam., sometimes 2–3 united in a common stroma; involucrellum present, extending into the associated photobiont colonies. Asci 40–60 × 13–18 µm. Ascospores 11.5–16 × 5–6.5 µm. Pycnidia 40–70 µm diam., conidia 2–2.5 × 1–1.5 µm.

On fronds of the seaweed *Pelvetia canaliculata* on sheltered sea shores, S.W. England, N. Scotland (Orkney Isles). France,

This species is of particular biological interest as forming a three-biont association in which the lichen grows epiphytically on a second photosynthetic partner, *Pelvetia* (Phaeophyceae). Not to be confused with the very common *Mycosphaerella ascophylli* Cotton (1907), which forms a systemic mycelium within *Pelvetia* thalli and has immersed ascomata 55–130(–160) μm diam., and larger ascospores 15–22.5(–25) \times 4.5–5.5(–6.5) μm .

Collemopsidium subarenisedum (G. Salisb.) ined.

Pyrenocollema subarenisedum (G. Salisb.) Coppins (1992)

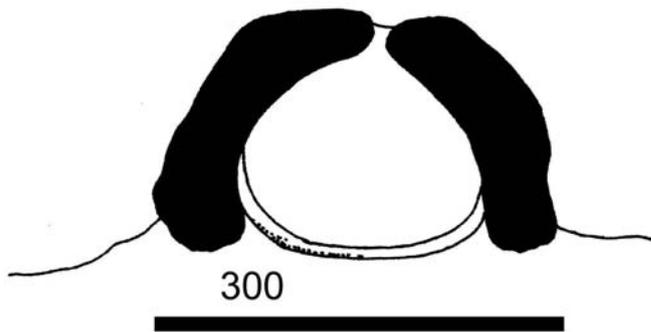
Thallus whitish or ashy grey, immersed. Ascomata 80–200 μm diam., \pm globose, semi-immersed. Asci 70–100 \times 13–14 μm , subcylindrical. Ascospores 15–19(–21) \times 5–7 μm , ovoid to ovoid-fusiform.

On soil in dune slacks and machair. S. and W. England (Devon, Hampshire), N.W. England (Lancashire), W. Scotland (Colonsay). Spain, Netherlands, Germany.

Distinguished from *C. arenisedum* by the smaller ascospores.

Collemopsidium sublitorale (Leight.) Grube & B.D. Ryan (2002)

Pyrenocollema sublitorale (Leight.) R.C. Harris (1987)



Thallus immersed, photobiont in scattered groups or absent. Ascomata 150–550(–1500) μm , usually sessile and globose, with a more or less appressed, hemispherical involucrellum, or semi-immersed with a spreading involucrellum. Ascospores 15–25 \times 5–10 μm . Pycnidia common to absent, immersed or semi-immersed, with a black, flattened involucrellum; usually smaller than Ascomata but size ranges

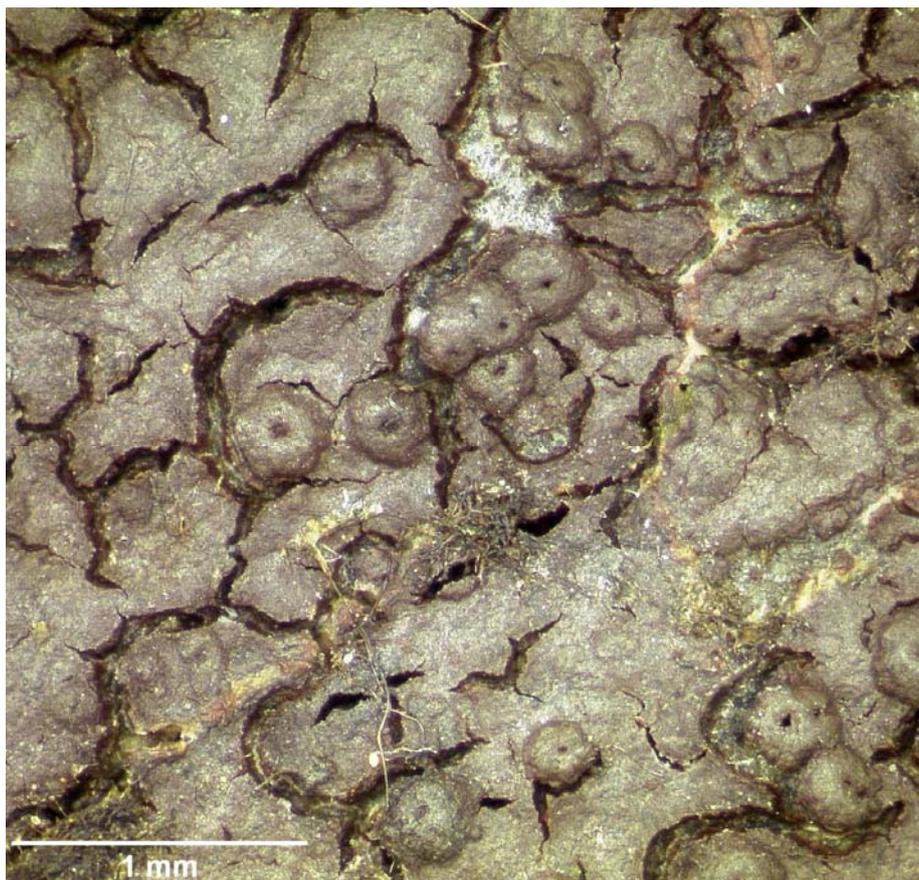
overlapping.

On calcareous rocks and shells (of barnacles and limpets) in the littoral zone of sea shores, common. Throughout Britain and Ireland. Scandinavia, ?New Zealand. Distribution elsewhere uncertain due to taxonomic confusion.

C. halodytes differs in the superficial thallus; *C. foveolatum* differs in the smaller, immersed ascomata. Variable; the largest ascomatal sizes have been reported from soft chalk.

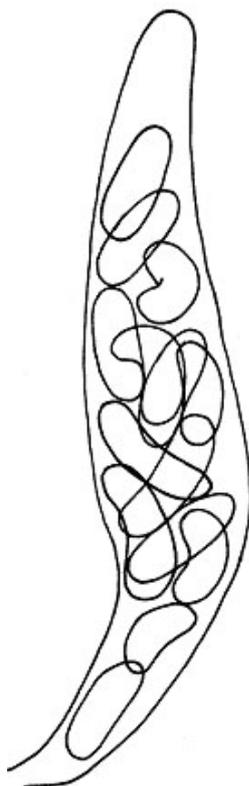
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Cryptothele rhodosticta (20494).

Cryptothele sp.



Thallus crustose, cracked, very dark brown, 100–130 μm thick; surface slightly uneven and roughened. Ascomata inconspicuous, forming low to moderate convex projections to 160 μm diam., opening by a pore at the apex. Centrum 110–180 μm wide. Exciple colourless, 8–15 μm thick at sides and base. Hymenial gel I + red, I + dull red after treatment with K. Hamathecium of branched and anastomosing periphysoids adjacent to upper part of exciple. Also, inconspicuous filaments much shorter than the asci, *c.* 35 μm long, occur mixed with the asci. Asci thin-walled, tapering above, I – , with at least 11–14 ascospores. Ascospores simple, colourless, reniform to allantoid, 7.8–12.5 \times 3.5–4.5 μm . Conidiomata not detected.

On siliceous rock beside an unshaded upland stream; Wales (Radnorshire).

This apparently undescribed species is known from a single collection. The ascospores agree in shape and size with *C. permiscens* (Nyl.) Th. Fr., but that species is said to have 8-spored asci (Henssen 1979). *C. neglecta* Henssen has 16(–24)-spored asci, but the ascospores are 7–8 μm long and the exciple is conspicuously thickened to 40–50 μm .

References:

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DERMATOCARPON Eschw. (1824)

Thallus squamulose to foliose, grey to brown, attached by one or more central or scattered holdfasts; both surfaces corticate, specialized vegetative propagules absent; some species with nodular or rhizine-like structures on lower surface. **Upper cortex** of pseudoparenchymatous cells, often with brown pigment near the surface. **Epinecral layer** thin, comprising cells which are either compressed (thallus surface usually epruinose) or broken and air-filled (often visible as a pale pruina). **Medulla** of filamentous hyphae. **Lower cortex** pseudoparenchymatous, of anticlinal rows of thick-walled cells, the inner cells larger than the outer, with brown pigment at surface. **Photobiont** green algae (*Myrmecia biatorellae* and *Protococcus dermatocarponis* reported). **Ascomata** perithecioid, immersed in the thallus. **Exciple** unpigmented except at apex. **Involucrellum** absent. **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, wall thickened above, I –, K/I –, 8-spored. **Ascospores** simple, colourless, ellipsoid, smooth, without perispore, 8–25 µm long, usually irregularly arranged in the ascus. **Conidiomata** pycnidia, of *Xanthoria*-type (multi-chambered), immersed in the thallus. **Conidia** aseptate, rod-shaped, c. 4–6 × 1 µm. **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.

Classification: Chaetothyriomycetidae, Verrucariales, Verrucariaceae.

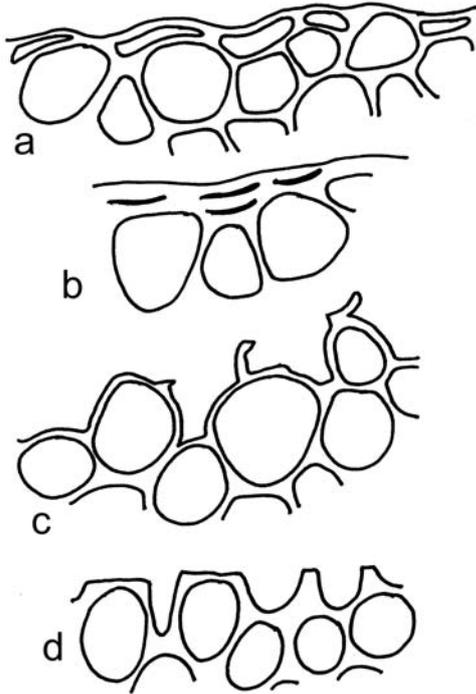
There are rather few taxonomically useful characters to differentiate the species; these include ascospore size, the colour of the lower surface, and the nature of the epinecral layer (view in thin section). The presence of pruina usually indicates an air-filled epinecral layer, but an absence of pruina is not conclusive. Care should be taken not to mistake a pale upper surface for pruina, nor the pale incrustations seen on some herbarium specimens. *Dermatocarpon arnoldianum* and *D. leptophyllum* have been incorrectly reported from the British Isles.

LITERATURE: Orange (1998), Heiðmarsson (1998, 2000)

1	Medulla I + red; thallus strongly lobed	2
	Medulla I –	3
2(1)	Thallus with scattered holdfasts; lobes 5–15 mm wide, epruinose	luridum
	Thallus with secondary holdfasts absent or rare; lobes 0.4–3(–6) mm wide, epruinose or pruinose	polyphyllizum
3(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 lobed thallus)	4
4(3)	Ascospores 6–12 × 4–8 µm, broadly ellipsoid; thallus thin, 130–300 µm thick	leptophyllum
	Ascospores larger, ellipsoid	5
5(4)	Ascospores (8–)9–14(–15) µm long	miniaturum
	Ascospores (12–)14–22(–25) µm	6
6(5)	Epinecral layer of ‘compressed’ type, upper surface of thallus epruinose	7
	Epinecral layer of ‘air-filled’ type, upper surface of thallus pruinose or not	8
7(6)	Thallus underside wrinkled (but variable in a single colony); thallus 100–380 µm thick when moist (measured between wrinkles and perithecia)	rivulorum

Thallus underside smooth, rarely with a few wrinkles or folds; thallus 240–500(–800) μm thick when moist (measured between perithecia) **meiophyllizum**

- 8(6) 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 up 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**



< cortex types in *Dermatocarpon*:
 a, b: compressed type; surface cells crushed
 c, d: air-filled type; surface cells broken.

Dermatocarpon deminuens Vain. (1921)

Thallus up to 22 mm diam., attached by a single central holdfast, more or less unlobed or slightly lobed. 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. Thallus 250–400 μm when mature, measured between the perithecia and veins. Medulla I –. Ascospores (14–)16–22(–25) \times (5.5–)6.5–8.5(–9) μm .

On intermittently inundated rocks on the shore of a small base-rich lake; very rare, known from one site in the British Isles at 615 m altitude (Brown Cove Tarn, English Lake District), but possibly overlooked. North-west Europe (N. England, Iceland, Faeroe Islands, Norway, Sweden, Finland, N.W. Russia).

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 epruinose above; *D. meiophyllizum* is slightly thicker and is never veined below; the lower surface of *D. meiophyllizum* is often darker but the colour overlaps in the two species. *D. miniatum* differs in the shorter ascospores. The description above is based both on British and extra-British material.



Dermatocarpon deminuens (12420)

***Dermatocarpon intestiniforme* (Korb.) Hasse (1912)**

Thallus repeatedly lobed, up 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 ellipsoid to ellipsoid, (8.0–)8.5–15(-16) × (5.0–)5.5–7.5(-8.0) μm.

On damp, siliceous, often slightly calcareous 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 in northern and western Britain and in southern and western Ireland.

Differs from *D. miniatum* only in the strongly divided thallus with numerous scattered holdfasts, but well-developed material of *D. intestiniforme* is striking, and it is more restricted to the north and west than *D. miniatum*. Young specimens of the two species can be difficult to distinguish, but generally intermediates are few in the region. For these reasons the two species are retained as separate species here. *D. luridum* differs in the epruinose upper surface and I + medulla. Illustrations: Jahns (1980) p. 251, Puntillo (1996) Tav. XV.

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

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 up to 30 mm or more diam.; a common 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.

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

Europe (British Isles, France, Czech Republic, Italy, Iceland, Norway, Sweden, N.W. Russia), western North America.

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.

Illustrations: Puntillo (1996) Tav. XV (as *D. lorenzianum*).



Dermatocarpon leptophylloides, moist (21530).

***Dermatocarpon leptophyllum* (Ach.) K.G.W. Lang (1910)**

Characterised by the single holdfast, thin thallus, 130–300 μm , presence of pruina, and small, broadly ellipsoid ascospores 6–12 \times 4–8 μm .

Calcareous rocks. Not reported for Great Britain.

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

Thallus repeatedly lobed, lobes 5–15 mm wide, attached by scattered holdfasts. Upper surface epruinose, grey to pale brown, rarely dark brown in exposed places. Lower surface smooth, pale brown. Medulla I + red (in section, best seen using Melzer's Reagent). Ascospores (10–)12–19(–23) × 5–8 μm.

On intermittently inundated rocks 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. Widespread in northern and western Britain, very rare in central and south-east England, near the coasts in Ireland; locally frequent, but intolerant of water pollution and acidification.

Distinguished by the large, lobed, epruinose thallus with scattered holdfasts. *D. intestiniforme* differs in the usually pruinose upper surface. Very young or difficult specimens are distinguished from all other British species by the I + medulla.

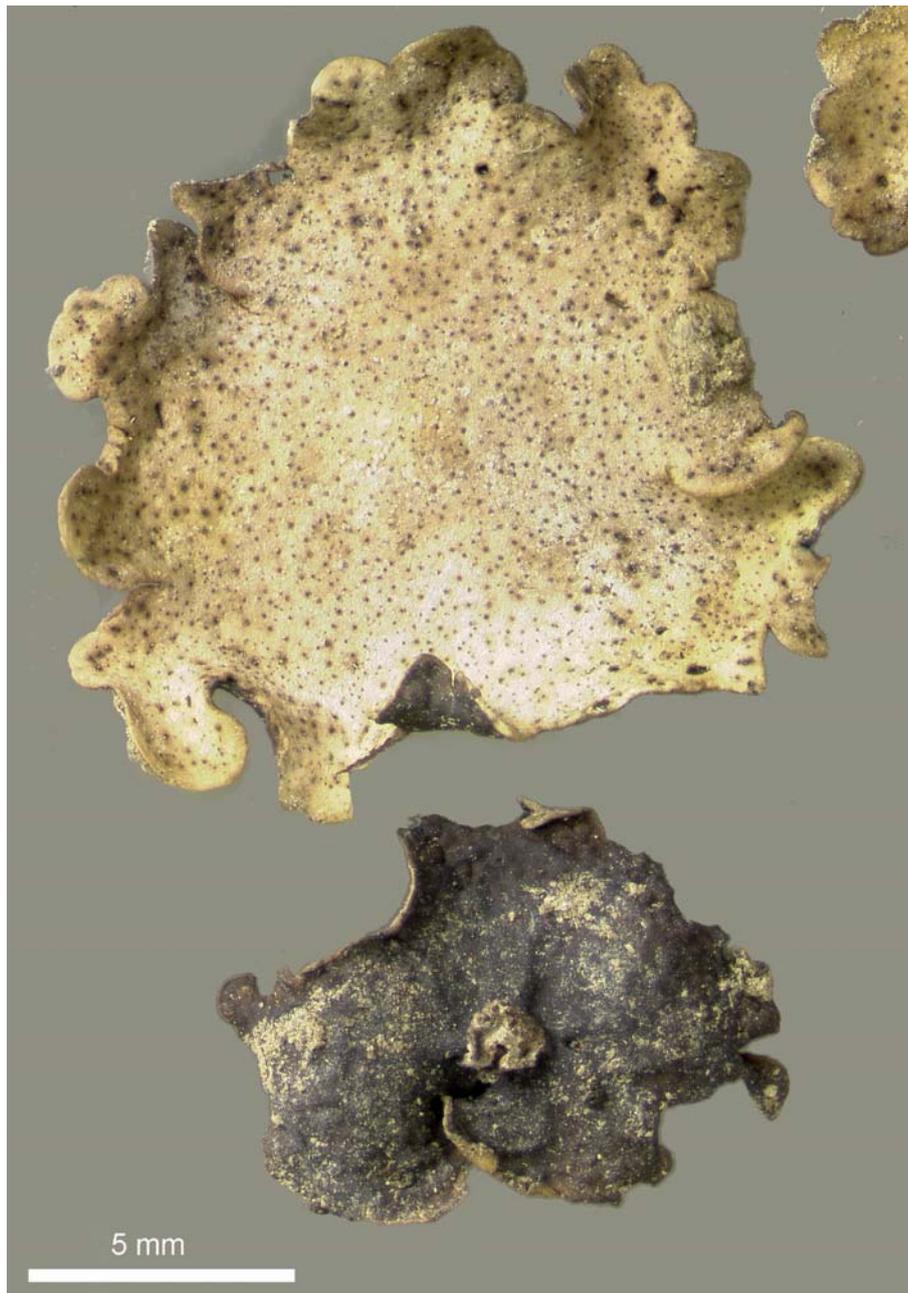
Illustrations: Brodo *et al.* (2001) p. 297, Wirth (1995) p. 371.

Dermatocarpon meiophyllizum Vain. (1921)

Thallus 8–18(–30) mm diam., attached by a central holdfast. 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.

On intermittently inundated siliceous rocks by rivers and lakes, in the lower part of the inundated zone. Widespread but local in north and west Britain and in mainly in the west in Ireland, possibly a little under-recorded. Europe (British Isles, Iceland, Faeroe Islands, Norway, Sweden, Finland, N.W. Russia, France, Austria, Czech Republic), N. America.

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.



Dermatocarpon meiophyllizum (10082).

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

Thallus up 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 $10\text{--}15 \times (4.5\text{--})5\text{--}6.5\text{--}(7) \mu\text{m}$.

On siliceous rocks or limestone, often where damp; inland or on sea cliffs, and on intermittently inundated rocks beside unpolluted streams and lakes. Widespread in the British Isles; in the lowlands mainly in limestone areas; occurrences beside streams are mainly in upland areas. Widespread in Europe; Madeira, N. America, Africa, Asia (including Israel, Himalaya, Korea, Taiwan, China, Japan). Incorrectly reported from Australia.

Variable in colour and in development of pruina; distinguished from other species with a single holdfast by the short ascospores. *D. intestiniforme* differs in the numerous scattered holdfasts.

Illustrations: Brodo *et al.* (2001) p. 298, Jahns (1980) p. 251, Puntillo (1996) Tav. XV., Wirth (1995) p. 372.

Dermatocarpon rivulorum (Arnold) Dalla Torre & Sarnth. (1902)

Thallus 15–35 mm diam., attached by a single holdfast. 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. Thallus 100–380 µm thick (between perithecia and wrinkles). Medulla I —. Ascospores $16.5\text{--}23(-24) \times (6\text{--})6.5\text{--}9$ µm.

On rocks beside montane streams and on flushed rock faces. Very rare in Great Britain, known from three localities in the Scottish Highlands; a record from N. Wales needs to be confirmed. Distribution Arctic-alpine: North Europe (British Isles, Iceland, Norway, Sweden, Finland) and the central European mountains (Austria, Italy); Greenland, N. America (Alaska, Colorado).

Dermatocarpon meiophyllizum has a thicker thallus which is usually smooth below (at most a few folds or wrinkles in some specimens in a colony).

Illustrations: Jahns (1980) p. 251, Thomson (1984) p. 220–221.



Dermatocarpon rivulorum (Finland)

References

- Heiðmarsson, S. (1998) Species delimitation in the long-spored species of *Dermatocarpon* in the Nordic countries. *Ann. Bot. Fennici* **35**: 59–70.
- Heiðmarsson, S. (2000) The genus *Dermatocarpon* (Verrucariales, lichenized Ascomycotina) in the Nordic countries. *Nordic J. Bot.* **20**: 605–639.
- Orange, A. (1998) *Dermatocarpon leptophyllodes* and related species in the British Isles. *Lichenologist* **30**: 1–20.

ENDOCARPON Hedw. (1789)

Thallus squamulose; upper cortex pseudoparenchymatous; medulla paraplectenchymatous or partly plectenchymatous; lower cortex absent or pseudoparenchymatous; rhizines often present. **Photobiont** *Stichococcus*, present in both thallus and hymenium. **Ascomata** perithecia, immersed in the thallus.

Exciple pigmented. **Involucrellum** absent. **Hymenium** I + red, K/I + blue. **Hamathecium** of periphyses and periphysoids; interascal filaments absent. **Asci** (1–)2(–8)-spored, wall thickened above, fissitunicate; apex with a plug staining in Congo Red. **Ascospores** multiseptate to muriform, colourless to brown. **Conidiomata** pycnidia, immersed. **Conidiogenous cells** elongate-ampulliform, enteroblastic. **Conidia** rod-shaped, simple, colourless. **Chemistry**: no lichens products detected by TLC. **Ecology**: on soil, rarely directly attached to rock.

Classification: Chaetothyriomycetidae, Verrucariales, Verrucariaceae.

The species which grow on soil (*E. pallidium* and *E. pusillum*) are very rare in Britain and material is sparse; the descriptions of these species below are based on McCarthy (1991).

LITERATURE: McCarthy (1991).

- | | | |
|---|--|-------------------|
| 1 | On periodically inundated rocks beside streams and lakes | adscendens |
| | On soil in non-inundated habitats | 2 |
| 2 | Lower cortex absent; underside of squamules white to pale brown; squamules 0.5–1.5(–2) mm wide, without rhizines | pallidum |
| | Lower cortex present, brown; underside of squamules dark brown to black; squamules 0.5–3(–4) mm wide | pusillum |

Endocarpon adscendens (Anzi) Müll. Arg. (1881)

Squamules divided into lobes 400–800 µm wide, margins appressed, or free and somewhat raised; upper surface grey-green to pale brown, lower surface pale brownish to pale brown; rhizines not observed. Epinecral layer sometimes present, *c.* 3 µm thick. Exciple brown. Asci 2-spored. Ascospores (29–)31.5–40(–51) × (10.5–)12.5–16(–17.5) µm [36/3].

On calcareous siliceous rocks or limestone beside shaded or unshaded streams and lakes, directly on rock or on mosses (*Thamnobryum*); rare. S. Wales (Glamorgan; Breconshire: River Usk), W. England (Herefordshire: Downton Gorge), N. England, W. Ireland (N. Kerry, Connemara). Europe, North America.



Endocarpon adscendens, fresh and moist (21281).



Endocarpon adscendens, dry (21281).

Endocarpon pallidum Ach. (1810)

Squamules white to pale brown below, 0.5–1.5(–2) mm wide, 120–180(–200) μm thick. Medullary hyphae loosely arranged. Lower cortex absent, lower surface formed by tightly packed and horizontally orientated medullary hyphae. Rhizines absent. Perithecia 160–220 μm diam.. Excipulum medium brown to brown-black. Asci 2-spored. Ascospores muriform, colourless to pale brown, (25–)34.5(–49.5) \times (14.5–)16(–19) μm . Pycnidia numerous, 100–200 μm diam. Conidia filiform, 3–5 \times 0.7 μm .

British distribution? Europe, N. Africa, C. America, Australia.

Endocarpon pusillum Hedw. (1789)

Squamules brown above, dark brown to black below, 0.5–3(–4) mm wide, 150–250(–300) μm thick. Medulla paraplectenchymatous. Lower cortex paraplectenchymatous, (20–)30(–50) μm thick, dark brown. Rhizines present, dark brown to black. Perithecia 150–250(–300) μm diam. Excipulum brown-black. Asci 2-spored. Ascospores pale to dark brown, (29.5–)44(–58) \times (14–)19(–28) μm .

On soil over chalk and limestone and over old walls; very rare. S. England (S. Devon, Norfolk, Sussex), S. Wales (Glamorgan). Europe, Macaronesia, N. America, Asia, Australia.

Literature

McCarthy, P.M. (1991) The lichen genus *Endocarpon* Hedwig in Australia. *Lichenologist* **23**: 27–52.

EOPYRENULA R.C. Harris (1973)

Thallus immersed, inconspicuous or whitish, effuse. **Photobiont** *Trentepohlia*, or absent. **Ascomata** perithecia, ± globose or hemispherical; with a dark brown involucrellum, which either clasps the sides of the centrum or spreads outwardly. **True exciple** pale brown, colourless or almost inapparent below; dark tissue K-. **Hamathecium** of numerous simple or sparingly branched or anastomosed paraphysoids; short periphyses sometimes evident near the ostiole; gel matrix I + yellowish or + pale bluish (especially around the asci). **Asci** subcylindrical, without apical ring-structure and usually without a distinct ocular chamber, the wall K/I- or + blue (especially below), 8-spored but often up to 6 spores aborting. **Ascospores** (1-)3- or more septate, brown, the end cells often paler, without conspicuous perispore or ornamentation. **Conidiomata** pycnidia, black. **Conidiogenous cells** ± cylindrical or narrowly lageniform, enteroblastic. **Conidia** of two types: macroconidia ellipsoid, oblong to cylindrical, brown, 1- or more septate; microconidia bacilliform to filiform, colourless, simple. **Chemistry**: lichen products not detected by t.l.c. **Ecology**: on bark in woodland.

Classification: Dothideomycetidae, Dacampiaceae.

A small genus with 4 European species. Distinguished from *Pyrenula* by ascospores without lenticular lumina, straight microconidia, and brown, septate macroconidia.

LITERATURE: Aptroot (1991), Coppins *et al.* (1992).

- 1 Involucrellum clasping sides of centrum; spores 3- or more septate; macroconidia with 1 pale septum or (5-)7 dark septa 2
 Involucrellum outwardly spreading; spores 3-septate; macroconidia with 3 pale septa and rounded locules 3
- 2(1) Ascospores mostly 18-26 x 6.5-10 µm and 3- to 5-septate; macroconidia with 1 pale septum; microconidia 6-10 µm long **leucoplaca**
 Ascospores mostly 21-34 x 9-10 µm and 5- to 7-septate; macroconidia with (5-)7 dark septa; microconidia 10-16.5 µm long **septemseptata**
- 3(1) Ascospores 10.5-16 µm long, macroconidia 9.5-13 µm long **avellanae**
 Ascospores (12-)14-19(-22) µm long, macroconidia (13-)14-19(-21) µm long **grandicula**

Eopyrenula avellanae Coppins (1992)

Thallus inconspicuous, scarcely discolouring the bark. Photobiont filaments sometimes present. True exciple indistinct. Perithecia 0.2-0.28 x 0.16-0.22 mm, broadly ellipsoid, with distinct ostiolar depression, ± hemispherical in section; involucrellum outwardly spreading. Ascospores 9.5-16 x (5-)6-7 µm, ellipsoid, (1-)3-septate; septa pale or mid septum becoming dark. Macroconidia 9.5-13 x (4-)4.5-6 µm, 3-septate, with rounded locules and pale septa; microconidia 2.8-4 x 0.7-1 µm, bacilliform.

On smooth bark of *Corylus* in old woodlands. W. Britain, N. Ireland. ?Endemic.

Easily mistaken in the field for *Arthopyrenia* species or *Pyrenula coryli*; the latter has ascospores with markedly lens-shaped lumina and curved microconidia (macroconidia not known).

Eopyrenula grandicula Coppins (1992)

Thallus usually causing a whitening or silvering of the bark. Perithecia similar to *E. avellanae*, but usually absent. Ascospores 3-septate, (12-)14-19(-22) x 6-7.5 µm; macroconidia 3-septate, brown, (13-)14-19(-21) x 6-7.5 µm.

Usually on smooth bark, especially *Corylus*, but also on plateaus of fissured bark of *Fraxinus*, *Platanus* and *Quercus*; usually in old woodland, often common in high rainfall areas. S.W. England, Wales, W. Scotland and W. Ireland. W. Norway, Belgium.

Close to *E. avellanae*, but with larger ascospores and macroconidia. Perithecia usually absent, but easily identified by the 3-septate brown macroconidia.

Eopyrenula leucoplaca (Wallr.) R.C. Harris (1973)

Thallus whitish. Photobiont present. Perithecia 0.2–0.35 mm diam., ± globose; involucrellum clasping centrum. Ascospores (13–)18–26 x 6.5–10(–12) µm, ellipsoid to clavate-fusiform, (1–)3- to 5(–7)-septate; septa dark; middle 2 cells darkest and the outer cells progressively paler. Macroconidia 6.5–9.5 x 3–4 µm, ellipsoid, ovoid or pyriform, (0–)1-septate, the septum pale; microconidia 6–10 x 0.5–0.7 µm, filiform.

On fissured bark of *Fraxinus* in old woodland. N. Scotland (Inverness); the only British record but perhaps overlooked. Europe (frequent in Scandinavia, rare and declining in C. and S. Europe).

Could be mistaken in the field for a morph of an *Anisomeridium*.

E. septemseptata Coppins (1992)

Similar in appearance and structure of perithecia to *E. leucoplaca*. Ascospores 5- to 7(–8)-septate, 21–34(–38) × 9–10 µm. Macroconidia (5–)7-septate, 18–26 × 4–5 µm, ± cylindrical, distal end ± obtuse, proximal end truncate with a distinct but unthickened scar; brown, but end cells often pale; microconidia (10–)13–16.5 µm long.

On *Corylus* in old woodlands, very rare. S.W. Scotland (Westernness, Argyll). S.W. Norway.

Literature:

Aptroot, A. (1991) A Monograph of the Pyrenulaceae (excluding *Anthracothecium* and *Pyrenula*) and the Requiellaceae, with Notes on the Pleomassariaceae, the Trypetheliaceae and *Mycomicrothelia* (Lichenized and Non-lichenized Ascomycetes). *Bibliotheca Lichenologica* **44**: 1-178.

Coppins, B.J., James, P.W. & Hawksworth, D.L. (1992) New species and combinations in *The Lichen Flora of Great Britain and Ireland*. *Lichenologist* **24**: 351-369.

FRIGIDOPYRENIA Grube (2005)

As the genus is currently monotypic, the description below constitutes the generic description.

Literature: Grube (2005)

Frigidopyrenia bryospila (Nyl.) Grube (2005)

Collemopsidium bryospilum (Nyl.) Coppins (2004)

Thallus squamulose when well-developed; squamules up to 0.5 mm diam., globose to flattened, dark olive-green to dark brown; outer parts pseudoparenchymatous; underside of squamules connected to each other and to bases of ascomata by brown hyphae *c.* 5-7 μm wide, with thickened walls *c.* 1.5-2 μm . Photobiont a chroococcoid cyanobacterium, the cells 4-5(-8) \times 3-4 μm , with thin walls. Ascomata perithecioid, globose to broadly pyriform, 400-450 μm diam., seated amongst the thallus squamules. Involucrellum absent. Exciple dark brown throughout, 55-65 μm thick in upper part, 25-35 μm thick near base; cells in basal parts tangentially flattened, more rounded above; pigment in intercellular spaces.

Hamathecium of strongly branched and anastomosing filaments (paraphysoids), cells 6-10 \times *c.* 1 μm , not constricted at the septa. Asci unitunicate, cylindrical, 130-140 \times 18-22 μm , 8-spored; wall becoming gradually thicker above, ocular chamber present. Ascospores 1-septate, (25-)28-44 \times 8-12 μm , colourless, becoming brownish and faintly warted when old.

On mosses and schistose soil in montane localities. N.E. Scotland (Easternness: Ben Alder; Mid Perthshire: Ben Lawers). Norway, Sweden, Slovakia, N. America (Alaska).

Collemopsidium species differ in the strictly crustose thallus.

Literature:

Grube, M. 2005: *Frigidopyrenia*—a new genus for a particular subarctic lichen, with notes on similar taxa. *Phyton (Austria)* **45(2)**: 305-318.

HENRICA B. de Lesd. (1921)

Thallus crustose, superficial, smooth to strongly verrucose or areolate. **Photobiont** Chlorophyceae; hymenial algae absent. **Ascomata** perithecia, partly immersed to sessile. **Involucrellum** 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** 8 per ascus, 30–71 × 17–33 µm, ellipsoid, muriform, medium to dark brown. **Conidiomata** unknown. **Chemistry**: lichen products absent. **Ecology**: on calcareous and siliceous rocks. **Distribution**: 2 species, Europe, N. America, Australasia.

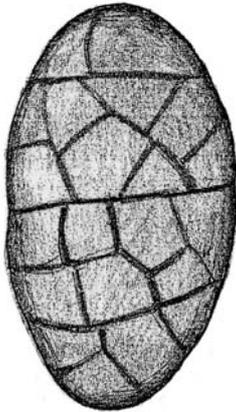
Formerly included in the genus *Polyblastia*; see the key under that genus.

LITERATURE: Gueidan et al. (2007)

- 1 Ascospores (20.5–)28.5–36(–38.5) µm long *melaspora*
Ascospores (51–)53.5–63.5(–70) µm long *theleodes*

Henrica melaspora (Taylor) S. Savić & Tibell (2008)

Polyblastia melaspora (Taylor) Zahlbr. (1921)



Thallus superficial, whitish, uneven to verrucose, thin to well-developed, up 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).

On damp calcareous sandstone, mica-schist, and limestone, on damp cliffs, below moist overhangs, and near streams, mainly upland; occasional. Wales, N. England, Scotland, W. Ireland. Europe, N. America, New Zealand.



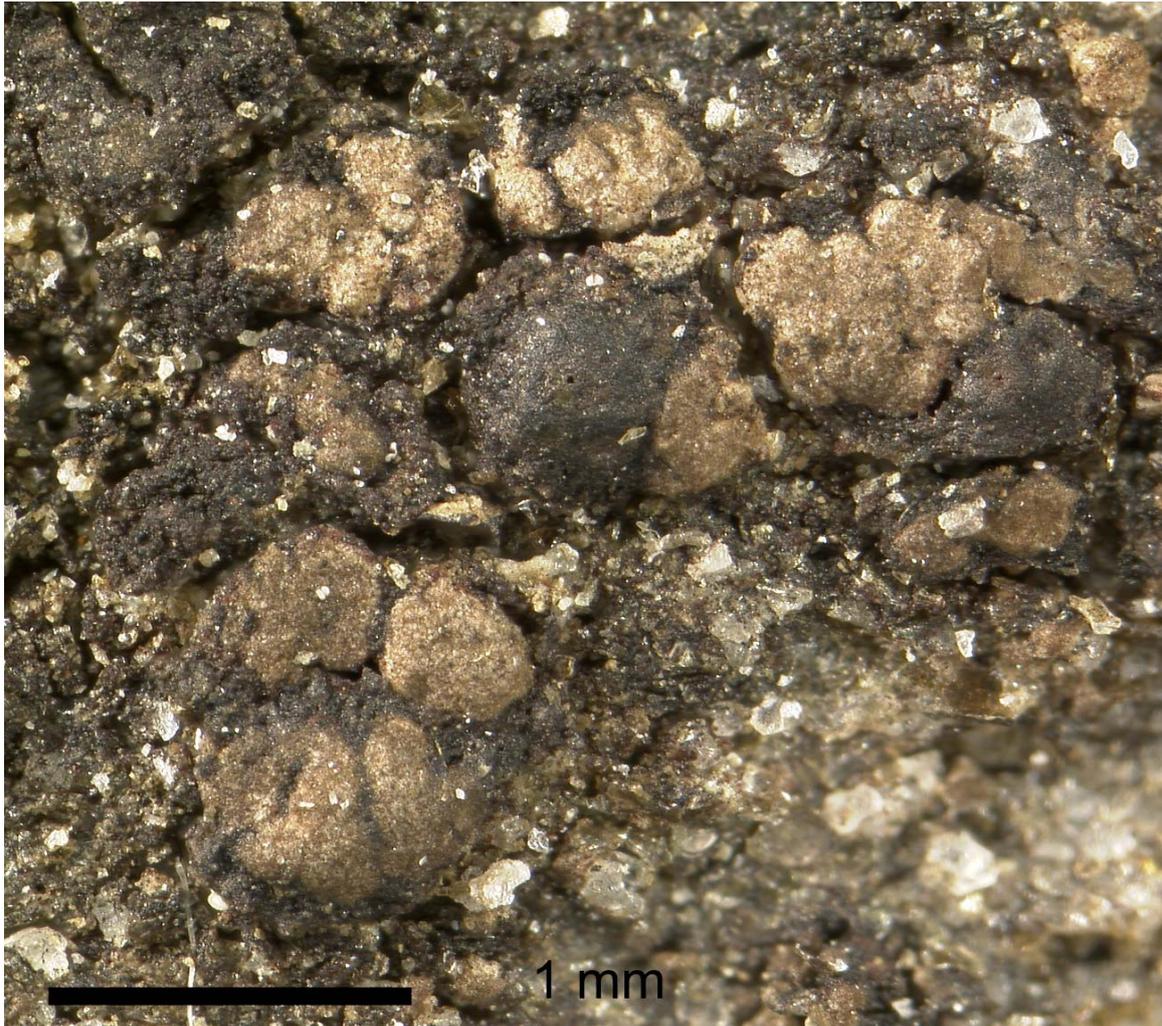
Henrica melaspora (8291).

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

Thallus superficial, areolate, areoles strongly convex, sometimes almost stalked, discrete to contiguous and forming lobed aggregations, 0.4–1.0 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 more or less 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).

On damp calcareous rock, apparently rare. C. Scotland (Craig Leek). Scandinavia, Spain, C. Europe, Greenland, N. America.

Most British and Irish records under the name *Polyblastia theleodes* refer to *Sporodictyon schaererianum*, which differs in the rough perithecia with an irregular thalline covering, and the presence of cephalodia.



Henrica theleodes, Scotland (15932).

Literature:

S. Savić and L. Tibell (2008) The lichen genus *Henrica* (Verrucariaceae, Eurotiomycetes) in northern Europe. *Nordic Journal of Botany* **26**: 237-247.

HETEROPLACIDIUM Breuss (1996)

Thallus crustose-areolate to squamulose, entirely paraplectenchymatous or subparaplectenchymatous. Perithecia immersed in the thallus. Involucrellum absent. Ascospores simple, 8 per ascus, rounded to ellipsoid. Pycnidia of Dermatocarpon-type.

Classification: Chaetothyriomycetidae, Verrucariales, Verrucariaceae.

Literature:

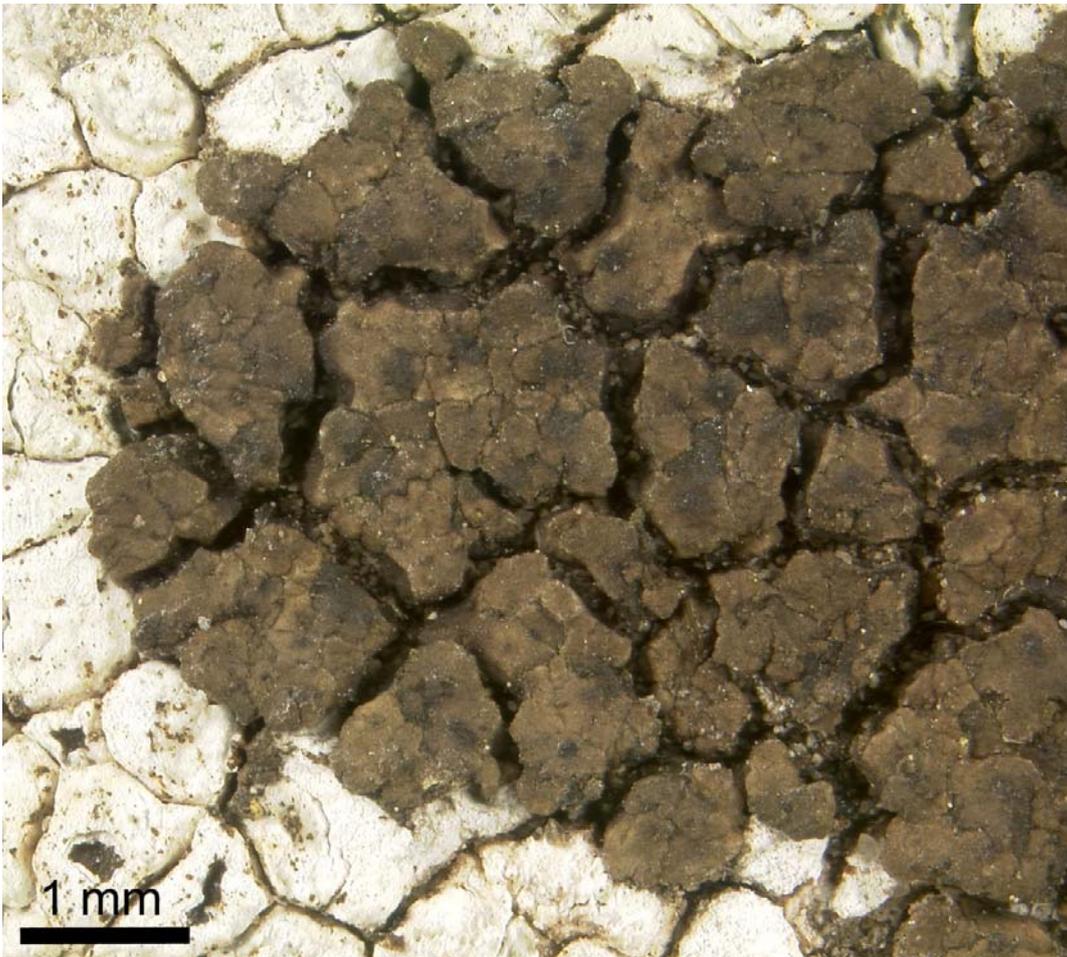
Heteroplacidium fusculum (Nyl.) Gueidan & Cl. Roux (2007)

Verrucaria fuscula Nyl.

Thallus brown, areolate or squamulose-areolate, parasitic on *Aspicilia calcarea*. Ascospores (7-)10-13(-15) × 6-10 μm. Conidia rod-shaped, 3-5 μm long.

On *Aspicilia calcarea* on limestone, North Somerset (David Hill).

This species has been incorrectly reported from Great Britain in the past, but is now confirmed from a recent collection.



Heteroplacidium fusculum (coll. David Hill).

HYDROPUNCTARIA Keller, Gueidan & Thüs (2009)

Thallus crustose, superficial, green (in shade), brown or black; subgelatinous; vegetative propagules unknown. **Cortex** poorly defined; pigment brown or dark green (only absent in shaded specimens). Thallus with darkly-pigmented inclusions which sometimes reach to surface. **Photobiont** Chlorophyceae. **Ascomata** perithecia, black (except rare albino morphs). **Involucrellum** 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 –, fissitunicate, wall thickened above. **Ascospores** 8 per ascus, simple, colourless, ellipsoid or oblong-ellipsoid, smooth, wall thin or only slightly thickened, rather small. **Conidiomata** pycnidia, immersed in the thallus. **Conidia** rod-shaped, aseptate, colourless. **Chemistry**: lichen products absent. **Ecology**: on rock in freshwater or marine habitats.

Classification: Chaetothyriomycetidae, Verrucariales, Verrucariaceae.

A morphologically reasonably distinctive genus segregated from *Verrucaria* by Gueidan *et al.* (2009). Orange (2012) distinguished several species formerly included in *V. maura*, and discussed the typification of the type species, *V. maura*. The recently distinguished species are best confirmed by molecular methods, but subtle characters separate them in the field and laboratory. It is probable that there are additional species remaining to be found in marine habitats.

Literature:

- Gueidan, C., Savić, S., Thüs, H., Roux, C., Keller, C., Tibell, L., Prieto, M., Heiðmarsson, S., Breuss, O., Orange, A., Fröberg, L., Amtoft, A.W., 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.
- Orange, A. (2012) Semi-cryptic marine species of *Hydropunctaria* (Verrucariaceae, lichenised Ascomycota) from North-west Europe. *Lichenologist* **44**: 299-320.

Provisional key to species in Europe

The following key is intended as a brief synopsis of the species treated here; until the variation within each species is better known, and until more regions have been investigated, positive identification of several of the species requires sequencing.

- 1 Ascospores small, (8.5-)11-12.7-14(-16) μm long; thallus thin, 60-95 μm , 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 Dark tissue in thallus reaching the surface as distinctly elongated bars 40-400 \times 40-60 μm , at least near the thallus margin, where they are perpendicular to the thallus margin; apex of perithecium plane or crenulate; cortical pigment brown; marine *amphibia*
- Dark tissue in thallus in the form of small isodiametric punctae or occasionally minute ridges c. 20-90 \times 20-40 μm , visible or not at the thallus surface 3
- 3 Thallus relatively thick, 60-300 μm , mostly cracked into discrete areoles; cortical pigment brown (rarely in part greenish brown); marine *maura*
- Thallus relatively thin, up 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 4

- 4 Cortical pigment brown; marine *oceanica* (Britain and Ireland) and *adriatica* (Mediterranean and Black Sea)
Cortical pigment dull green to green-brown 5
- 5 Thallus typically uncracked when fresh (fine cracks may appear on storage); freshwater *scabra*
Thallus usually with cracks when fresh; marine *aractina* and *orae*
(More studies are needed to determine whether these can be distinguished by morphology).

Hydropunctaria adriatica (Zahlbr.) Keller & Gueidan (2009)

Dermatocarpon adriaticum Zahlbr. (1904), *Verrucaria adriatica* (Zahlbr.) Zahlbr (1916).

This is a poorly understood species known from the shores of the Mediterranean and the Black Sea (but it is not the only taxon there). Zschacke (1933-34) distinguished it from *H. maura* by the generally thinner thallus, lack of a dark basal layer, and exciple unpigmented below. In Zahlbruckner, *Lichenes rariores exsiccati* no 61 (probably a syntype) and in a recently collected specimen, the cortical pigment is brown.

The basionym of this species is *Dermatocarpon adriaticum* Zahlbr. The name *Verrucaria adriatica* is a new combination, as clearly stated by Zahlbruckner (in Ginzberger 1915).

Hydropunctaria amphibia (Clemente) Orange (2012)

Verrucaria amphibia Clemente (1807)

Prothallus inapparent, or rarely whitish, very local. Thallus superficial, dark greenish brown to blackish brown (black to unaided eye), abundantly cracked, often into discrete areoles, 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 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 oblong-ellipsoid, (13–)15–**16.6**–18(–19.5) × (5–)5.5–**6.2**–7(–7.5) µm, length/width ratio (2.1–)2.4–**2.7**–3.1(–3.5) [29/4].

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

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

The species was described from calcareous marine rocks in Spain, but the location of the type specimen is uncertain.

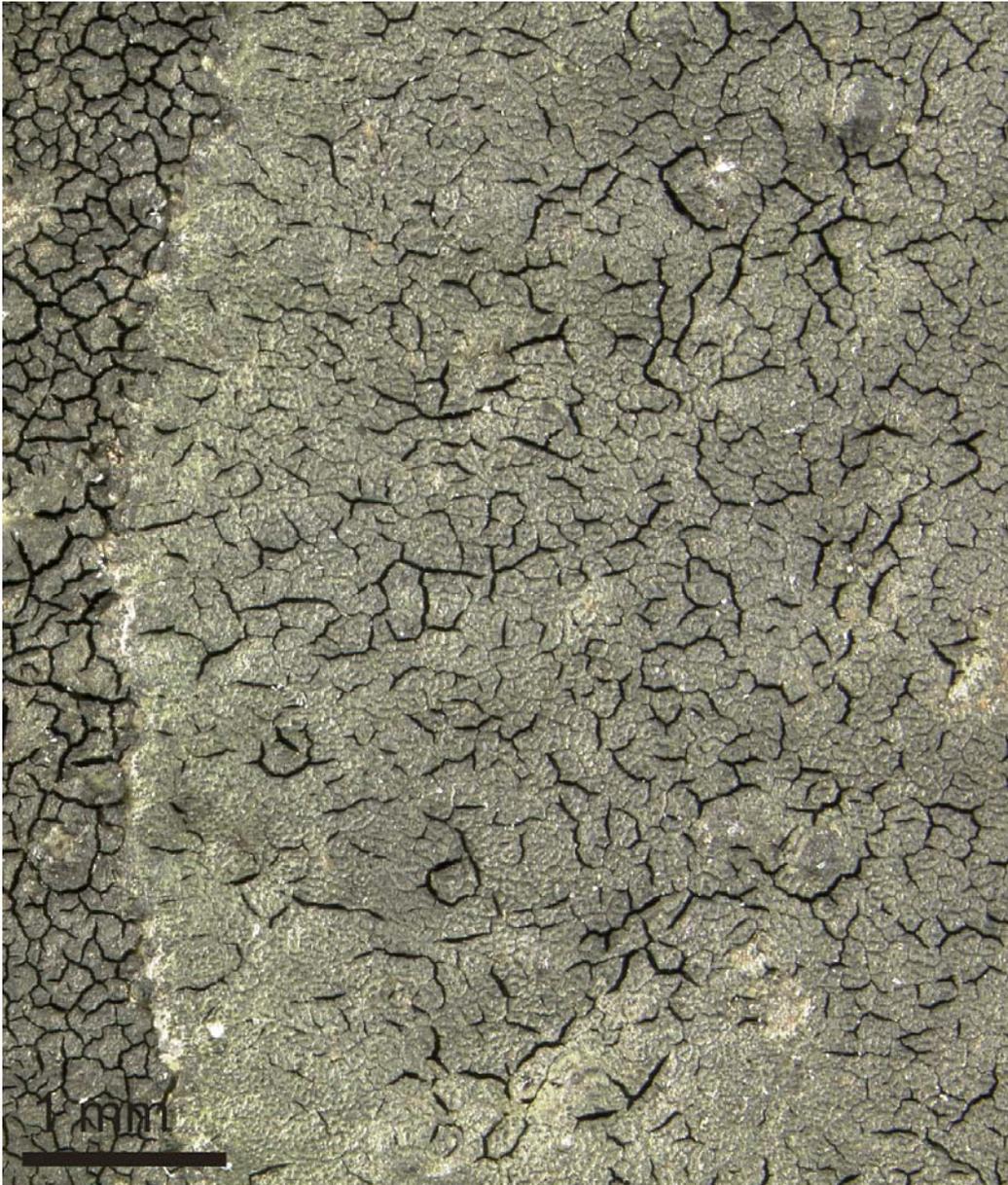
Hydropunctaria aractina (Wahlenb.) Orange (2012)

Verrucaria aractina Wahlenb. in Ach., *Methodus, Suppl.*: 17 (1803); lectotype: [Norway, Finnmark, Alta], Finmarkia Norvegiae ad Påsekop [Bossekop] in scopulis maritimis d. 25 April 1802, G. Wahlenberg (UPS - [L-164364] 381395, Fragment 4, Thallus 1!); epitype: Norway, Alta kommune, Alta, north side of Komsa, Skjåbukta, 69°59.37'N, 23°16.51'E, on rocks on sea shore, 30 June 2010, A. Orange 19118 (NMW - C.2010.001.208); GenBank accession nos JN638257, JN638289).

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 plane, 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 photobiont layer, sometimes reaching 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 diameter, but often too indistinct to measure accurately; surface smooth to roughened. *Ascospores* oblong-ellipsoid, (12-)13.5-**14.6**-16(-17) × (6.5-)7.0-**7.5**-8.0 µm, 1.7-**1.9**-2.2(-2.5) times as long as wide [n = 46/4].

Habitat and distribution. With *Hydropunctaria maura* in the littoral zone of the sea shore. N.W. Scotland. Norway (Troms and Finnmark).

Notes. Differs from contiguous thalli of *Hydropunctaria 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.



Hydropunctaria aractina (right) with *H. maura* (left) (21010).

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

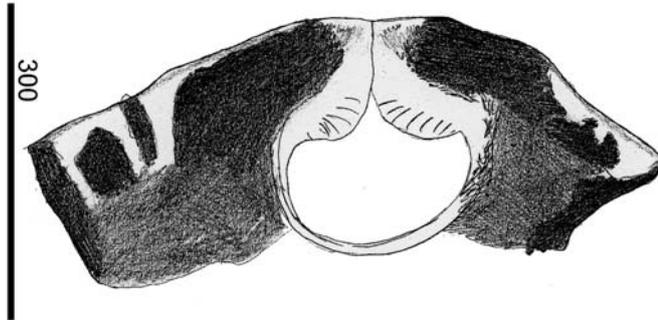
Taxon 58: 208 (2009). — *Verrucaria maura* Wahlenb. in Ach., *Methodus, Suppl.*: 19 (1803); lectotype: [Norway, Finnmark, Alta], Finmarkia Norvegiæ in insula sinus Altensis, 10-11 May 1802, G. Wahlenberg (UPS - [L-048912] 84247, Fragment 5!); epitype: Norway, Finnmark, Alta kommune, Alta, north side of Komsa, Skjåbukta, 69°58.39'N, 23°16.41'E, on rocks on sea shore, 30 June 2010, A. Orange 19131 (NMW - C.2010.001.238; GenBank accession nos JN638266, JN638296).

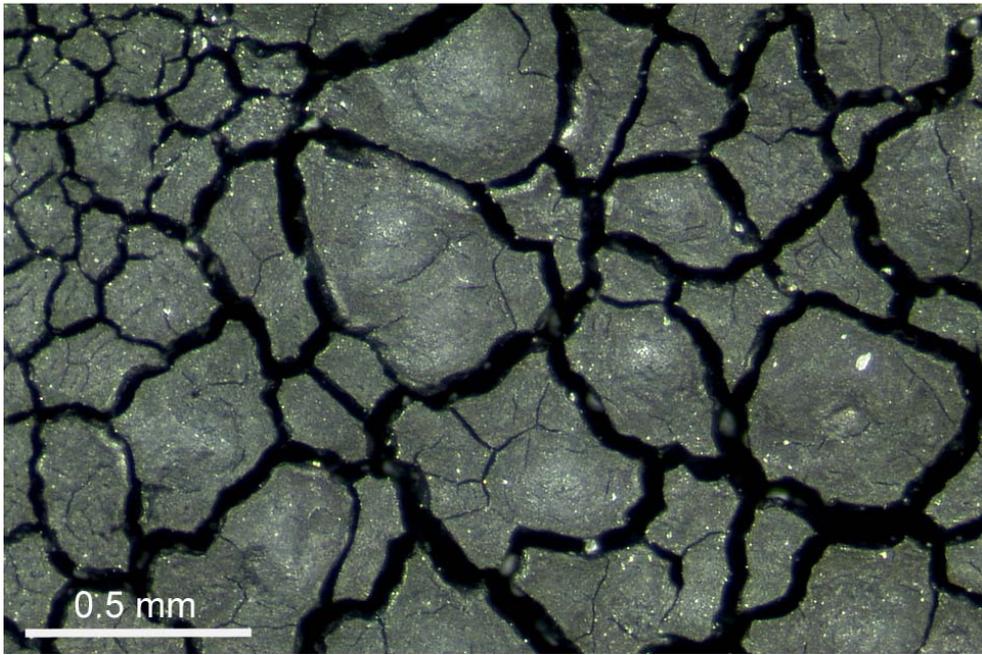
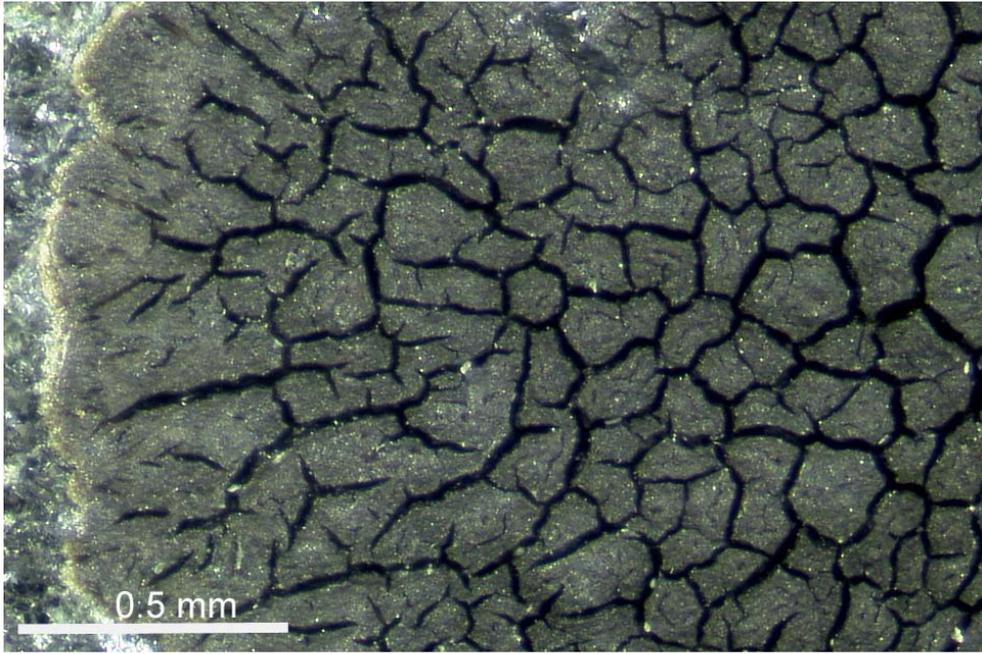
Prothallus narrow, sometimes scarcely visible, whitish to pale brown, not or scarcely fimbriate. *Thallus* moderately thick, 60-300 µm thick, greenish black to brownish black, sometimes brown near margin, or green-brown in shade, but typically very dark and appearing almost black to unaided eye; young margin thin, continuous, soon cracked into separate areoles 100-600 µm diameter (sterile) or 300-600 µm diameter (fertile), areoles plane or slightly concave to slightly convex, matt or rarely slightly glossy, surface smooth or most frequently roughened by slightly raised punctae or short ridges *c.* 20-60(-90) × 20-30 µm, 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 + 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 wide when measurable, conical-hemispherical and sometimes slightly irregular in shape, but not distinctly angular nor with projections. *Exciple* 70-190 μm diameter (few measured), exciple darkly pigmented; involucrellum well-developed, merging with parts of the dark basal layer. *Ascospores* oblong-ellipsoid, (14.5-)15.5-16.6-18(-19) \times (7.0-)7.5-8.0-8.5(-9.0) μm , (1.6-)1.9-2.1-2.3(-2.5) times as long as wide [$n = 37/7$]. *Pycnidia* immersed, with colourless wall and ostiole, 90 \times 50 μm ; conidia rod-shaped, 4.1-5.7(-6.6) \times 1.2-1.6 μm .

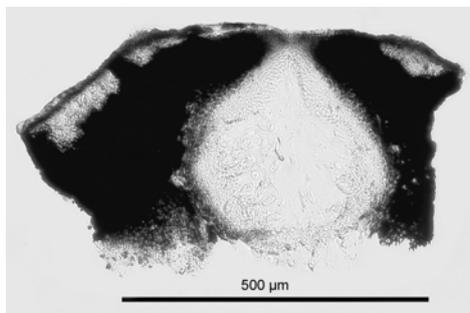
Habitat and distribution. Widespread and often abundant on sea shore rocks; specimens confirmed by ITS sequence from Wales, Ireland, The Faroe Islands, Iceland and Norway. At all sites studied, *H. maura* is much more abundant than *H. aractina*, *H. oceanica* and *H. orae*, and appears to be more tolerant of drought and exposure than those species. This is usually the most abundant species of *Verrucariaceae* on the sea shore in Great Britain, but in northern Norway it is often less abundant than other species, and often confined to sheltered gullies.

Notes. 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*).





Hydropunctaria maura (epitype, Norway). (19131).



Hydropunctaria oceanica Orange (2012)

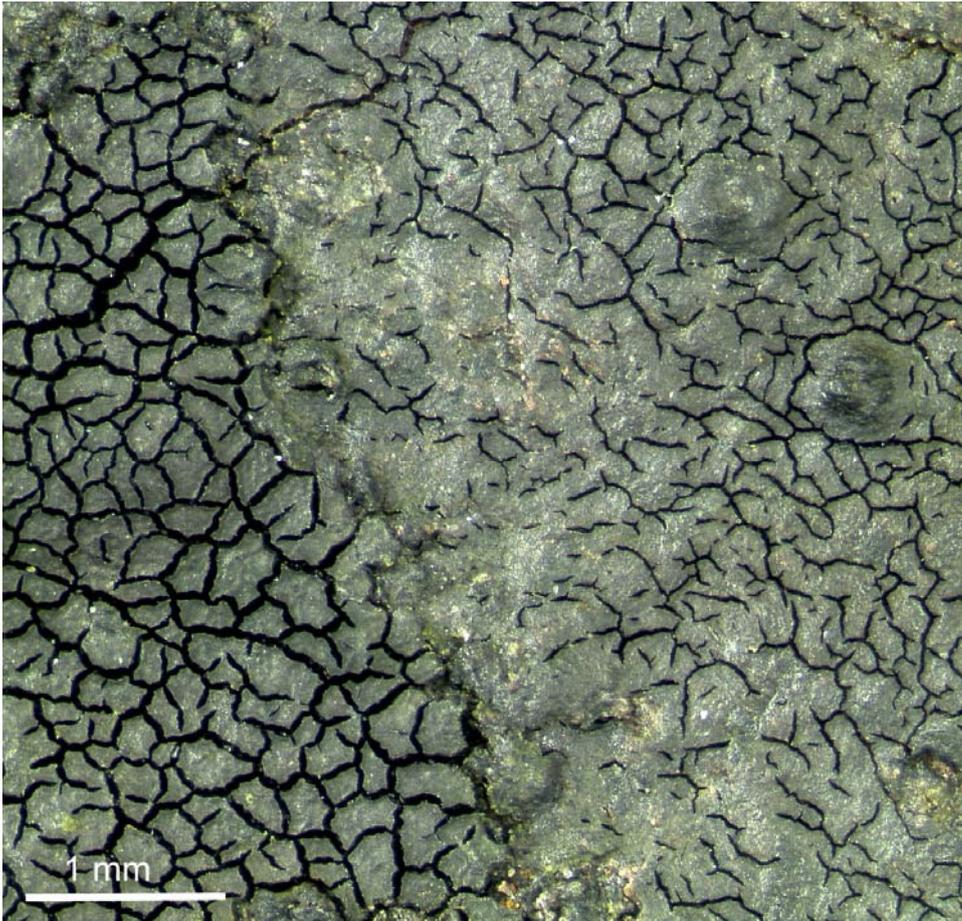
MycoBank no: MB 563381

Typus: Great Britain, Wales, Pembrokeshire, near Haverfordwest, St Brides, national grid reference 12/8005.1108, 51°45'18.56"N, 005°11'17.42"W, on gently sloping ledge on siliceous rocks on sea shore, 26 March 2011, A. Orange 20479 (NMW - C.2011.014.53 - holotypus, BG, BM, MA, UPS - isotypi; GenBank accession nos JN638279, JN638299).

Prothallus whitish, non-fimbriate. *Thallus* episubstratal, thin, c. 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, c. 20-90 × 20-40 µm, but often too indistinct to measure; thallus gradually thinning to margin. Pseudocortex with dilute to moderately dense pigment, pigment brown, K - or almost; cells of photobiont layer c. 2.5-3.7 × 2-3.3 µm. Epinecral layer sometimes present, c. 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 basal layer into photobiont layer, pigment dark red-brown, K + dark grey-brown. *Perithecia* forming conspicuous conical-hemispherical projections 260-500 µm diameter, roughened below like the thallus, above smooth, concolorous with thallus or black, apex rounded or slightly flattened; ostiolar region concolorous, inconspicuous. *Involucrellum* well-developed, merging with dark basal tissue. Exciple 170-210 µm diameter (few measured). Asci 8-spored, c. 45-82 × 18-29 µm. *Ascospores* oblong-ellipsoid, (12.5-)13.5-**15.0**-16.5(-18.0) × (5.5-)7.0-**7.3**-8.0(-8.5) µm, (1.4-)1.8-**2.1**-2.3(-2.7) times as long as wide [n = 66/8].

Habitat and distribution. On gently to steeply sloping rocks on the sea shore, often in places which are occasionally lightly irrigated by rain water; usually growing with *Hydropunctaria 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, Channels Islands, Ireland.

Notes. This species is often found contiguous with *Hydropunctaria maura*, which is then thicker, 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 perithecia 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.



Hydropuntaria oceanica (right) with *H. maura*. Holotype (20479).



Hydropunctaria oceanica (holotype; 20479).

Hydropunctaria orae Orange (2012)

MycoBank no: MB 563382

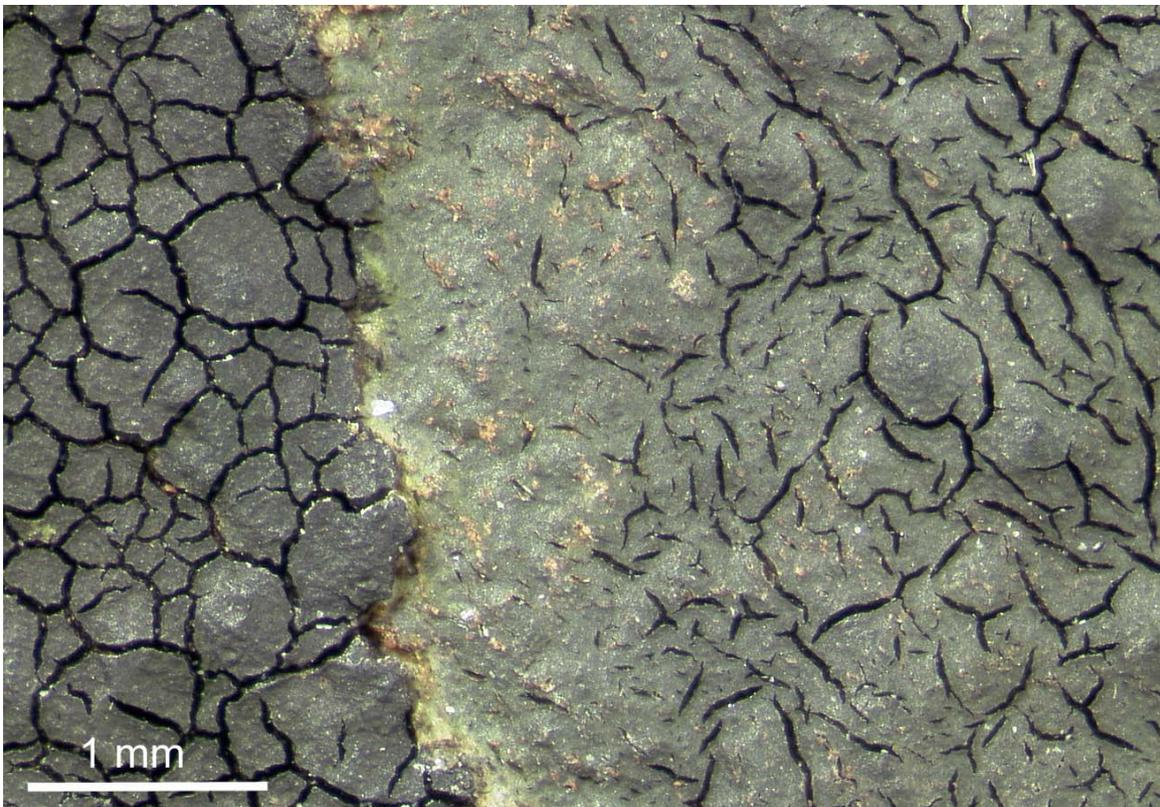
Typus: Great Britain, Wales, Pembrokeshire, near Haverfordwest, St Brides, national grid reference 12/8024.1108, 51°45'18.83"N, 005°11'07.52"W, on steep rocks on NW-facing sea shore, 11 June 2011, A. Orange 20571 (NMW - C.2011.014.48 - holotypus; GenBank accession nos JN638285, JN638294).

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 cracks few to numerous, but rarely forming discrete 'islands' of thallus. Thallus surface minutely roughened by low punctae *c.* 20-40 μm wide, occasionally forming minute ridges up to 80 \times 30 μm , punctae concolorous, or darker than surrounding surface in shaded specimens. Thallus comprising cells in vertical columns, in upper part of thallus 2-4 \times 1.6-3.3 μm , walls sometimes slightly thickened. Pseudocortex present, but a surface layer *c.* 5 μm thick 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, up to 5 μm thick, comprising collapsed and scarcely recognisable cell remains. Photobiont cells 5-10.5 \times 3.7-9 μm . *Perithecia* forming low to moderately projecting, occasionally rather prominent, warts in the thallus 300-840 μm diameter, apex rounded, rarely depressed, ostiole inconspicuous. Asci 8-spored, *c.* 43-52 \times 21-26 μm . *Involucrum* well-developed, merging with dark

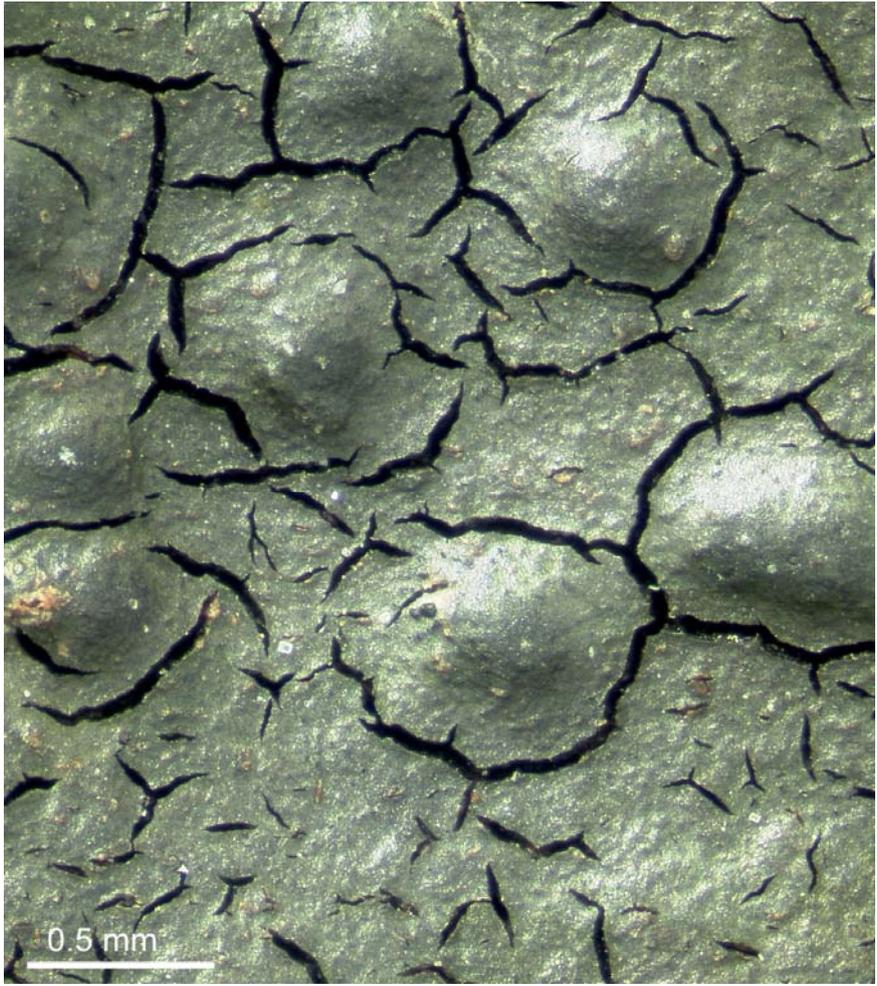
basal tissue. Exciple 260-270 μm diameter (few measured). Ascospores oblong-ellipsoid, simple, colourless, filled with small oil droplets when mature, (13.0-)14.5-16.1-17.5(-19.5) \times (6.0-)7.0-7.4-8.0(-8.5) μm , (1.7-)1.9-2.2-2.5(-2.8) times as long as wide [$n = 75/4$].

Habitat and distribution. 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.

Notes. 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 in some specimens is partly due to a green pigment in the pseudocortex. In mixed collections, thalli of *H. maura* are thicker, more extensively cracked, less green, and with less prominent perithecia. In Orange 20572, from a relatively shaded rock face, *H. maura* is green-brown whereas adjacent *H. orae* is mid green to dark grey-green. In Orange 20575 *H. orae* had green pigment in the pseudocortex whereas adjacent *H. maura* had brown pigment. In one mixed collection (Orange 20577) of *H. orae* with *H. oceanica*, the latter looked browner (dark grey-brown, with brown pigment in pseudocortex) than the *H. orae* (dark grey green, with dull green pigment in the pseudocortex), and the *H. oceanica* also looked slightly thinner and with smaller perithecia.



Hydropunctaria orae (right), with *H. maura*. Holotype (20571).

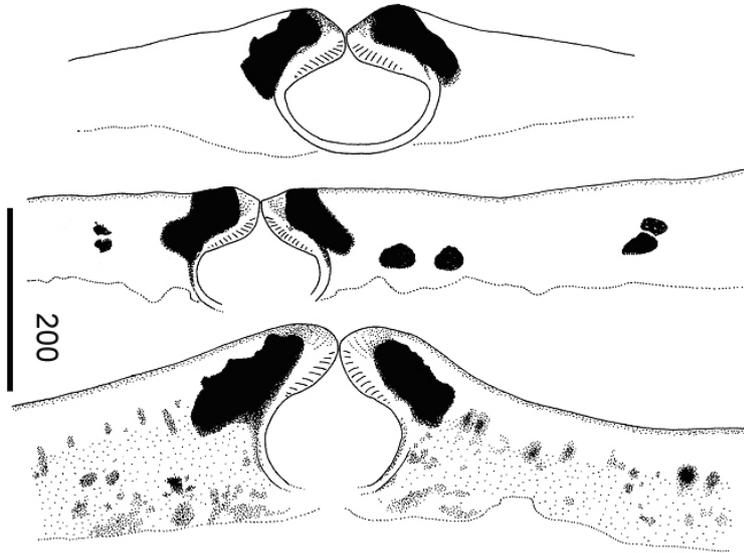


Hydropunctaria orae. Holotype (20571).



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

Verrucaria rheitrophila Zschacke



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 more or less distinct columns of cells; cortex poorly defined, cell walls with brown pigment (dilute or absent in shade). Lower part of

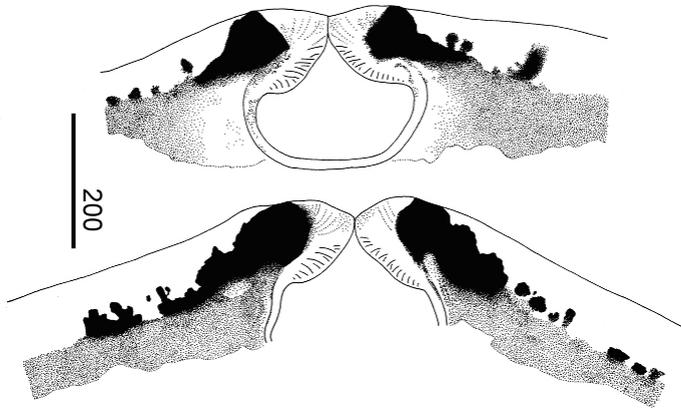
thallus often forming an ill-defined medulla; in this zone living algal cells are often few, and the fungal cells contain oil drops; this zone is colourless to dilute brown, locally with intensely pigmented patches near its upper edge, often appearing as more or less discrete punctae in section. Perithecia 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 up to 220 μm diam., often roughened or surrounded by a few punctae. Exciple 110–210 μm diam., sides and base colourless or partly brown. Involucrellum present, well-developed in the upper half of the exciple, often spreading outwards and downwards and grading into the punctae of the upper layer of the medulla. Ascospores ellipsoid, (8.5–)11–12.7–14(–16) \times (6–)6.5–7.4–8(–9.5) μm , length/width ratio (1.3–)1.5–1.7–1.9(–2.3), without perispore [112/8].

On long-submerged rocks, tolerant of shade; frequent. Widespread in Britain; Ireland. Widespread in Europe; N. America.

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

Verrucaria scabra Vězda (1970).

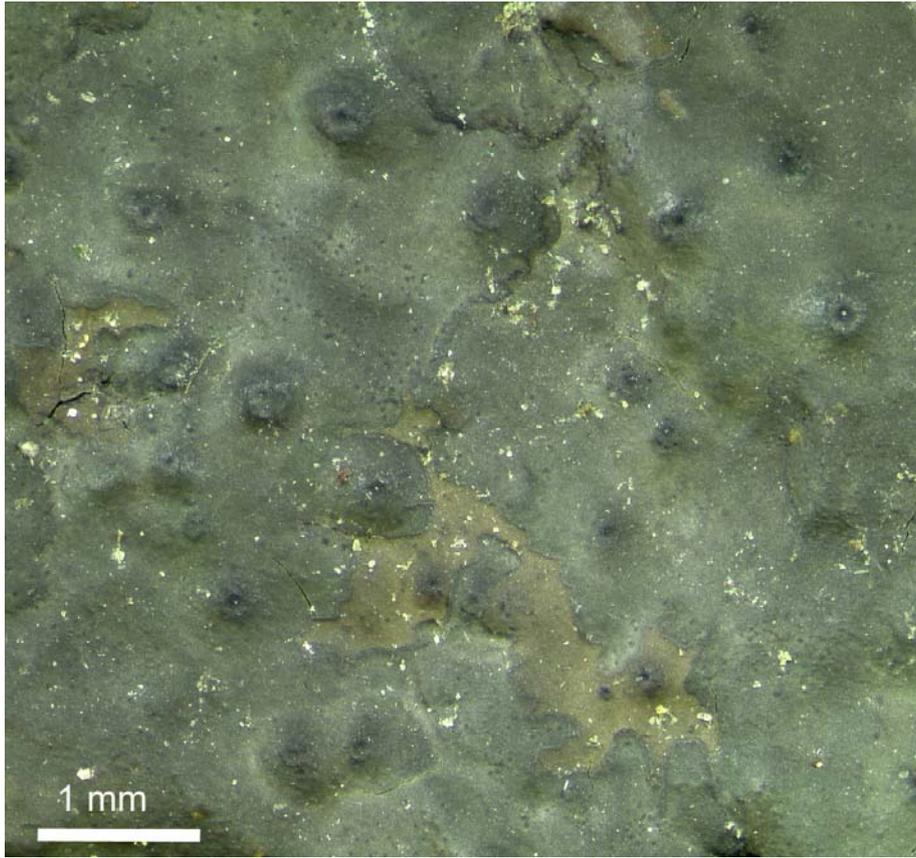


Prothallus whitish, not fimbriate; contiguous conspecific thalli often separated by thin black lines. Thallus dull green to dark grey-green or dark green (sometimes blackish to unaided eye), well-developed, 35–150 μm thick, subgelatinous, uncracked (rarely with fine splits forming in the herbarium), surface smooth to slightly scabrid with concolorous papillae, occasionally with very local black punctae c. 30 μm diam. Thallus in section composed of more or less 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 more or less 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. Exciple 275–290 μm diam., sides and base colourless or partly brown. Involucrellum present, well-developed in the upper half of the exciple, often spreading outwards and downwards and grading into the punctae of the upper layer of the medulla; sometimes (where medulla is thin), involucrellum conical and reaching base of thallus. Ascospores ellipsoid to (mostly) oblong-ellipsoid, (11–)14–15.7–17.5(–21.5) \times (7–)7.5–8.4–9(–10.5) μm , length/width ratio (1.4–)1.7–1.9–2.1(–2.4) [116/6], without perispore. Conidia straight or slightly curved, 3.5–5 \times 1.2 μm .

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. Iceland, Faroe Islands, Germany, Switzerland, Slovakia.

Differs from *V. rheitrophila* in the green (rather than brown) thallus pigment, the slightly larger and more oblong 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 *V. rheitrophila*. Some thalli superficially resemble *V. 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.



Hydropuntaria scabra (green), with small brown thalli of *H. reitrophila*. (16223).

JULELLA Fabre (1979)

Thallus crustose. **Photobiont** (if present) *Trentepohlia*, not or only facultatively lichenized. **Ascomata** perithecia, circular to ellipsoid in outline. **Involucrellum** present, dark, usually laterally spreading, composed of compacted hyphae and bark cells; wall pigment greenish or brown, K+ greenish, N-. **True exciple** thin, pale or colourless, surrounding the centrum. **Hymenium** I-. **Hamathecium** of abundant, richly branched and anastomosing, slender paraphyses. **Asci** (2-)8-spored, cylindrical to clavate, I-, the inner wall thickened towards apex, ± with a shallow, broad ocular chamber. **Ascospores** ellipsoid, submuriform to muriform, colourless, with a distinct gelatinous perispore. **Conidiomata** pycnidia, black. **Conidia** bacilliform to shortly thread-like, simple, colourless. **Chemistry**: no lichen products detected by T.L.C. **Ecology**: on bark. **Distribution**: cosmopolitan in temperate to tropical regions, c. 13 species.

Classification: Ostropomycetidae, Thelenellaceae.

Distinguished from *Mycoglaena* by the halonate ascospores, less cylindrical asci, more richly branched, hamathecial filaments, and the N- ascomatal pigments.

LITERATURE: Aptroot & van den Boom (1995), Barr (1985), Morgan-Jones & Swinscow (1965).

Julella sericea (A. Massal.) Coppins (1992)

Thallus effuse, pale grey or yellowish grey, often inconspicuous. True exciple 200–400 µm diam. Perithecia 0.3–0.6 mm diam., flattened-hemispherical, 1/2– to 1/5-immersed, blackish, but covered by a thin layer of bark cells; involucrellum dark brown. Ascospores 15–25 × 10–15 µm (excluding gelatinous perispore), muriform, with 5–7 transverse septa and 1–2 longitudinal septa. Pycnidia not seen.

On smooth bark of branches of *Corylus* and *Quercus*, very rare. S.W. Ireland (Glengarriff). Italy.

Closely resembles *Arthopyrenia analepta* when examined under a hand lens but that species has 1-septate ascospores. The more widely recorded (C. Europe, U.S.A., Canada) *J. fallaciosa* (Stizenb. ex Arnold) R.C. Harris (1987) is possibly a synonym.

MERISMATIUM Zopf (1989)

Thallus immersed, or absent. **Ascomata** perithecia, black, more or less superficial to half-immersed. **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). **Involucrellum** absent. **Hamathecium** of periphyses and periphysoids; interascal filaments absent. **Hymenial gel** I + red (+ blue at very low concentrations of iodine), K/I + blue (hemiamyloid). **Asci** subcylindrical to clavate, thick-walled when young, (6–)8-spored, ocular chamber absent or small; I –. **Ascospores** broadly ellipsoid to oblong-ellipsoid, submuriform to muriform, brown, perispore sometimes present. **Conidiomata** unknown. **Chemistry:** lichen substances absent. **Ecology:** parasitic on lichens, or possibly sometimes lichenized.

Classification: Chaetothyriomycetidae, Verrucariales, Verrucariaceae.

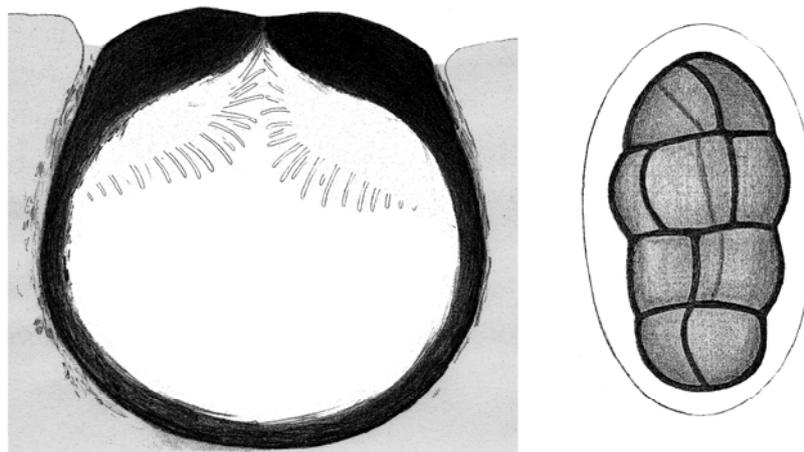
A genus of 9 species; distinguished from *Polyblastia* mainly by the lichenicolous habit. *M. deminuta* has recently been transferred to *Merismatium* from *Polyblastia*, but its biological status needs more study.

LITERATURE: Roux *et al.* (2002), Triebel (1989).

- | | | |
|------|---|--------------------|
| 1 | Ascospores (18–)22.5–27.5(–31) μm long, muriform with 6–15 cells visible in optical section, with a distinct perispore | deminutum |
| | Ascospores without a perispore | 2 |
| 2(1) | Ascospores (11–)13–15.5(–16.5) μm long, submuriform, divided by oblique septa into a total of <i>c.</i> 4 cells | discrepans |
| | Ascospores (14–)15–25(–32) μm long, submuriform to muriform, <i>c.</i> 8–24 cells visible in optical section | nigritellum |

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

Polyblastia deminuta Arnold (1861)



Thallus immersed. Perithecia in pits in limestone, not projecting, or projecting from pit by up to a third, 200–280 μm diam. (few measured). Involucrellum absent. Exciple pigmented throughout,

brown to dark brown, K + darker brown, with faint violet pigment around ostiolar region. Hyphae surrounding 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–**25.1**–27.5(–31) × (10.5–)11.5–**12.7**–14(–16.5) μm, length/width ratio (1.2–)1.8–**2.0**–2.1(–2.4) [65/10]; perispore present, 1.5–2.5 μm thick, but often much thicker in immature spores.

On limestone, frequent. Widespread in Europe.

A recent study suggests 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. Despite this, the placement in *Merismatium* is followed here due to the rather small, brown ascospores and presence of a perispore.

Merismatium discrepans (J. Lahm) Triebel (1989)

Non-lichenized. Perithecia one-third to half-immersed in host, 190–220 μm diam. (few measured). Exciple brown throughout, K + darker brown; ostiolar region dull greenish blue. Ascospores dark brown, submuriform, divided by oblique septa into (3–)4 cells, (11–)13–**14.3**–15.5(–16.5) × (8.5–)9–**9.7**–10(–11.5) μm, length/width ratio (1.1–)1.4–**1.5**–1.6(–1.7) [37/3], perispore absent.

On the thallus of *Protoblastenia calva* and *P. rupestris* on limestone, frequent. Europe, North Africa.

Additional hosts reported from outside the region.

Merismatium nigrillum (Nyl.) Vouaux (1913)

Non-lichenized. Perithecia 200–300 μm diam. Ascospores submuriform to muriform, c. 8–24 cells visible in optical section, (14–)15–25(–32) × (6–)8–12(–15) μm, perispore absent.

Associated with *Catapyrenium lachneum*, very rare. Scotland (Ben Lawers).

Additional hosts reported from outside the region.

Literature:

Roux, C., Gueidan, C. & Navarro-Rosinés, P. (2002) La position systématique de *Polyblastia deminuta*. *Mycotaxon* **84**: 1–20.

Triebel, D. (1989) Lecideicole Ascomyceten. Eine Revision der obligat lichenicolen Ascomyceten auf lecideoiden Flechten. *Bibliotheca Lichenologica* **35**: 1–278.

MYCOMICROTHELIA Keissl. (1936)

Thallus crustose, immersed, rarely superficial, silvery or cream, sometimes \pm lacking, sometimes with a \pm black limiting fringe. **Photobiont** absent in most species, when present *Trentepohlia*. **Ascomata** perithecia, \pm globose to flattened, usually lacking a lower wall, black; involucrellum present, dark brown, often olivaceous in K, extending laterally and sometimes forming a distinct fringe around the perithecia, formed of hyphae and incorporated bark cells (clypeate in structure). **True exciple** \pm globose to flattened, often poorly developed to absent below, of interwoven brown to colourless hyphae. **Hamathecium** of pseudoparaphyses, branched and anastomosed, septate; gel I– or I + violet (not blue). **Asci** 8-spored, elongate-clavate or broadly clavate to subcylindrical, with two functional wall layers, discharge fissitunicate, with an internal ocular chamber, I–. **Ascospores** ellipsoid to slipper-shaped, 1(–3)-septate, the upper cell usually larger, brown, usually distinctly warted, often with a thin gelatinous sheath swelling in K. **Conidiomata** pycnidia, similar to the ascomata in structure. **Conidiogenous cells** enteroblastic, elongate-ampulliform, unbranched, acrogenous. **Conidia** bacilliform, simple, colourless, or ellipsoid, 1-septate and brown, or ellipsoid, simple, with centrally thickened walls and brown. **Chemistry**: lichen products not detected by t.l.c. **Ecology**: on bark, cosmopolitan but mainly in the tropics.

Classification: Dothideomycetidae, Pleosporales, Arthopyreniaceae.

This genus includes 26 species world-wide, most of which are \pm host-specific and not lichenized. It is close to *Arthopyrenia* s. str., from which it differs in that the ascospores turn brown within the ascus before discharge and also have warted walls. Old degenerating ascospores in some *Arthopyrenia* species can become brownish, but then their walls are not usually warted. Reports of *M. melanospora* (Hepp) D. Hawksw. (1982) from the British Isles are based on misidentifications; that species has ascospores (12.5–)13.5–15.5(–17) \times (6–)6.5–7.5(–8) μm , cells \pm equal in size and with rounded apices, and elongate-ellipsoid, brown, 1-septate conidia 13–14.5 \times 5.5–6.5 μm ; it occurs on smooth bark of *Mespilus germanicus* and (?)*Crataegus* in C. Europe.

LITERATURE: Hawksworth (1985).

- | | | |
|------|---|-------------------|
| 1 | Basal fringe around the perithecia inconspicuous, <125 μm wide, \pm circular | 2 |
| | Basal fringe around the perithecia conspicuous, 125–300 μm wide, ellipsoid to broadly fusiform | wallrothii |
| 2(1) | Ascospores (12.5–)13.5–16(–17.5) \times (5.5–)6.5–8(–9) μm ; pycnidia present | atlantica |
| | Ascospores (15.5–)17.5–21(–25) μm long; pycnidia absent | confusa |

Mycomicrothelia atlantica D. Hawksw. & Coppins (1985)

Thallus silvery grey to \pm indistinct, lacking a delimiting fringe, sometimes loosely associated with *Trentepohlia*, probably not lichenized. Perithecia (0.15–)0.2–0.3(–0.35) mm diam., 90–120 μm tall, with a purple-black fringe 30–50 μm wide; hymenial gelatin I+ pale violet when young. Asci 40–55 \times 12–17 μm , clavate. Ascospores (12.5–)13.5–16(–17.5) \times (5.5–)6.5–8(–9) μm , ellipsoid, 1-septate, scarcely constricted at the septum, the cells \pm equal in size; apices rounded. Pycnidia 45–75 μm diam., scattered amongst the perithecia. Conidia 3–4 \times 0.5–0.7 μm , bacilliform, colourless, simple.

On smooth bark of *Corylus*, generally in deep shade; very rare. W. Scotland (W. Inverness, Skye), S.W. Ireland (Kerry, Clare, Donegal). Endemic.

Mycomicrothelia confusa D. Hawksw. (1985)

Thallus creamy or whitish, often with a delimiting purplish black fringe, loosely associated with algae, facultatively lichenized with *Trentepohlia*. Perithecia 0.2–0.3(–0.4) mm diam., basal fringe to 25 μm wide; hymenial gelatin I–. Asci 55–70 \times 12–18 μm , elongate-clavate. Ascospores (15.5–)17.5–

21(–25) × (6–)7–9(–10) μm, sole-shaped, 1-septate, markedly constricted at the septum, the upper cell generally larger and rounded, the lower generally attenuated. Pycnidia unknown.

On smooth bark, particularly of *Corylus*, but also *Betula*, *Fraxinus*, *Ilex*, *Quercus*, and *Sorbus*, in shaded, ± constantly humid situations; local. W. British Isles. Norway, Spain (Cataluña).

Most British records of “*Microthelia micula* Körber (1855)” are misidentifications for this species. *Mycomicrothelia confusa* is distinguished from *M. atlantica* by the larger and ± slipper-shaped ascospores, with an attenuated lower cell, and the absence of pycnidia.

***Mycomicrothelia wallrothii* (Hepp) D. Hawksw. (1980)**

Thallus inconspicuous, not delimited, with algal cells occasionally scattered on the surface, but not lichenized. Perithecia 0.15–0.25(–0.3) mm diam., situated in an ellipsoid, dark grey basal fringe to 0.3 mm wide; hymenium I–. Asci 35–60 × 14–16(–20) μm, elongate-clavate. Ascospores (12–)14–18(–20) × 6–8(–8.5) μm, ellipsoid, 1-septate, not to slightly constricted at the septum; apices rounded. Pycnidia 50–100(–120) μm diam., intermixed with the ascomata or present alone. Conidia (9–)11–12.5(–14) × 4–6.5 μm, ellipsoid to doliiform, brown, thickened centrally internally and sometimes ± distoseptate.

On trunks of *Betula*; very rare. Scotland (Highlands, E. Ross). Probably circumboreal in the Northern Hemisphere. Also known from *Populus* in Norway.

Superficially recalling *Leptorhaphis epidermidis*, which also occurs on *Betula* bark; microscopic examination is necessary to conclusively separate these taxa.

NORMANDINA Nyl. (1855)

Thallus crustose or squamulose; soralia sometimes present. **Photobiont** a green alga. **Ascomata** perithecioid, subglobose or conical-globose, black. **Exciple** of tangentially slightly flattened cells (*textura angularis*), 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, wall thickened above, I –. **Ascospores** ellipsoid-fusiform, usually 7-septate, rarely a proportion submuriform, slightly constricted at the septa, colourless or faintly brownish, smooth. **Conidiomata** unknown. **Chemistry**: lichen products not detected by TLC. **Ecology**: on bryophytes or other lichens in somewhat oceanic regions. **Distribution**: three species in temperate and tropical regions.

Classification: Chaetothyriomycetidae, Verrucariales, Verrucariaceae.

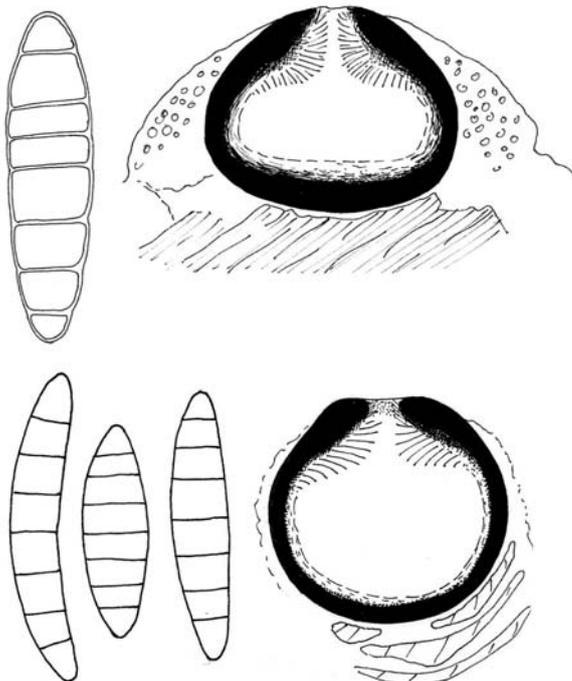
Distinguished by the multiseptate ascospores, absence of interascal filaments, and I + red hymenial gel. *Thelidium* differs in the broader ascospores with fewer septa, and the habit on rock.

LITERATURE: Aptroot (1991), David & Hawksworth (1989), Wirth (1996).

- | | | |
|---|--|-------------------|
| 1 | Thallus crustose, or forming a collar around each ascoma | |
| | | acroglypta |
| | Thallus squamulose; ascomata immersed in thallus | |
| | | pulchella |

Normandina acroglypta (Norman) Aptroot (1996)

Lauderlindsaya acroglypta (Norman) R. Sant. (1993), *L. chlorococca* (Leight.) Diederich & Sérus. (1993), *L. erichsenii* (Keissl.) Diederich & Sérus. (1991), *Normandina erichsenii* (Keissl.) Aptroot (1991).



Thallus grey-green, forming a diffuse crust over the substratum, and often forming a collar surrounding each ascoma; thallus in section comprising goniocyst-like units; soralia scattered, diffuse, concolorous; soredia 20–40 µm diam., surface hyphae of ± isodiametric and often projecting colourless cells. Ascomata 200–430 µm diam., one-quarter to three-quarters immersed in thallus. Exciple with irregularly distributed pigmented areas, thus tending to break up into ‘plates’ in squash preparations. Ascospores (5–)7-septate, 25–35(–45) × 6–9 µm.

On bryophytes over base-rich bark or rock, or directly on bark; occasional. S.W. England, N. England, Wales, Scotland, Ireland. Scandinavia, Portugal, France, Belgium, Germany, Estonia, Italy.

Normandina pulchella (Borrer) Nyl. (1861)

Thallus squamulose, glaucous to pale grey or greenish grey, up to 5 mm diam., composed of one to several broadly rounded shell- or ear-like lobes up to 1.7 mm wide, upper surface concentrically ridged, margins sharply raised, 0.05-0.10 mm wide; squamules scattered or crowded; soralia often present on lobe surface and margins, green or concolorous with lobes; soredial granules 40-80 μm diam.; lower surface whitish, slightly felted, broadly attached by numerous hyphae. Upper cortex pseudoparenchymatous or indistinct, cells similar in shape to those of photobiont layer. Photobiont layer of more or less isodiametric hyphal segments. Medulla of filamentous hyphae. Lower cortex absent. Ascomata immersed in thallus, similar in structure to *N. acroglypta*, but exciple with more evenly distributed pigmented areas, thus not tending to break into 'plates' in squash preparations.

On mossy deciduous trees or rocks in woodland and parkland, growing over bryophytes or other lichens, rarely on bare bark; frequent. S. & W. British Isles. Cosmopolitan.

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. Ascomata are rather rare.



Literature:

Aptroot, A. (1991) A conspectus of *Normandina* (Verrucariaceae, lichenized Ascomycetes). *Willdenowia* **21**: 263-267.

David, J.C. & Hawksworth, D.L. (1989) *Lauderlindsaya*, a new genus in the Verrucariales for *Sphaerulina chlorococca*. *Sydowia* **41**: 108-121.

Wirth, V. (1996) *Flechtenflora. Bestimmung und ökologische Kennzeichnung der Flechten Südwestdeutschlands und angrenzender Gebiete*. 2. Auflage. Stuttgart: Ulmer.

PHYLLISCUM Nyl. (1855)

Thallus squamulose, gelatinous and swelling when wet, or fruticose and subgelatinous; homoiomerous, lacking a central hyphal cord; the mycobiont cells forming a loose network. **Photobiont** a coccoid cyanobacterium, with yellowish brown, red, reddish brown or purplish sheath. **Ascomata** apothecia, disc expanded or punctiform. **Hamathecium** of periphyses, interascal filaments absent. **Ascus** cylindrical, thin-walled, apex rounded or pointed, 8–16(–24)-spored. **Ascospores** simple, colourless. **Conidiomata** pycnidia. **Conidia** rod-shaped to thread-like.

Classification: Lichinomycetes, Lichinales, Lichinaceae.

LITERATURE: Schultz & Büdel (2002).

Phylliscum damangeonii (Moug. & Mont.) Nyl. (1855)

Thallus squamulose, colonies attached at the centre and with lobed margin, black. Ascomata with punctiform disc, immersed in thalline warts. Paraphyses absent, periphysoids present. Asci slender, with pointed tips, (8–)16(–24)-spored. Ascospores 7–10 × 4–5 µm. Conidiomata pycnidia. Conidia thread-like.

On quartzite boulder below waterfall; very rare. N.W. Scotland (W. Sutherland). Temperate Northern Hemisphere.



Phylliscum damangeonii (19150, Norway)

Illustrations: Schultz & Büdel (2002: 46), Wirth (1995: 723).

References:

Schultz, M. & Büdel, B. (2002). Key to the genera of the Lichinaceae. *Lichenologist* **34**: 39-62.
Wirth, V. (1995) *Die Flechten Baden-Württembergs. Teil 2*. Stuttgart: Ulmer.

PHYLLOBLASTIA Vain. (1921)

Thallus crustose to very minutely squamulose; isidia sometimes present. **Photobiont** chlorococcoid. **Ascomata** perithecia, pale orange to black. **Hamathecium** of periphysoids. **Asci** fissitunicate. **Ascospores** mostly 8 per ascus, oblong to cylindrical, transversely septate to muriform, colourless. **Conidiomata** unknown. **Chemistry**: no substances detected by TLC. **Ecology**: foliicolous.

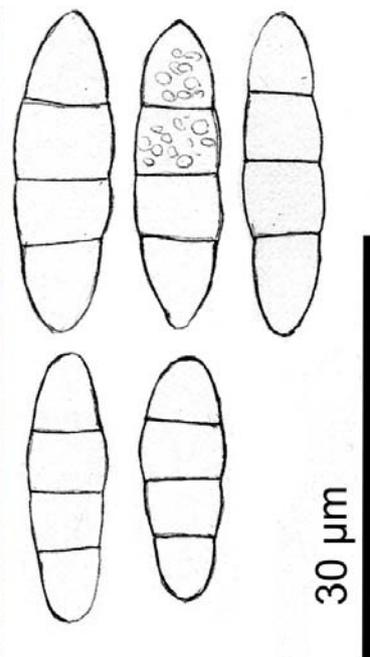
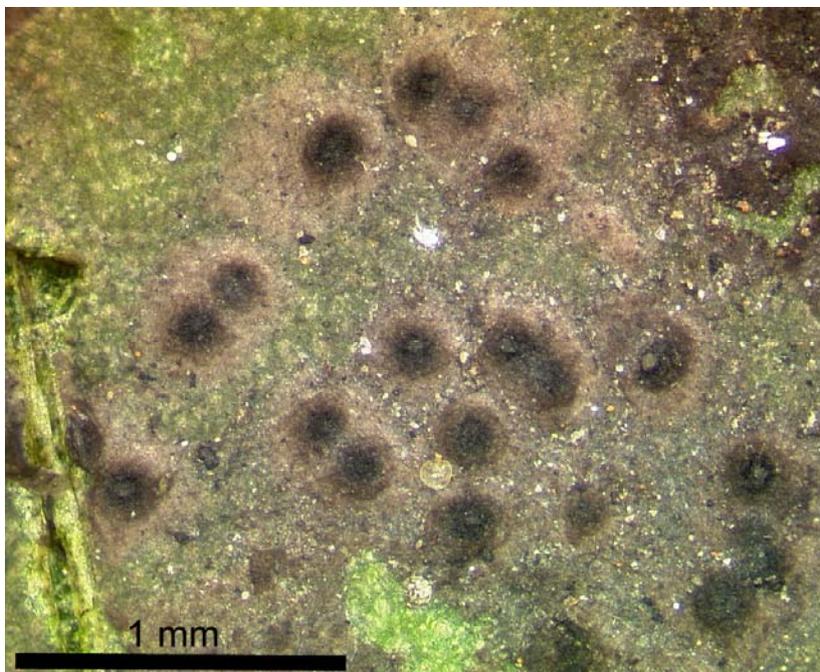
The two species reported from Great Britain appear to the writer to be non-lichenised members of the Chaetothyriaceae, living as sooty moulds on evergreen leaves.

- 1 Ascospores 3-septate **inexpectata**
 Ascospores 6–8-septate or submuriform **fortuita**

Phylloblastia inexpectata Sérus., Coppins & Lücking (2007)

Thallus thin, 15-25 µm thick, brown or pale grey-green, smooth, comprising brown, branched hyphae with cells mostly 7.5–22 × 2.5–6.5 µm. Photobiont possibly absent, algal cells absent or very sparse, sometimes with hyphae curving around them but not enveloping them. Perithecia hemispherical or somewhat flattened above, 100–240 µm diameter, brown to black. Hymenial gel I + red (no I + blue reaction at very low concentrations of iodine). Asci 8-spored, wall thickened above, with ocular chamber. Ascospores (10–)14–21.5 × (4–)4.5–7(–7.5) µm, colourless, 3-septate, containing numerous oil-droplets when fresh.

On living evergreen leaves, including leaves of *Buxus*, *Hedera*, *Prunus laurocerasus* and *Rhododendron*. Great Britain (probably widespread), Spain, Italy, Madeira.

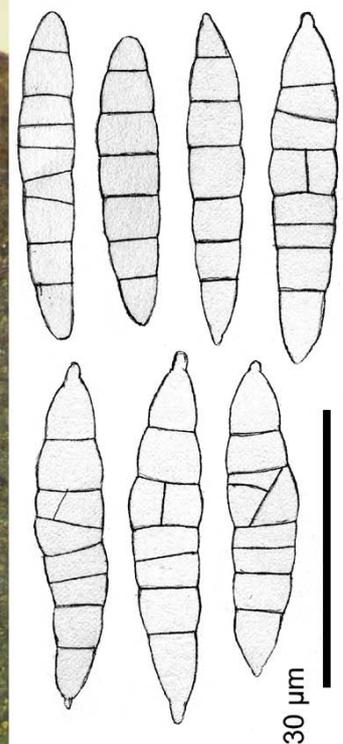
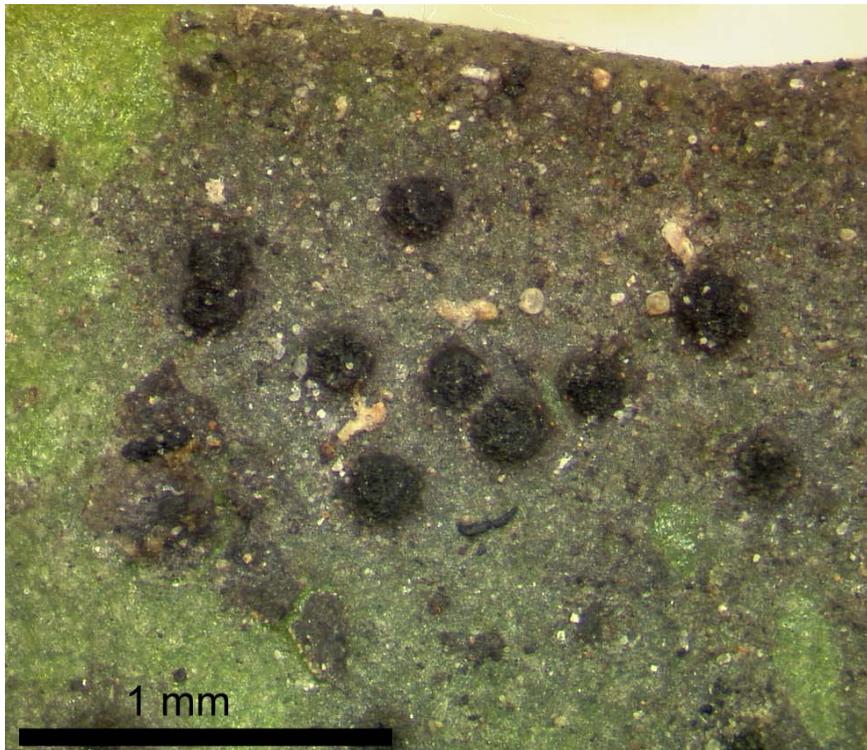


Phylloblastia inexpectata (17459)

Phylloblastia fortuita Llop & Gómez-Bolea (2009)

Thallus thin, greenish grey or brown. Perithecia subglobose to hemispherical, flattened above, 100-240 μm diameter. Hymenial gel I + red (no I + blue reaction at very low concentrations of iodine), K/I + blue. Asci 8-spored, I -, thick-walled above when young, thin later but somewhat thickened at apex; possibly ascus wall becoming gelatinised and indistinct. Ascospores (16-)20-39(-42) \times (4-)5-9(-109) μm , L/W = (3.6-)4.1-5.4(-5.8), colourless; when mature or almost so often 5-septate, slightly constricted at the septa, with rounded apices, but soon 5-7-septate, the additional septa less constricted, with 0-2 longitudinal septa, and the spore apices often produced into a papilla (papillate spores sometimes seen within asci, otherwise loose in hymenial preparations or extruded from ostiole when kept in a moist chamber).

On living evergreen leaves. Wales (on *Hedera* in suburban garden). Spain (on *Buxus*, *Hedera*, *Ilex aquifolium* and *Quercus ilex*).



Phylloblastia fortuita (17250)

PLACOPYRENIUM Breuss (1987)

Thallus crustose to subsquamulose, without vegetative propagules, always divided into areoles, these often with dark sides; attached by lower surface or by localized hapters. **Cortex** poorly defined; pigment, when present, brown epinecral layer often present. **Photobiont** Chlorophyceae. **Ascomata** perithecia, immersed in the thallus, exciple colourless to brown. **Involucrellum** absent.

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 –, fissitunicate, wall thickened above, ocular chamber usually present. **Ascospores** 8 per ascus, simple, colourless, ellipsoid or oblong-ellipsoid, smooth, wall thin or only slightly thickened, perispore present or absent.

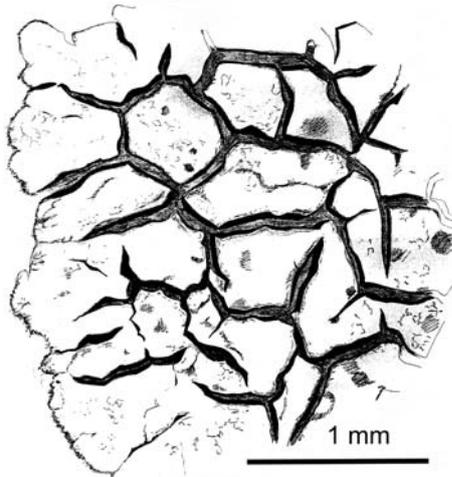
Conidiomata pycnidia, *Dermatocarpon*-type, immersed in the thallus. **Conidia** rod-shaped, aseptate, colourless. **Chemistry**: lichen products absent. **Ecology**: on rock and soil, some species in freshwater habitats, several species initially parasitic on other lichens.

Classification: Chaetothuriomycetidae, Verrucariales, Verrucariaceae.

A distinctive monophyletic group of approximately 11 currently accepted species, several of which were formerly placed in *Verrucaria*. The species are included in the key to *Verrucaria*.

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

V. aspiciliicola R. Sant. (1984), *V. canella* Nyl. (1883)



Prothallus absent or indistinct. Thallus epilithic, well developed, 260–600 μm thick. Margin thin, often more or less continuous, initially not broken into discrete areas, but very early divided by cracks; thallus rapidly increasing in thickness from the margin. Mature areoles discrete, separated by deep cracks; 220–1000 μm diam., angular in outline, mostly plane, sometimes a few slightly concave or convex, pale grey (under dissecting microscope) or locally brownish, pruinose, margin usually dark brown, sides black; upper surface rarely to occasionally rather frequently subdivided by dark lines. Epinecral layer to 10 μm thick. Cortex poorly defined, the cell walls with dilute brown pigment. 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; apex black, 100–180 μm wide, plane or occasionally slightly convex; ostiole inconspicuous or visible as a small depression *c.* 20 μm wide. Exciple 175–280 μm wide, thickened at apex, colourless to brown below, dense brown above, pigment brown, K + slightly darker or dull greenish brown. Involucrellum absent. Ascospores narrowly oblong-ellipsoid or ellipsoid, (18.5–)21.5–**23.9**–26.5(–30.5) \times (6.5–)7.5–**8.5**–9.5(–10.5) μm , (2.1–)2.5–**2.8**–3.1(–3.8) times as long as wide [*n* = 59/9]; perispore present, up to 1.2 μm thick, sometimes difficult to distinguish from ascospore wall, sometimes separating from the spore wall in K by swelling or by forming blisters. Conidiomata not seen.

On unshaded limestone, initially growing on the thallus of *Aspicilia calcarea*, later independent. S.W. and N. England, Wales. Sweden, France, Spain, Italy, Greece, Hungary, Romania, Yugoslavia.

Differs from *P. fuscillum* and *Verrucaria polysticta* in the larger ascospores and the presence of a perispore. A prothallus is scarcely apparent, 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. fuscillum* 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)

Verrucaria cinereoatrata Degel.

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 500–1200 µm diam., upper surface plane or uneven, occasionally convex when older, pale grey to mid brown, faintly to distinctly pruinose; areoles undivided or occasionally upper surface divided by a few dark lines; sides of areoles adjacent to cracks black; also parasitic on the thallus of *Staurothele fissa*, and then thallus thin, cracked, without a distinct margin. Areoles attached by the lower surface, without rhizines or hapters. Epinecral layer usually present, up 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, apex often inconspicuous in surface view, sometimes visible as a small brown dot, occasionally apex easily visible as a plane or slightly projecting black disc 60–120 µm diam. Exciple 140–300 µm diam., brown at apex, colourless below. Ascospores (13–)16–**18.5**–21.0(–25.5) × (5.5–)6.5–**7.2**–8.0(–9.5) µm, length/width ratio (1.9–)2.2–**2.6**–2.9(–4.0) [n = 110/10], ellipsoid, 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 ostiole; conidia simple, colourless, rod-shaped, 4–6 × 1.2 µm.

On siliceous rocks beside streams and rivers, sometimes parasitic on *Staurothele fissa*; associated species include *Collemopsidium angermannicum*, *Dermatocarpon meiophyllizum*, *Ionaspis lacustris*, *Leptogium plicatile*, *Staurothele fissa*, *Verrucaria aethiobola*, *V. latebrosa*, *V. pachyderma*, and the bryophytes *Amblystegium fluviatile* and *Cinclidotus fontinaloides*; uncommon. Wales, N. England. Norway, Sweden, Finland.

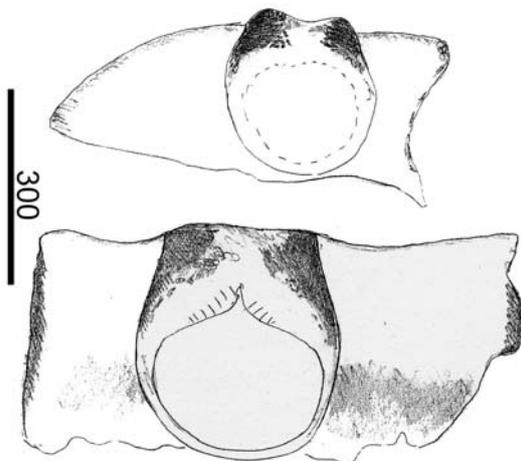
Placopyrenium formosum also grows in freshwater habitats, but in that species the ascospores are slightly larger, with a more distinct perispore, a prothallus is better developed, the areoles are more frequently gently convex, and young thalli are parasitic on *Aspicilia*. ITS sequences indicate that 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 cinereoatratum

Placopyrenium formosum Orange (2009)

Verrucaria crustulosa auct.



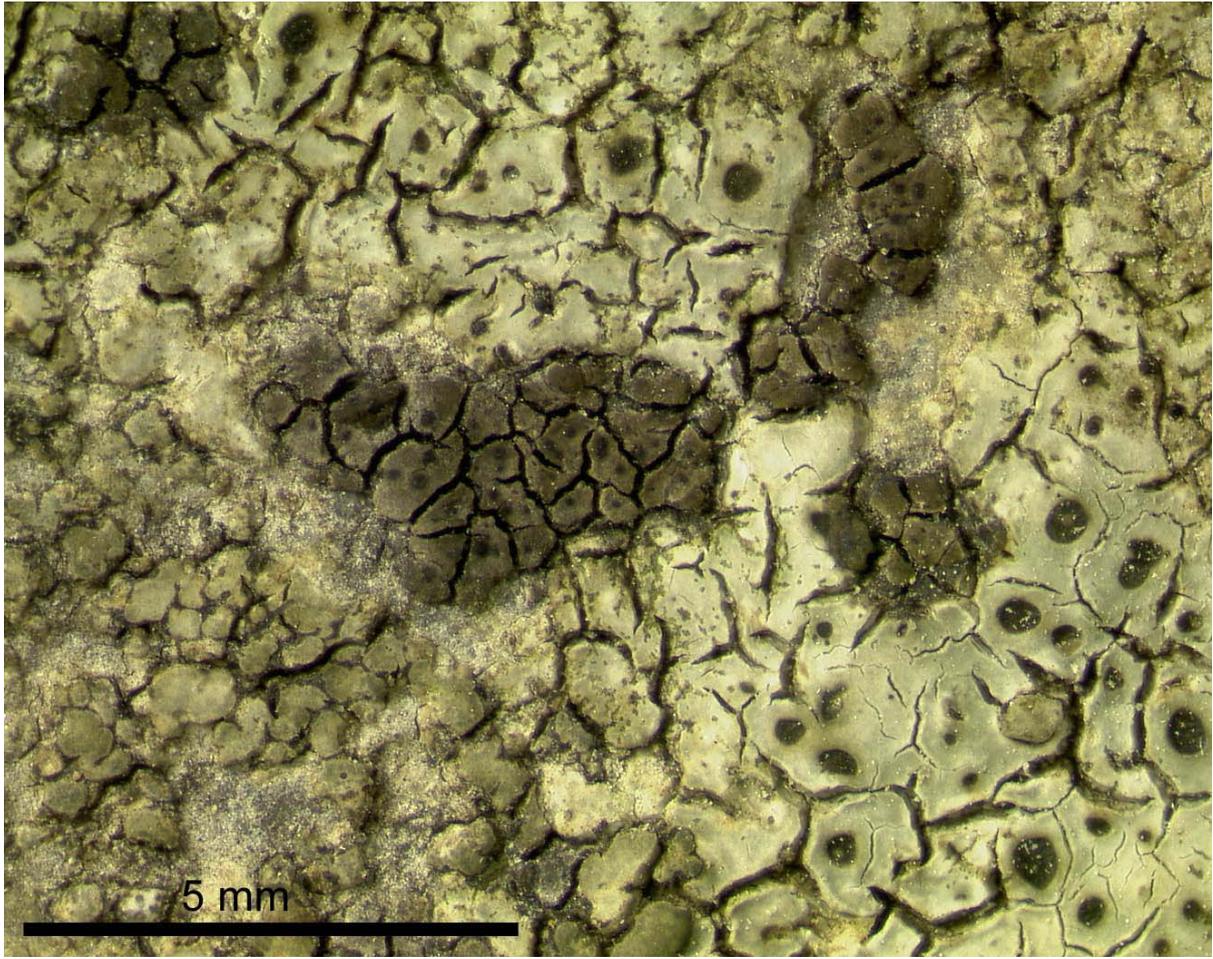
Prothallus brown, non-fimbriate, often present around areoles on rock. Thallus initially invading *Aspicilia* thalli, killing the host; superficial, well-developed, 130–400 µm thick; areoles discrete from early on, soon separated by deep cracks, at first c. 200–400 µm wide, later up to 1200 µm wide, at first plane, but mature areoles plane to gently convex, sometimes becoming subdivided by grooves; upper surface grey-brown to brown, epruinose or pruinose, the sides black. Areoles attached by the lower surface, without rhizines or hapteres. 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, apex black, plane or slightly convex, up to 180 µm diam. Exciple 140–220 µm diam., colourless or brown below, thickened and brown above.

Ascospores (14–)17.5–**20.2**–22.5(–28) × (7–)8.0–**9.0**–10(–11) µm, length/width ratio (1.6–)2.0–**2.3**–2.5(–3.0) [n = 114/6], 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 simple, colourless, rod-shaped, 3.7–5.3 × 1.2 µm.

Initially parasitic on *Aspicilia aquatica* on siliceous rocks beside streams, later free-living; rare. N. Wales, Scotland, Ireland. Italy, France, Iceland, Finland.

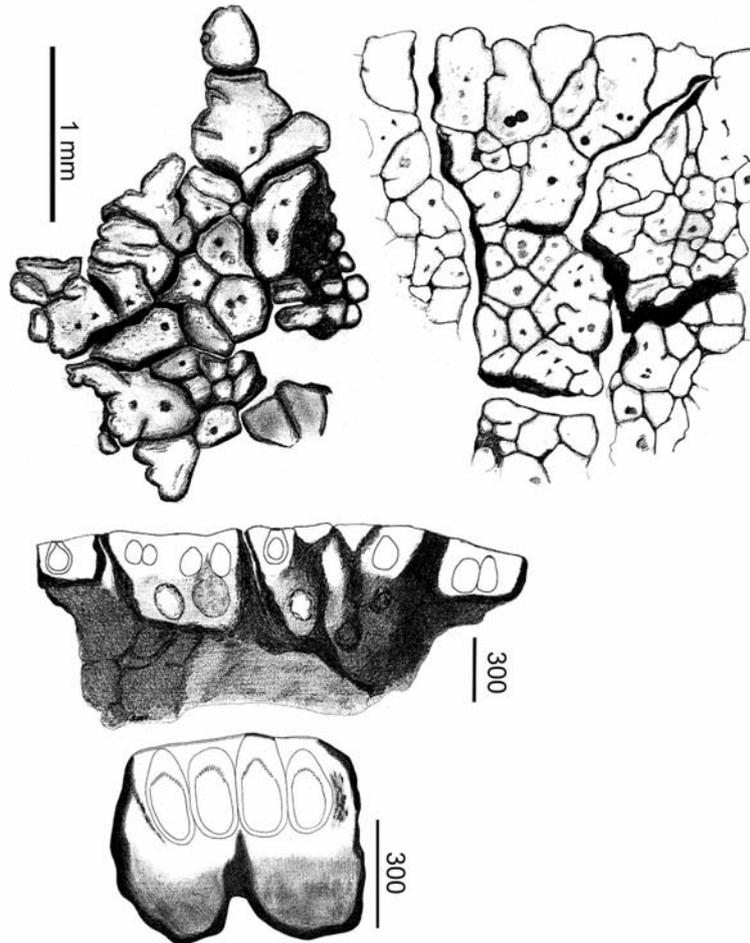
Placopyrenium canellum differs in the larger ascospores and the different host (*Aspicilia calcarea*). See under *P. cinereoatratum* for the distinction from that species.



Placopyrenium formosum on *Aspicilia aquatica* (18820).

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

Verrucaria fuscella (Turner) Winch (1807)



Prothallus inapparent. Thallus epilithic, well developed, 250–800 μm thick, often forming small patches to about 10 mm wide, but sometimes forming extensive colonies 60 mm wide; actively growing thallus margin usually thick, formed of discrete areoles, these often elongated and lobed, 300–1400 \times 180–700 μm ; upper surface of areoles in surface view becoming divided into smaller units by dark lines; thallus becoming cracked into mature areoles 600–2000 μm diam.; all areoles light brown to grey, lightly pruinose, often tinged red, often with brown edge in surface view; 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 \rightarrow HCl + red \leftrightarrow 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; apex 60–120 μm diam., plane to slightly convex, brown to black. Exciple 190–225 μm wide, colourless to dilute brown below, brown above, pigment brown, K + darker brown or greenish brown. Involucrellum absent. Ascospores oblong-ellipsoid, (11.5–)13–15.1–17(–20.5) \times (4.5–)5–5.7–6(–7.5) μm , (1.9–)2.3–2.7–3(–3.7) times as long as wide [68/8]; perispore absent. Conidiomata pycnidia, very rare (detected once), immersed in marginal areole, 75 \times 33 μm , wall colourless, cells at ostiole faintly brown, conidia *c.* 4.5 \times 1.2 μm .

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. Norway, France, Turkey.

The thallus margin in *P. fuscillum* 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.

The name *Placopyrenium trachyticum* (Hazsl.) Breuss appears to have been applied to this species by some authors, but the type of that species is more distinctly squamulose, with a nodular lower surface.

POLYBLASTIA A. Massal. (1852)

Thallus crustose, immersed or superficial, white, green, grey or brown; rarely with vegetative propagules (soredia). **Cortex** usually poorly defined, rarely a *textura intricata* of gelatinized hyphae; pigment, when present, usually brown. **Photobiont** usually Chlorophyceae. **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–, fissitunicate, 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 to dark brown. **Chemistry**: lichen products absent. **Ecology**: on siliceous rock, limestone, and on soil or over bryophytes. **Distribution**: c. 125 species, cosmopolitan.

The genus as defined here is artificial; recently, several natural genera have been segregated from *Polyblastia sensu lato* (see under *Atla*, *Henrica* and *Sporodictyon*), and many of the remaining species are likely to be reassigned in future. *Staurothele* differs in the presence of photobiont cells in the hymenium. *Agonimia* differs in the combination of somewhat layered perithecial wall, absence of an involucrellum, presence of papillae on the thallus cortical cells, and habitat often on soil, mosses or bark. *P. deminuta* has been transferred to *Merismatium*, which differs in the combination of brown ascospores, frequent presence of a perispore, and often lichenicolous habit. *Thelidium* differs in the septate ascospores, but a proportion of spores in some species can have some longitudinal septa. *Protothelenella* differs in the presence of interascal filaments and the I + ascus. The key below includes *Merismatium deminutum* and all British and Irish species of *Atla*, *Henrica* and *Sporodictyon*.

- 1 Soralia present; perithecia 0.30-0.95 mm diam., ascospores colourless, 36-50 µm *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 partly immersed in thallus or in soil, involucrellum present 5
- 3(2) Ascospores dark brown, (18-)22.5-27.5(-31) µm, with a perispore usually visible *Merismatium deminutum*
 Ascospores colourless, perispore absent 4
- 4(3) Ascospores muriform, with c. 10-36 cells visible in optical section *albida*
 Ascospores submuriform, with 3-4 transverse and 1-2 longitudinal septa, with c. 6-14 cells visible in optical section *dermatodes*
- 5(1) 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 small, (15-)20-38.5 µm long 7
 Ascospores 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 *gothica*
- 8(6) Involucrellum absent, ascospores large, 70-160 µm long 9
 Involucrellum present, ascospores smaller, 48-98 µm long 10
- 9(8) Asci (1-)2-spored, spores cylindrical-ellipsoid *helvetica*
 Asci (3-)4-8-spored, spores ellipsoid or oblong-ellipsoid *Atla wheldonii*

- 10(8)** 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 11
- 11(10)** 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. 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 15
- 14(13)** Ascospores 12–20 μm long *quartzina*
Ascospores 30–45(–68) μm long *verrucosa*
- 15(13)** Ascospores small, 17–45 μm long 16
Ascospores larger, 38–81 μm long 17
- 16(15)** 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*
- 17(15)** Asci 2-spored; involucrellum absent *agraria*
Asci 8-spored 17
- 18(17)** 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 terrestris*

P. agraria Th. Fr. (1864)

Thallus superficial, thin and film-like to uneven, green to green-brown, composed of goniocysts with brown pigment in the cortical cells. Perithecia 0.14–0.23 mm diam. when moist, sometimes collapsed when dry, half- to two-thirds immersed, or a few almost superficial, without a thalline covering. Involucrellum absent. Asci 2-spored. Ascospores colourless, becoming brownish when over-mature, narrowly oblong-ellipsoid, (42.5–)49–60(–65.5) \times (14–)16–21.5(–27) μm , length/width 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, Ireland. N. Europe.

Distinguished by the small perithecia lacking an involucrellum, the 2-spored asci and the colourless ascospores.

P. albida Arnold (1858)

Thallus immersed. Perithecia immersed in well-defined pits in limestone, apex of perithecium separated from side of pit by a fine crack. Involucrellum absent. Exciple brown throughout, but often paler at base, 0.2-0.4(-0.5) mm diam. 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).

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

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

P. cupularis A. Massal. (1852)

Thallus immersed, partly immersed, or superficial, whitish to pale grey, often cracked. Perithecia forming moderately prominent projections 0.28-0.54(-0.59) mm diam., not covered by thallus, apex plane or slightly depressed. Involucrellum well-developed, clasping the exciple and spreading slightly. Asci 8-spored. Ascospores colourless, muriform, ellipsoid to rather broadly ellipsoid, (21.5-)26-38.5(-45) × (14-)17.5-23(-29.5) μm, length/width ratio (1.3-)1.4-1.9(-2.4).

On limestone and on slightly calcareous siliceous rocks, including epidiorite and schist, rarely on soil. Throughout British Isles, but rare in S. England. Europe, N. America.

P. dermatodes A. Massal. (1855)

Thallus immersed, grey. Perithecia immersed in pits in limestone, 0.3-0.5 mm diam. Involucrellum absent. Exciple pigmented throughout. Asci 8-spored. Ascospores colourless, submuriform with 3-4 transverse septa and 1-2 longitudinal septa, 25-50 × 12-25 μm.

On limestone, chalk and old mortar. Throughout the British Isles. Europe, Australia (Tasmania).

This species is provisionally retained here, but the distinction from *Thelidium incavatum* is currently arbitrary; see under that species for discussion.

P. efflorescens Coppins (1991)

Thallus superficial, of scattered to confluent areoles, often in extensive patches; areoles 0.2-0.4 mm diam., plane to convex, grey-green, soon dissolving almost entirely into soralia; soralia irregularly convex to globose, 0.2-1 mm diam., sometimes more or less stipitate and up to 0.7 mm high, plae greyish green (bright green when moist and fresh), soredia c. 25-50 μm diam. Perithecia rare, (0.3-)0.4-0.8(-0.95) mm diam., three-quarters to one-quarter immersed, often partly hidden by areoles or soralia. Involucrellum well-developed. Exciple 0.2-0.48 mm diam., colourless below. Asci 8-spored. Ascospores muriform, colourless, 36-50 × 22-33 μm.

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

P. gothica Th. Fr. (1865)

Thallus subgelatinous, black, granular, effuse. Perithecia one-quarter to one-half immersed, 0.2-0.3 mm diam. Involucrellum absent. Asci 8-spored. Ascospores (156-)20-30(-36) × (8-)10-15 μm, submuriform, brown.

On mica-schist soil between squamules of *Catapyrenium cinereum*. C. Scotland (Mid Perthshire: summit of Ben Lawers); not collected since 1864. Europe, N. America.

P. helvetica Th. Fr. (1865)

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, cylindrical-ellipsoid, $70-135 \times 30-60 \mu\text{m}$.

On base-rich, mossy soil, montane; very rare. Scotland (Highlands). Scandinavia (Iceland, Norway), Alps, Greenland.

P. philaea Zschacke (1933)

Thallus superficial, very thin or up to $120 \mu\text{m}$ thick, pale brownish; when well-developed, forming a coherent crust which is smooth to uneven or with indistinct areole-like convex areas up to 0.16 mm diam.; a distinct cortex sometimes present, up to $30 \mu\text{m}$ thick, composed of colourless more or less elongated 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 thallus, $0.48-0.60 \text{ mm}$ diam.; apex black, not covered by 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, $(37.5-44-54.5(-58) \times (17-)19-24(-24.5) \mu\text{m}$, length/width ratio $(1.8-)2.1-2.5(-2.8)$.

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

Distinguished by the perithecia immersed in soil, and the colourless ascospores. 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.

P. quartzina Lynge (1928)

Thallus superficial, smooth or finely granular, somewhat cracked, pale to dark grey, green-grey or dark red-brown; possibly lichenicolous. Perithecia $0.15-0.25 \text{ mm}$ diam., half-immersed, often covered up to 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, ellipsoid, $12-20 \times 6-10 \mu\text{m}$.

On siliceous, frequently inundated rocks in sunny streams, on *Verrucaria aethiobola* and *Ionaspis lacustris*, and on *Verrucaria maura* in brackish seepage on seacliffs; very rare. Wales, W. & C. Scotland. ?Endemic.

Characterized by the small perithecia, well-developed involucrellum, and the small submuriform ascospores.

P. sendtneri Kremp. (1855)

Thallus superficial, pale grey to pale brown, uneven, formed of coalescing convex units *c.* $0.15-0.5 \text{ mm}$ diam.; surface smooth, slightly glossy, with a slightly translucent, cartilaginous appearance. Cortex distinct, $30 \mu\text{m}$ thick, formed of gelatinized, colourless, filamentous hyphae $1.5-2 \mu\text{m}$ wide, forming a *textura intricata*; base of cortex becoming subcellular, and sometimes with brown pigment. Perithecia half- to three quarters-immersed in thallus and substratum, sometimes a few more exposed, often clustered; apex of perithecium exposed as a blackish projection up to 0.3 mm diam. Involucrellum present, mainly near apex of exciple, scarcely spreading. Asci 8-spored. Ascospores colourless, muriform, $(17-)21.5-25.5(-28) \times (10.5-)12-14.5(-16.5) \mu\text{m}$, length/width ratio $(1.2-)1.6-2(-2.2)$.

On exposed mossy soil over mica-schist and epidiorite, over 900 m , very rare. N. Scotland (Highlands: Ben Lawers, Coire Cheap near Ben Alder). Scandinavia, Alps, N. America.

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*.

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 *c.* 6-10 cells in total, 30-45(-68) × 15-20 μm.

On mica schist at 600 m; very rare. C. Scotland (Breadalbane: Creag na Caillich, Creag an Lochain). Scandinavia, Alps.

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

PORINA Ach. (1809), nom. cons. emend.

Thallus crustose, immersed to superficial. **Cortex** absent or present. **Epinecral layer** sometimes present. **Medulla** ill-defined. **Isidia** sometimes present. **Photobiont** *Trentepohlia* or (mostly in foliicolous species) *Phycopeltis*. **Ascomata** perithecioid, immersed in the thallus to prominent, or forming pits in limestone. **Exciple** with or without dark pigment. **Involucrellum** present, composed of thick-walled more or less elongated cells; sometimes containing numerous photobiont cells or crystals. **Hamathecium** of paraphyses, simple or rarely branched, periphyses present or absent. **Hymenial gel** I –, K/I –. **Asci** clavate-cylindrical, wall thin throughout, functionally unitunicate (dehiscence by rupture of the apex, with no extruded inner layers), I –, K/I –; apex either truncate and containing a refractive ring which stains with Congo Red, or rounded (to somewhat tapering) and without a ring. **Ascospores** 3-many-transversely septate, rarely with 1–3 longitudinal septa, colourless, narrowly ellipsoid to acicular, smooth, with perispore, 15–90(–140) µm long, usually irregularly biseriolate in the ascus. **Conidiomata** pycnidia, frequent. **Conidia** aseptate, oblong-ellipsoid to rod-shaped or rarely filiform. **Chemistry:** acetone-soluble secondary products absent; at least 4 acetone-insoluble pigments present, including a yellow to orange, K + orange or dark orange, HCl + yellow to orange pigment (Porina-yellow; the dominant pigment in involucrellum of *P. ahlesiana*, *P. lectissima*, *P. leptalea*, *P. rhodostoma* and *P. rosei*, and found in at least the upper exciple of *P. aenea*, *P. coralloidea*, *P. curnowii*, *P. guentheri*, *P. interjungens* and others), and a range of dark pigments which need more study; these often occur mixed together and are difficult to distinguish; the following are examples which may be part of a continuum of colour reactions, perhaps due to overlapping: 1. purple-violet to purple, K + dark bluish grey, HCl + purple to red-purple (Sagedia-red; the dominant pigment in the involucrellum of *Porina byssophila*, *P. linearis* and others, also found in some *P. lectissima*), 2. purple-brown, K + dark grey-brown, HCl + red-purple to red-brown (?Pseudosagedia-violet in part; involucrellum of *P. borrieri*, *P. coralloidea*, *P. guentheri*, *P. hibernica* and others), 3. purplish brown, K + dull purplish-brown, HCl + purplish-brown (?Pseudosagedia-violet in part; involucrellum of *P. aenea*, *P. borrieri*, *P. chlorotica* and others), 4. pigments brownish in water and K, red-brown in HCl (mixed with other pigments in involucrellum of several species). **Ecology:** on siliceous or calcareous rock, often in damp habitats; bark, evergreen leaves (mainly in tropics), rarely on soil (and then usually overgrowing bryophytes).

Classification: Ostropomycetidae, Ostropales, Porinaceae.

Attempts have been made to subdivide the genus using features of the ascus apex, the presence or absence of periphyses, the presence or absence of isidia, and the type of pigment present in the involucrellum and exciple, but these features correlate poorly, even in the European species, and the units which have been distinguished intergrade with each other. *Strigula* differs in the thickened ascus apex.

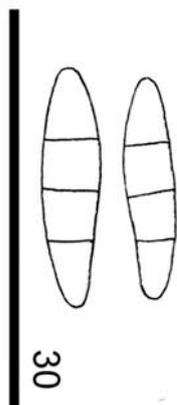
Literature: Aptroot (2002e), Hafellner & Kalb (1995), McCarthy (2000), McCarthy & Malcolm (1997), Sérusiaux *et al.* (2007).

- 1 Isidia present, perithecia present or absent 2
Isidia absent, perithecia present 5
- 2(1) Thallus dull dark grey, isidia mostly simple and tapering to the apex, which is formed of pale elongated hyphae *coralloidea*
Thallus cream to grey-green or orange, isidia simple or usually becoming branched, apex similar to rest of isidium, not formed of elongated hyphae 3
- 3(2) Isidia with a papillose surface formed by projecting fungal cells (microscope), often large, up to 0.50 mm high and the branches 0.05-0.08 mm wide *atlantica*
Isidia with a more or less smooth surface, fungal cells sometimes rounded but not strongly projecting 4

4(3) Isidia with a distinct cortex of fungal cells, isidia slender, the individual branches 0.025-0.05 mm wide	<i>rosei</i>	
Isidia with only a thin and indistinct cortex of fungal cells, isidia coarser, the individual branches 0.03-0.10 mm wide	<i>hibernica</i>	
5(1) Growing on soil, plant remains, or on bryophytes over rock; perithecia black, involucrellum with dark (purple, brown or grey) pigment, ascospores 3-5-septate		6
Growing on rock or bark; if on bryophytes over rock then perithecia yellow or pinkish, involucrellum yellow to orange, or ascospores with 7 or more septa		7
6(5) Ascospores 3-septate	<i>mammillosa</i>	
Ascospores 3- to 5-septate	<i>sudetica</i>	
7(5) Ascospores 3-septate		8
Ascospores (3-)6- to 16(-17)-septate		15
8(7) Involucrellum in section yellow to orange; dark pigments in shades of purple, brown and grey absent		9
Involucrellum in section with dark pigments (shades of purple, brown or grey); but yellow to orange pigments often present as well		11
9(8) Isidia present; on bark or rarely on bryophytes over rock.....	<i>rosei</i>	
Isidia absent; on bark or on rock		10
10(9) Perithecia 0.1-0.3 mm diam. (measured <i>in situ</i>), ascospores 14.5-23 × 3.5-5 μm	<i>leptalea</i>	
Perithecia 0.22-0.5 mm diam., ascospores 16-30(-40) × 4-8 μm	<i>lectissima</i>	
11(8) Involucrellum with a purple pigment which is K ⁺ blue-grey, often mixed with other pigments		12
Involucrellum purple-brown to grey-brown or brown in K, but not blue-grey		14
12(11) Involucrellum containing much Porina-yellow; perithecia (<i>in situ</i>) up to 500 μm diam.; growing on damp siliceous rocks	<i>lectissima</i>	
Involucrellum with Porina-yellow confined to area near ostiole; perithecia up to 0.3 mm diam.; on calcareous rocks		13
13(12) Thallus endolithic, perithecia often immersed in pits in rock	<i>linearis</i>	
Thallus superficial, well-developed, perithecia not in pits	<i>byssophila</i>	
14(11) On bark	<i>aenea</i>	
On rock	<i>chlorotica</i>	
15(7) Involucrellum in section yellow to orange (Porina-yellow), without additional dark pigments		16
Involucrellum with purple, grey or brown pigments, sometimes locally with Porina-yellow as well		18
16(15) Isidia present; ascus without a ring structure in apex, ascospores 6- to 10-septate, 56-66 × 11-14 μm; on bark	<i>atlantica</i>	
Isidia absent		16
17(16) Ascospores (6-)7-septate, 30-50(-70) × 6-9(-15) μm; ascus with a ring structure in apex	<i>ahlesiana</i>	
Ascospores 7- to 14-septate, 40-90 × 8-12 μm; ascus without a ring structure	<i>effilata</i>	

18(15) Ascospores (5-)9- to 16(-17)-septate	19
Ascospores (3-)7(-9)-septate	20
19(18) Thallus dull dark grey, isidia mostly unbranched, narrowed to apex; ascospores (5-)9- to 11(-12)-septate, (35-)40-57(-63) × (5-)8-13(-15) μm	<i>coralloidea</i>
Thallus grey-green to pale orange, isidia unbranched or becoming branched, often forming granular-coralloid mats; ascospores (7-)12- to 16(-17)-septate, (55-)60-90(-95) × 5-7(-8) μm	<i>hibernica</i>
20(18) Ascospores with a proportion containing 1-2(-3) longitudinal septa	21
Ascospores all without longitudinal septa	22
21(20) Ascospores (4-)5- to 7-septate, 20.5-29(-34.5) × (6-)7-8(-10) μm, 2.5-4.5 times as long as wide	<i>interjungens</i>
Ascospores (5-)7(-8)-septate, (29-)31.5-40(-43.5) × (6-)6.5-7(-7.5) μm, (4-)4.5-5.5(-6) times as long as wide	<i>guentheri</i> var. <i>lucens</i>
22(20) Ascospores 3- to 7-septate; involucrellum with some purple, K+ blue-grey pigment	<i>byssophila</i>
Ascospores (5-)7(-9)-septate	23
23(22) Thallus mostly endolithic, on limestone	<i>ginzbergii</i>
Thallus superficial, usually well-developed	24
24(23) On bark, ascus with ring structure	25
On rock	26
25(24) Ascospores (3-)4.5-5(-5.5) μm wide	<i>borreri</i>
Ascospores 2.5-3.5(-4) μm wide	<i>leptospora</i>
26(25) Ascospores narrow, 3-5 μm	<i>curnowii</i>
Ascospores wider, 5-10 μm wide	26
27(26) Ascospores (4.5-)5-6.5 μm wide, (4.5-)5.5-8(-9.5) times as long as wide; ascus without a ring structure	<i>guentheri</i> var. <i>guentheri</i>
Ascospores (6-)7-9(-10) μm wide, 4-5(-5.5) times as long as wide; ascus with a ring structure	<i>grandis</i>

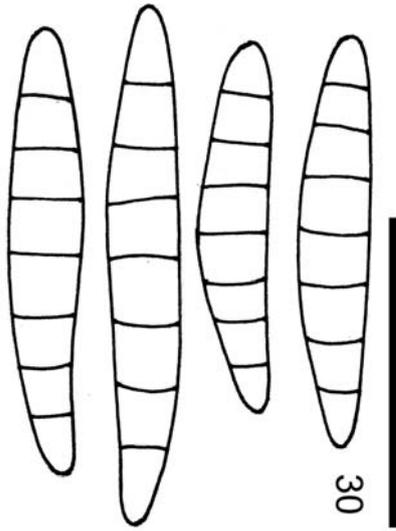
Porina aenea (Wallr.) Zahlbr. (1922)



Thallus thin, smooth or locally cracked, deep red-brown to green-brown or dark brown. Perithecia black, 120–260(–300) μm diam. Involucrellum purple-brown, dulling in K. Exciple dark or colourless. Ascospores 3-septate, 1–20(–24) × 3.5–5 μm. Conidia ellipsoid, straight or more or less curved, 2 × 0.5 μm.

On smooth bark on trunks and branches, including twigs, often on trees with bark of high pH (*Acer*, *Fraxinus*), but also frequent on bases of conifers in plantations; shade-tolerant. Europe, N. America. Most collections have perithecia no more than 200 μm diam. Very similar to *P. chlorotica*, which usually grows on rock. Material of *P. chlorotica* on bark is said to have a more olivaceous and oily thallus than *P. aenea*.

Porina ahlesiana (Körb.) Zahlbr. (1931)



Thallus superficial, thin, greenish grey, pale yellow-grey or olivaceous, continuous or more or less cracked. Perithecia pale orange-brown, translucent when wet, occasionally greyish at base, 300–500(–700) μm diam., 0.25–0.5-immersed in thallus. Involucrellum of thick-walled cells, containing numerous photobiont cells, yellow in section (Porina-yellow). Exciple yellow. Ascus apex truncate, with ring structure. Ascospores (6–)7-septate, 30–50(–70) \times 6–9(–15) μm . Pycnidia pale grey-pink, inconspicuous. Conidia 6–7 \times 0.5 μm .

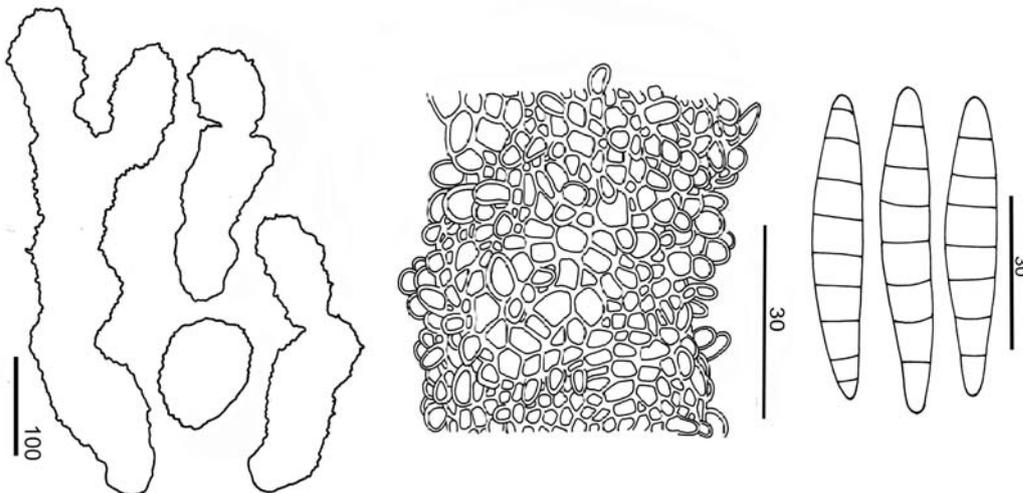
On damp shaded siliceous rock with slight base-influence, near rivers and lakes and on damp outcrops and in seepages; shade-tolerant, sometimes in cave entrances or below several layers of boulders; rare. Western Britain, one old record for Ireland. Norway, Spain, France, S.W. Germany, Austria, ?W. Africa, New Zealand.

Characterized by the greenish grey thallus, the pale perithecia which are translucent when moist, and the 7-

septate ascospores. *P. lectissima* has 3-septate ascospores.

Porina atlantica (Erichs.) P.M. Jørg.

Porina rhodostoma auct. non Müll. Arg. (1885), *P. guaranitica* auct. p.p. non Malme (1929), *P. heterospora* auct. p.p. non (Fink) R.C. Harris (1975).



Thallus superficial, pale brownish cream, often with lightly convex areas separated by furrows. Isidia present, discrete or crowded, isodiametric when young, soon oblong to cylindrical, branched and coralloid, fragile, to 500 μm high, branches 50–80 μm wide, papillose under the microscope, with a cortex which has numerous projecting cells. Perithecia frequent, mostly immersed (in Irish material) to prominent, apex light reddish brown. Involucrellum containing numerous large crystals, orange (Porina-yellow). Exciple yellow. Ascus apex rounded, without a ring structure. Ascospores 6–9(–10)-septate, 56–66 \times 11–14 μm .

On base-rich bark of *Quercus*, sometimes overgrowing bryophytes, very rare. S.W. Ireland (N. Kerry, W. Cork). Madeira, Cuba.

Sterile material can be distinguished from *P. hibernica* by the often larger isidia with a papillose surface.

Porina borrieri (Trevis.) D. Hawksw. & P. James (1980)

Thallus superficial, well-developed, grey-brown to green-brown or blackish olive, continuous to cracked. Perithecia 200–360(–500) μm diam., black, prominent (0.33–0.5-immersed in thallus). Involucrellum purple-violet to purple-brown or brown, dulling in K, or K + grey-brown to brown, containing some photobiont cells. Exciple colourless or faintly brown below. Ascus apex truncate, with ring structure. Ascospores 6–7(–8)-septate, (22.5–)28–**31.4**–35(–40) \times (3–)4.5–**4.8**–5(–5.5) μm . Conidia oblong-ellipsoid, 2–3.3 \times 1.2 μm .

On rough bark of old trees, particularly *Quercus*, *Fraxinus* and *Acer pseudoplatanus*, in old woodlands and parklands, on roughened bark on young trees (for instance *Sorbus aucuparia*), and on old smooth bark of *Ilex* and *Fagus*, rarely spreading to bryophytes, widespread but local. S. and S.W. England, Wales, Scotland, Ireland. Sweden, Denmark, France, Switzerland, Germany, Austria, Italy, Macaronesia, ?U.S.A.

P. aenea has smaller perithecia, and 3-septate ascospores.

Porina byssophila (Körb. ex Hepp) Zahlbr. (1903)

Thallus epilithic, well-developed, dull grey-green to green-brown or grey-brown, smooth to uneven, continuous to cracked. Perithecia 0.1–0.5-immersed, 130–300 μm diam. Involucrellum purple-violet to purple-brown, K + blue-grey to dark grey-brown. Exciple dark. Ascus with ring-structure. Ascospores 3(–7)-septate, (17–)18.5–**21.4**–24(–29) \times (3.5–)4–**4.7**–5.5(–6) μm , (3.5–)4–**4.6**–5(–6.5) times as long as wide. Conidia oblong, 2.9–3.3 \times 1.2 μm .

On limestone and on slightly basic siliceous rocks, on shaded rocks and stones, usually on surfaces sheltered from rain; rare but under-recorded. Wales, S.W. Scotland, Western Ireland.

Most collections have only 3-septate ascospores. Close to *P. linearis*, which differs in the endolithic thallus. *P. chlorotica* differs in the usually browner and thinner thallus, and the different pigment in the involucrellum, and grows on acid rocks.

Porina chlorotica (Ach.) Müll. Arg. (1884) **f. chlorotica**

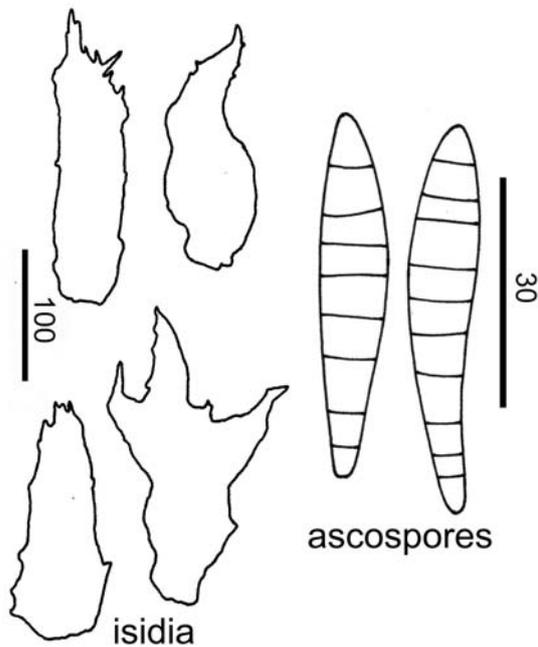
Thallus thin, superficial, dull brown to dark green-brown or blackish, continuous or cracked. Perithecia black, 140–220(–300) μm diam. Involucrellum purplish brown, dulling in K, or K + grey-brown. Exciple dark. Ascospores 3-septate, (12.5–)14.5–**15.9**–18(–32) \times 3.5–**4.1**–4.5(–6) μm . Conidia oblong-ellipsoid, 2.5–3.7 \times 1–1.2 μm .

On siliceous rocks and stones, rarely brickwork, often in shade and in damp situations, in woodland and beside rivers and lakes; occasionally on smooth bark; frequent. Throughout British Isles, especially in the north and west. Europe, N. and E. Asia, N. America, N. and S. Africa, Australia, New Zealand, Pacific Islands.

Very similar to *P. aenea*, which grows on bark; there appear to be no reliable features to distinguish the two species.

Porina chlorotica f. tenuifera (Nyl.) Swinscow (1962) differs in the ascospores 25–35 \times 3–4 μm .

Porina coralloidea P. James (1971)

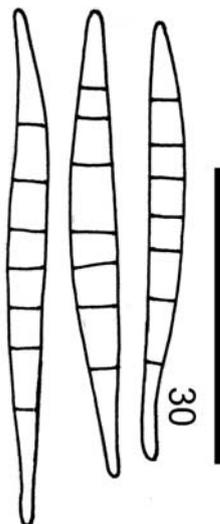


Thallus superficial, dull dark grey with a pinkish or purplish tinge; isidia present, often crowded, simple or rarely branched, cylindrical or elongate-ovoid, usually tapering to apex, 160–210 × 40–70, apex often pale, formed of a tuft of colourless filamentous hyphae (Figs. NEW). Perithecia black, 300–400 µm diam., 0.25–0.75-immersed, scattered and sometimes not obviously associated with thallus. Involucrellum dark purplish-brown, K + grey-brown. Exciple yellow (Porina-yellow), or with some pigment like the involucrellum. Ascospores (6–)9–11(–12)-septate, (35–)40–57(–63) × (5–)8–13(–15) µm.

On bark of medium-aged to very old trees, especially *Quercus*, rarely on *Fraxinus* and *Fagus*, in old forests and parklands, local. S. England (especially New Forest in Hampshire), N.W. England (Lake District), Wales, W. Scotland. France (Brittany), N. Spain, Canary Islands, Azores, Hong Kong.

Recognized in the field by the dark colour and the pointed isidia; the dark purplish brown thallus resembles that of *Catinaria atropurpurea*, which occurs in similar habitats, but which has no isidia. *Gyalideopsis anastomosans* has pointed isidia-like structures, but these are pale grey and contain a trebouxioid photobiont.

Porina curnowii A.L. Sm. (1911)



Thallus superficial, thin, dull grey-brown, cracked or not. Perithecia black, prominent, 300–500 µm diam. Involucrellum dull purple-violet, K + dark grey or grey-brown. Ascus apex rounded, without ring structure. Ascospores (6–)7–(–9)septate, 34–54 × 3–5 µm, 9.5–13 times as long as wide.

Mainly on siliceous coastal rocks in sheltered damp sites, and in seepage tracks, very local. S.W. England (Cornwall), S.W. Wales, Isles of Scilly, Channel Isles, S.W. Ireland. France (Brittany), N.W. Spain.

Similar to *P. guentheri* var. *guentheri*, which has wider ascospores.

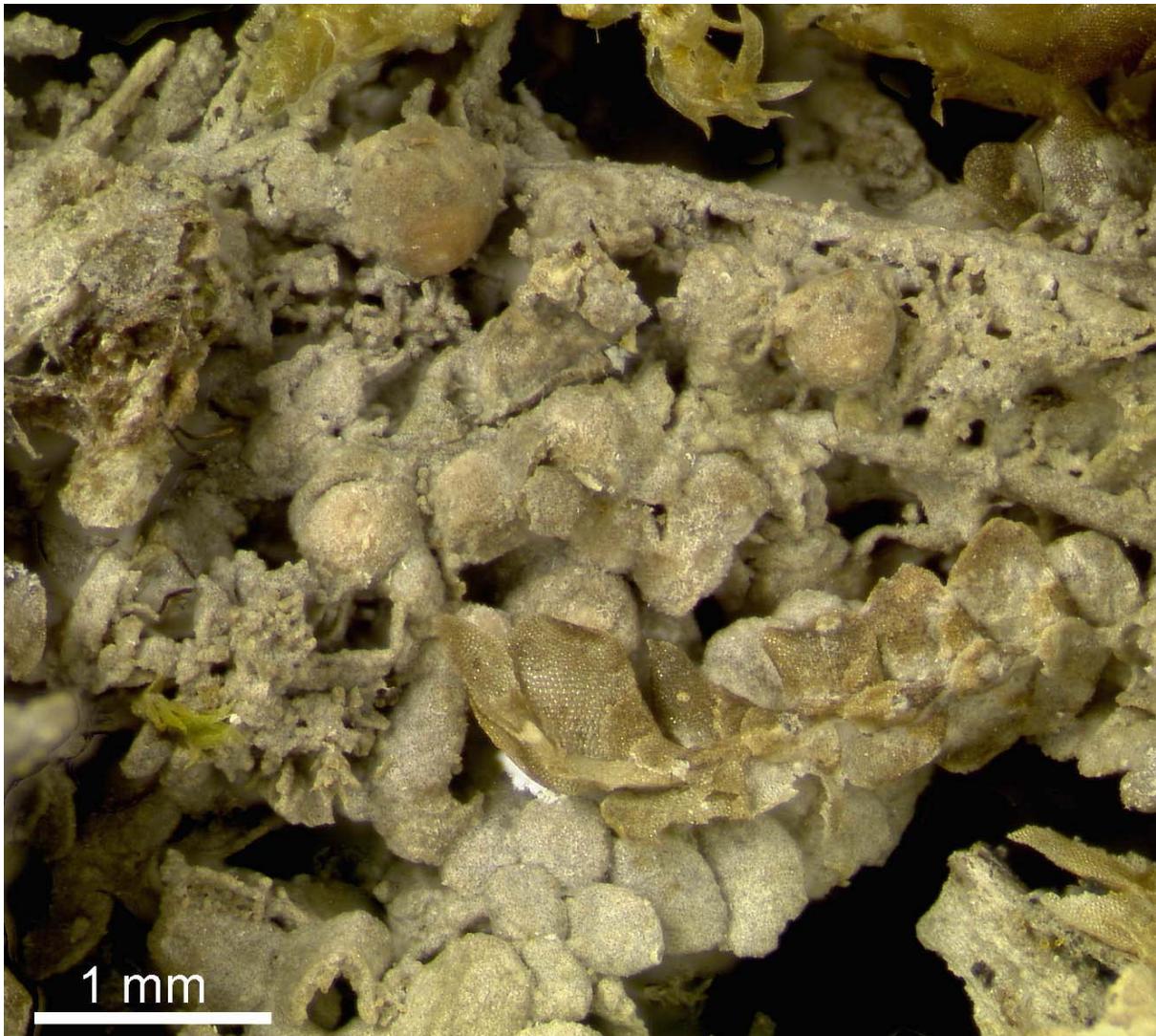
Porina effilata Brand & Sérus. (2007)

Porina atlantica auct. p.p. non (Erichs.) P.M. Jørg. (2000), *P. guaranitica* auct. p.p. non Malme (1929), *P. heterospora* auct. p.p. non (Fink) R.C. Harris (1975).

Thallus superficial, well-developed, more or less smooth to granular or verrucose, dull grey-green to dull orange-brown, orange or pinkish when fresh, pale grey to green-grey in the herbarium. Perithecia 360-900 µm diam., pale pinkish cream to orange-pink, pale pink-brown or yellow-brown, 0.25–0.75-immersed in thallus, sometimes pruinose when prominent. Involucrellum and exciple yellow (Porina-yellow). Ascus apex more or less truncate to rounded, without a ring structure. Ascospores 7–14-septate, 40–90 × 8–12 µm.

On base-rich bark, on sheltered bases of mossy trees, especially *Quercus* in old woodland, or on slightly calcareous siliceous rock in overhangs (often overgrowing bryophytes); rare, very locally frequent. S.W. Ireland, W. Wales (Cardigan, Merioneth), S.W. England (N. Devon). Europe (Spain), Madeira, N. America, Cuba, S. America (Brazil, Paraguay, Uruguay), S. Africa.

Characterized by the large pale perithecia and the large ascospores. *P. rhodostoma* differs in the shorter ascospores and presence of isidia.



Porina effilata (10998).

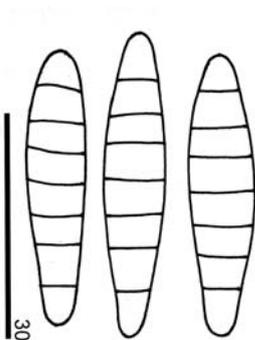
Porina ginzbergeri Zahlbr. (1903)

Thallus immersed and inconspicuous, to superficial, cracked; pale green-grey to orange-brown, rarely greyish black. Perithecia 250–400 µm diam., 0.25-immersed to prominent and more or less sessile. Involucrellum violet, K + blue-grey, also with Porina-yellow at apex of exciple. Exciple violet. Ascus apex rounded, without ring structure. Ascospores (5–)7(–8)-septate, (19–)21.5–40(–45) × 4–7 µm.

On shaded limestone and calcareous siliceous rocks, rare. England (Dorset, Derbyshire), S. Wales (Pembrokeshire), W. Scotland (Skye); W. Ireland. Mediterranean region of Europe from S. France to Greece.

P. byssophila and *P. linearis* differ in the ascus with a ring structure in the apex, and in the smaller, 3-septate ascospores, but some specimens of *P. ginzbergeri* can have a proportion of the ascospores relatively short.

Porina grandis (Körb.) Zahlbr. (1922)



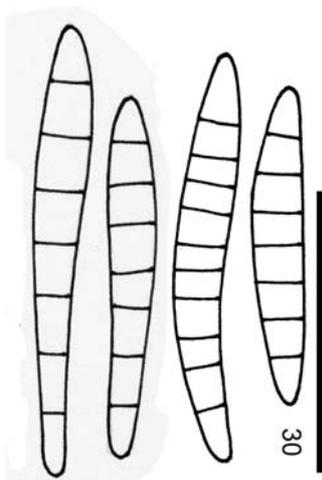
Thallus brown, continuous or cracked. Perithecia 400–800 µm diam., 0.25-immersed in thallus. Involucrellum purple-brown to purple-grey, dulling in K or K + dark grey. Ascus apex truncate, with ring structure. Ascospores (6–)7-septate, (30.5–)33.5–40.5(–50) × (6–)7–9(–10) µm, 4–5(–5.5) times as long as wide.

On damp rocks by streams, sometimes in woodland; rare. N. Wales, N. and W. Scotland (Inverness, Isle of Skye). Norway, Sweden, Denmark, Germany, Czech Republic.

Distinguished from *P. guentheri* by the wider ascospores and different ascus apex. Some specimens of *P. grandis* have larger perithecia than *P. guentheri*, but others are similar in size.

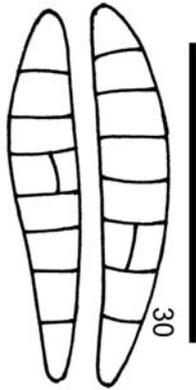
Porina guentheri (Flot.) Zahlbr. (1922) **var. guentheri**

Thallus superficial, well-developed, continuous or cracked, dull green-brown to dark purple-grey. Perithecia black, 300–700 µm, 0.25–0.5-immersed. Involucrellum purple-violet to purple-brown, K + dark grey to brown. Ascus apex rounded, without ring structure. Ascospores (6–)7(–9)-septate, (28–)32–45(–49) × (4.5–)5–6.5 µm, (4.5–)5.5–8(–9.5) times as long as wide.



On damp siliceous rocks on shaded outcrops and by lakes and upland rivers. Local in W. Britain and W. Ireland, rare elsewhere. Norway, Sweden, S.W. Germany, Austria, Italy (Lombardy and Sardinia), 'U.S.S.R.', N. America, S. Africa, Australia (Tasmania), New Zealand.

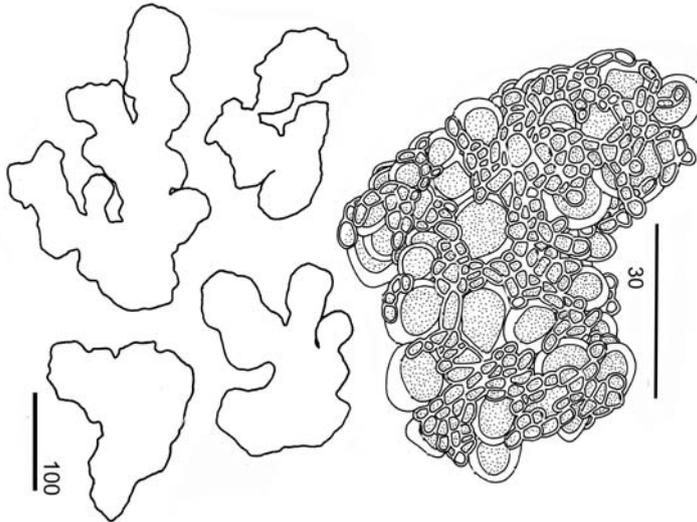
Porina guentheri var. lucens (Taylor) Swinscow (1962)



Similar to *P. guentheri* var. *guentheri*, but ascospores (6–)7(–8)-septate, some spores with 1–2(–3) longitudinal septa, (29–)31.5–40(–43.5) × (6–)6.5–7(–7.5) μm, (4–)4.5–5.5(–6) times as long as wide.

On periodically inundated siliceous rocks by rivers and lakes, in shaded or unshaded sites, often on steep faces. Very local in W. Britain and W. Ireland; rare in Scotland, N.W. and S.W. England, locally frequent in N.W. Wales, where it is the commoner of the two varieties beside rivers. Spain.

Porina hibernica P. James & Swinscow (1962)

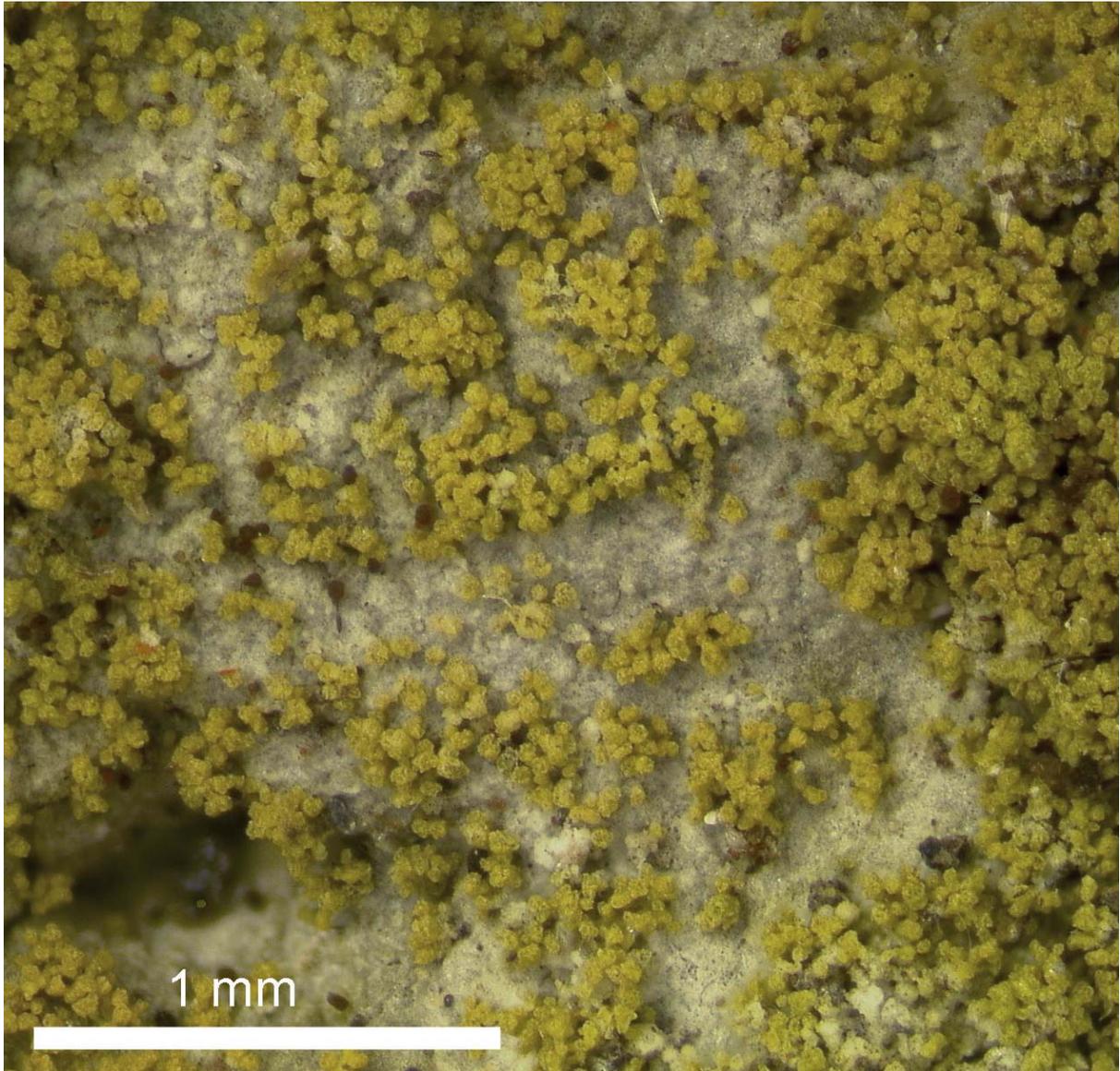


Thallus superficial or partly immersed, thin, grey-green to grey-ochre or pale orange. Isidia present, dull orange, isodiametric when young, becoming cylindrical and branched, fragile, remaining discrete or forming nodular-coralloid mats in which the individual isidia are difficult to distinguish; isidia up to 290 μm high, branches 30–100 μm wide, with a thin and inconspicuous cortex (Figs. NEW). Perithecia occasional, black, 0.5–0.75-immersed, to 700 μm diam. Involucrellum purplish brown, K + dark grey-brown. Asci rounded at the apex, without a ring structure.

Ascospores (7–)12–16(–17)-septate, (55–)60–90(–95) × 5–7(–8) μm.

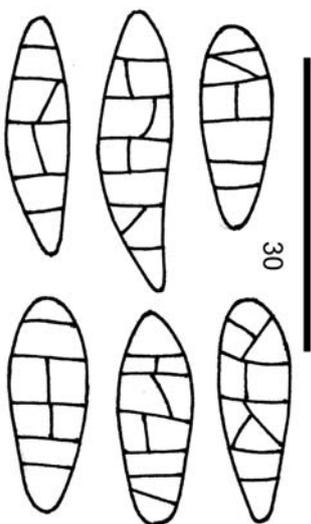
On rather dry base-rich bark of mature *Quercus* in ancient woodland and parkland, sometimes overgrowing bryophytes; rare, very locally frequent. S. England (New Forest, Hampshire; Boconnoc Park, Cornwall), N. Wales (Merioneth, Cardigan), S.W. Scotland (Castle Kennedy, Wigtown), S.W. Ireland (Killarney). France, Spain (Navarra, W. Pyrénées), Czech Republic.

Sterile specimens are similar to *P. rosei*, which differs in the usually more slender isidia with a well-developed cortex forming a colourless layer around the photobiont (Fig. NEW).



Porina hibernica (14033).

***Porina interjungens* (Nyl.) Zahlbr. (1922)**

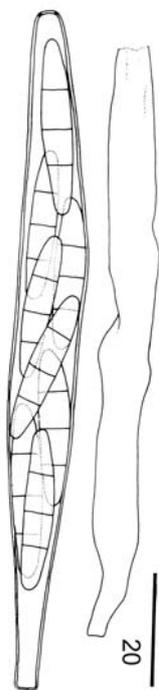


Thallus superficial, grey to dark brown, continuous to cracked. Perithecia black, 220–400 µm diam., 0.3–0.5-immersed in thallus. Involucrellum purple-brown, K + grey or grey-brown. Exciple almost colourless below, yellow above (Porina-yellow). Ascospores narrowly ellipsoid, with (4–)5–7 transverse septa, and 1–4 longitudinal septa, 20.5–29(–34.5) × (6–)7–8(–10) µm, 2.5–4.5 times as long as wide.

On damp siliceous rocks, shaded or unshaded, on cliffs and by rivers and lakes, rare. Scotland, N.W. England (Lake District), Wales, S.W. England (Devon). Norway, Sweden, Belgium.

Porina guentheri var. *lucens* also has longitudinal septa in some of the ascospores, but the ascospores in that species are longer and narrower.

Porina lectissima (Fr.) Zahlbr. (1903)



Thallus superficial, well-developed, continuous or cracked, pale ochre to orange-brown, reddish brown or brownish green. Perithecia red-brown (brighter red when wet) to black (often black only at apex), 0.25–0.3-immersed, 220–500 μm diam. Involucrellum thick, containing photobiont cells, orange (Porina-yellow). Ascus with ring structure. Ascospores 3-septate, 16–30(–40) \times 4–8 μm . Pycnidia orange, more or less immersed. Conidia narrowly ellipsoid to cylindrical, 3–4.5 \times 0.7–1 μm .

On damp siliceous rocks on flushed outcrops and in seepages, and beside rivers and lakes, often forming extensive patches, sometimes in frequently inundated situations, especially in shade, locally abundant. N. and W. British Isles. Norway, Sweden, Finland, Germany, Alps, Italy, Slovakia, N. America.

Usually recognized in the field by the large perithecia which are orange or reddish when wet. *P. ahlesiana* differs in the 7-septate ascospores, *P. leptalea* differs in the smaller perithecia.

Porina leptalea (Durieu & Mont.) A.L. Sm. (1911)

Thallus superficial, very thin, smooth or finely granular, grey-green to dark olive-green. Perithecia 100–300 μm diam., 0.25–0.5-immersed, brownish orange. Involucrellum orange (Porina-yellow), containing numerous photobiont cells. Exciple colourless to yellow. Ascospores 3-septate, 14.5–23 \times 3.5–5 μm . Pycnidia c. 100 μm diam., red-brown. Conidia ellipsoid to cylindrical, straight to slightly curved or dumb-bell-shaped, 1.7–2.5 \times 1 μm .

On bark of broad-leaved trees (*Alnus*, *Fagus*, *Ulmus*, *Corylus*, *Ilex* and others), but also frequent on the bases of conifers in plantations; also on damp rocks and stones, shade-tolerant, frequent. W. Britain, Ireland. Sweden, W. and Middle Europe, Slovakia, N. America, N. and S. Africa, Australia (Tasmania), New Zealand, Pacific Islands.

P. lectissima has larger perithecia and ascospores, and *P. aenea* and *P. chlorotica* have blackish perithecia.

Porina leptospora Nyl. (1864)

Porina leptospora (Nyl.) D. Hawksw.

Like *P. borreri*, but with narrower ascospores 30–55 \times 3–4 μm .

On *Ilex*. S.W. Ireland (Killarney). Macaronesia

Porina linearis (Leight.) Zahlbr. (1922)

Thallus endolithic to thinly superficial in part, continuous or cracked, pink, grey or discoloured brownish. Perithecia black, 240–400 μm diam., 0.5-immersed in pits in the rock to more or less superficial. Involucrellum purple-violet to purplish brown, K + dark blue-grey to grey-brown.

Ascospores 3-septate, $(15.5-16.5-22(-23.5) \times (3.5-4-6(-7)) \mu\text{m}$. Pycnidia black, more or less immersed in pits. Conidia oblong, straight to slightly curved, $3.3-4.5 \times 1.2 \mu\text{m}$.

On shaded and sheltered hard limestone, sometimes forming extensive patches in shaded overhangs, locally frequent. Throughout British Isles. Europe from Norway and Sweden to Greece, N. America.

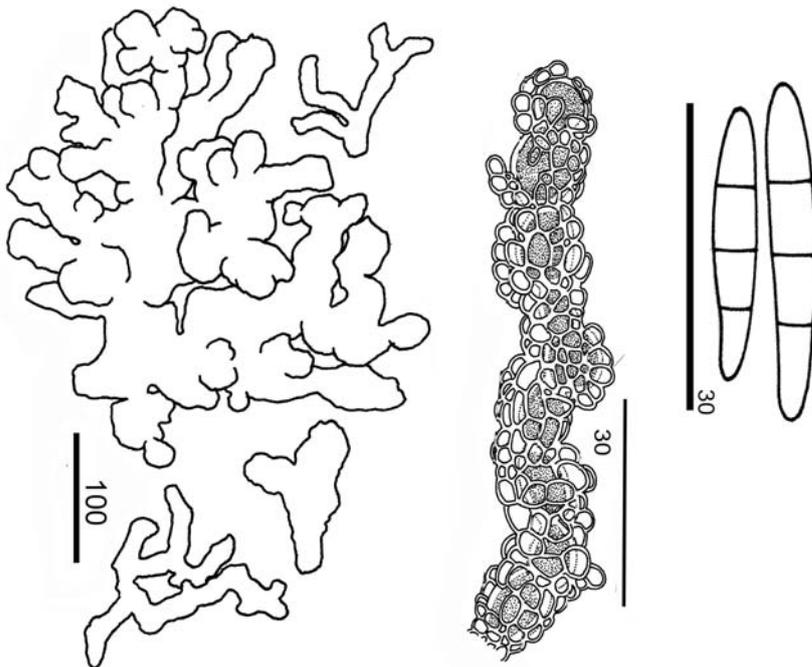
P. byssophila differs in the well-developed epilithic thallus. Easily confused in the field with *Arthopyrenia saxicola*, which has 1-septate ascospores.

Porina mammillosa (Th. Fr.) Vain. (1922)

Thallus smooth or \pm granular, rather thick, nodular, warted, effuse, blackish grey or green-grey often tinged brown-purple. Perithecia 300–500 μm diam., globose, partly covered by a thalline layer. Involucrellum thick, dark, with purple, K + blue-grey pigment (Sagedia-red), inner layers pinkish orange (Porina-yellow). Exciple yellow to pale orange. Ascospores 3-septate, $25-40 \times 4-6 \mu\text{m}$. Pycnidia unknown.

On bryophytes, small woody plants and soil in more or less protected or sheltered soil crevices of mountain rocks, also at lower altitudes, rare. N. Scotland (Ben Lawers, Cairngorm, Caenlochan), W. Ireland (Connemara, Galway). Norway, Sweden, Switzerland, Italy, 'U.S.S.R.', N. America, Japan.

Porina rosei Sérus. (1990)



Thallus superficial, thin, grey-green to grey-brown. Isidia present, ochre to orange-brown when fresh, scattered to crowded, simple or frequently becoming branched and coralloid, often forming mounds of congested branches, up to 180 μm high, branches 25–50 μm wide, sometimes containing only a single filament of the photobiont, with a well-defined cortex which often forms a colourless surrounding to the branch.

Perithecia very rare, pale dull orange, sometimes same colour as thallus below, 360–400 μm diam., 0.25–0.5-immersed. Involucrellum and exciple yellow (Porina-yellow). Ascus apex with a ring structure. Ascospores 3-septate, $22-33 \times 4-6(-7) \mu\text{m}$. Pycnidia yellow; conidia bacilliform, $4.5-5.7 \times 1.5 \mu\text{m}$.

On usually base-rich bark of *Quercus*, *Fraxinus* or *Taxus*, rarely overgrowing bryophytes on calcareous rock, in ancient woodland, rare. S. England (New Forest, Hampshire), Wales. Spain (Navarra), France (Vercors and W. Pyrénées), Madeira.

Found fertile once in Britain (S. Wales). Sterile specimens are similar to *P. hibernica*, which typically has larger isidia with a poorly defined cortex.

Porina sudetica (Körb.) Lettau (1912)

Thallus overgrowing bryophytes. Perithecia black. Involucrellum dull purple, K + dark grey to brown. Ascospores 3–5-septate (up to 7-septate when overmature), 25–39 × 3.5–8 µm.

On bryophytes on slightly basic siliceous montane rock, or on heavy-metal-rich scree, very rare. S.W. England (W. Cornwall: Botallack), Scotland (Mid Perthshire).

Apparently close to *P. mammillosa*, which differs in the 3-septate ascospores. The pigments in British material of *P. sudetica* may also differ from those in *P. mammillosa*; a wider range of material of the two species should be compared.

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PROTOTHLENELLA Räsänen (1943)

Thallus not lichenized, or distinctly lichenized and then crustose, granular to cracked-areolate, margin effuse, usually bright green when fresh, whitish to grey-brown when dry, ± gelatinous when wet, anatomically hardly differentiated. **Photobiont** *Elliptochloris bilobata*, or absent. **Ascomata** perithecia, mostly single and scattered, immersed, globose to pear-shaped, dark brown to blackish. **Involucrellum** absent. **True exciple** brown to greenish blue in upper part, mostly colourless towards the base, of strongly anastomosing, to 1 µm wide, conglutinate hyphae with narrow lumina. **Hamathecium** of paraphysoids, persistent, strongly branched and anastomosed; periphysoids absent. **Hymenial gel** hemiamyloid: I + dull red (I + blue at low concentrations of iodine), I after K + blue. **Asci** (6–)8-spored, ± cylindrical, thick-walled, (2–5 µm) with two functional wall layers, the outer wall layer I + dull reddish, I after K + blue, the apex with an I + blue, ± layered *Xylaria*-like apical apparatus (Fig. 9C). **Ascospores** colourless, transversely multi-septate, submuriform or strongly muriform, the outer wall distinctly thicker than the septa. **Conidiomata** not known. **Ecology**: lichenized taxa on acid substrata including rocks, soil, mosses, plant detritus or wood, in moist situations; non-lichenized taxa lichenicolous or on living mosses. **Chemistry**: unidentified C + red substance, or lichen substances absent.

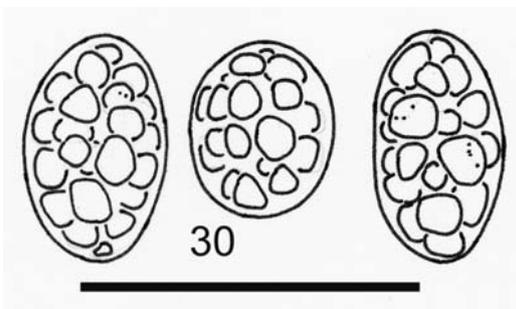
Classification: Ostropomycetidae, Protothelenellaceae.

Polyblastia differs in the absence of interascal filaments and the I – ascus. *Thelella* differs in the I – ascus. *Protothelenella leucothelia* (Nyl.) H. Mayrhofer & Poelt (1985) has been incorrectly reported from the British Isles; it has a whitish, C + red thallus and grows on decaying bryophytes or on soil.

LITERATURE: Mayrhofer & Poelt (198), Mayrhofer (1987)

- 1 Ascospores elongate to elongate-ellipsoid; on wood, soil, decaying plants, mosses and other lichens; thallus C – 2
Ascospores broadly ellipsoid; on rocks; thallus often C + red **corrosa**
- 2(1) Ascospores 22–33 × 7–10 µm, submuriform; perithecia <0.3 mm diam.
..... **sphinctrinoidella**
Ascospores 38–50 × 10–15 µm, strongly muriform; perithecia 0.4–0.6 mm diam.
..... **sphinctrinoides**

Protothelenella corrosa (Körb.) H. Mayrhofer & Poelt (1985)



Thallus smooth to granular-uneven, warted, or forming a cracked crust; often in ± dispersed areoles surrounding single or several perithecia, or inapparent, dirty yellowish, green or brownish white. Perithecia 0.2–0.5 mm diam., scattered, rarely 2–3 contiguous, partly immersed, forming low to prominent black projections, apex often a with a small central depression, exciple pigmented in upper half, dull greenish brown, K + brown going into solution; lower part colourless.

Ascospores 18–32 × 10–15 µm, muriform, broadly ellipsoid or ovoid. Thallus often C + red.

On damp siliceous rocks on flushed faces, boulders, scree and beside streams; very local. Upland Britain, Ireland. C. & N. Europe, U.S.S.R., Canada.

The green colour of some specimens is striking in the field, suggesting free-living algae rather than a lichen.

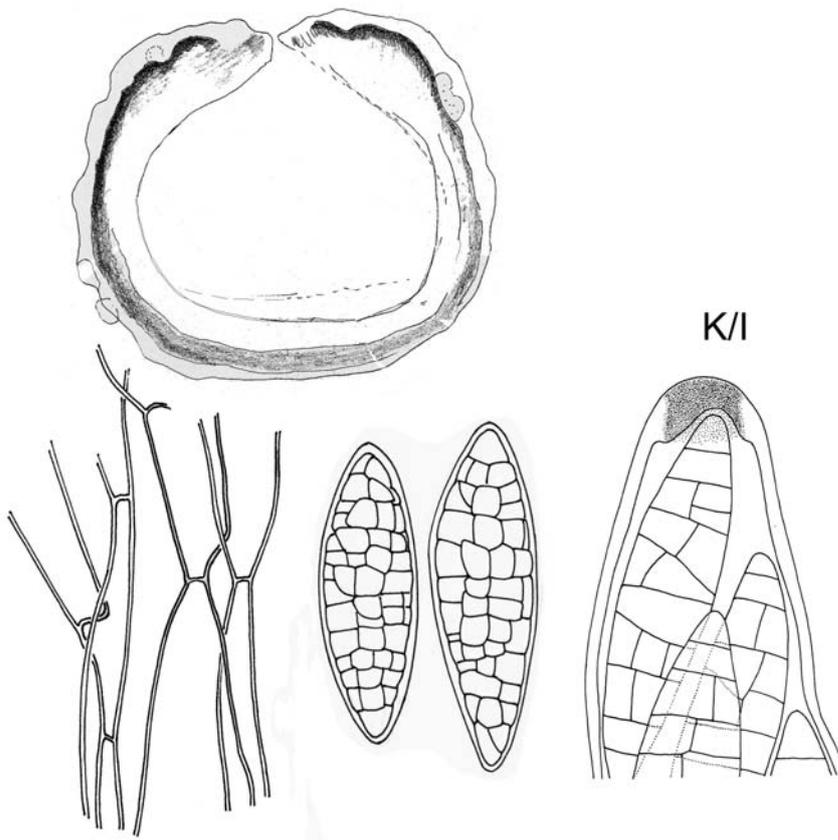
Protothelenella sphinctrinoidella (Nyl.) H. Mayrhofer & Poelt (1985)

Thallus indistinct, thin, membrane-like or diaphanous, evanescent, pale grey or dirty white, greenish when fresh. Perithecia 0.1–0.3 mm diam., superficial sessile to quarter-immersed, black, ± shiny, rounded to ± pyriform, single, very rarely 2–4 contiguous; true exciple dark brown above, ± opaque, paler below, sometimes colourless, semi-opaque to translucent; ostiole sometimes extended as a short papilla. Ascospores 22–23 × 7–10 μm, elongate or elongate-ellipsoid, submuriform, with 7–9 transverse and 4–6 longitudinal septa in optical section of each spore.

Overgrowing hepatics on acid soils or rocks, mainly above 600 m. N. Scotland (Highlands, especially Breadalbane and Cairngorm Mtns.). Fennoscandia, Portugal, Pyrénées, Alps, U.S.S.R., N. America.

Differs from *P. sphinctrinoides* in the smaller perithecia and smaller, submuriform spores. The thallus may be almost absent and partially saprophytic with few associated photobiont cells.

Protothelenella sphinctrinoides (Nyl.) H. Mayrhofer & Poelt (1985)



Thallus thin, film-like to finely warted, evanescent, dirty white when dry, greenish or pale brown, at times gelatinous when wet. Perithecia 0.4–0.6 mm diam., one-third to completely immersed, rounded or ± pyriform, scattered, brown to black, paler when wet; exciple densely pigmented above, brown, K –, pale brown to more or less colourless below; above with a superficial colourless layer c. 10 μm thick; ostiole sometimes depressed. Ascospores 38–50 × 10–15 μm, ellipsoid to broadly spindle-shaped, strongly muriform, with up to 4 longitudinal walls per tier of cells in optical section in middle part of spore.

Overgrowing bryophytes on acid soils or over schistose or granitic rocks, above 800 m. N. Scotland (Highlands, Breadalbane and Cairngorm Mtns.). Europe, from the Alps to N. Fennoscandia, U.S.S.R., Spitzbergen, Greenland, U.S.A.

P. sphinctrinoidella differs in the smaller, submuriform ascospores. *Thelenella muscorum* has larger ascospores and an I – ascus apex.

Literature:

Mayrhofer, H. (1987) Ergänzende Studien zur Taxonomie der Gattung *Protothelenella* . *Herzogia* **7**: 313-342.

Mayrhofer, H. & Poelt, J. (1985) Die Flechtengattung *Microglaena* sensu Zahlbruckner in Europa. *Herzogia* **7**: 13-79 (1985).

PSOROGLAENA Müll. Arg. (1891)

Macentina Vězda (1973)

Thallus crustose or minutely filamentous, cortical cells often with small papillae. **Photobiont** green (Trebouxiophyceae). **Ascomata** perithecioid, 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 elongated in section, sometimes with a surface layer of isodiametric cells. **Hamathecium** of periphyses, interascal filaments absent, gel I + red. **Asci** 1–8-spored, fissitunicate, clavate-cylindrical, thickened at apex when young, I–. **Ascospores** 8–26 × 2–6 µm, transversely (1–)3-septate to submuriform, elongate-ellipsoid, smooth, without a perispore, colourless. **Conidiomata** unknown. **Chemistry:** lichen products not detected. **Ecology:** on bark, leaves, bryophytes on leaves, rock and mossy soil.

Classification: Chaetothiomycetidae, Verrucariales, Verrucariaceae.

A genus of approximately ten species in tropical and temperate regions, united by the usually papillose hyphae (often inconspicuous) and usually pale ascomata. *Macentina aurantiaca* McCarthy & Vězda (1985) is a synonym of the non-lichenized *Nectria pseudopeziza* (Desm.) Rossman (1979).

LITERATURE: Coppins & Vězda (1977), Orange (1989).

- 1 Amongst bryophytes and other lichens over rock; perithecia three-quarters to completely immersed in the substratum; ascospores 1-septate (3-septate when overmature?)
..... **infossa**
On bark; perithecia prominent 2
- 2(1) Thallus minutely filamentous, often disintegrating into soredia-like granules; perithecia 200–380 µm wide; ascospores 3–5-septate **stigonemoides**
Thallus immersed or thin and leprose; perithecia 80–120 µm wide; ascospores 1–3-septate
..... **abscondita**

Psoroglaena abscondita (Coppins & Vězda) Hafellner & Türk (2001)

Macentina abscondita Coppins & Vězda (1977)

Thallus superficial, very thin, leprose, dull green; cortical hyphae with inconspicuous papillae. Perithecia 80–120 µm wide, pale brown when dry, almost translucent and colourless when wet; exciple 10–12 µm thick, colourless or pale yellowish. Asci clavate-cylindrical or sometimes pyriform. Ascospores 12–20 × 3.5–4.5 µm, 1–3-septate.

In fissures of bark of *Sambucus* or on stems of shaded *Juniperus* in coastal scrub. S.E. England (West Kent, East Sussex), N.E. Scotland (East Ross). Poland

Psoroglaena infossa Orange ad int.

Thallus grey-green, green, or yellowish green; granular-verrucose, or finely granular with loose granules 20–30 µm diam.; thallus composed of goniocysts 20–40 µm diam., rather readily separating from each other in water mounts; surface layer of goniocysts of fungal cells ± isodiametric and 3.5–10 × 3–6.5 µm in surface view, colourless, sometimes bearing papillae 0.8–1.2 µm high; some surface cells occasionally strongly convex. Perithecia three-quarters immersed to completely immersed in the substratum, orange-pink, 335–495 × 270–365 µm, pyriform, the upper part often narrowed to apex. Exciple 35–100 µm thick at sides and base, and here usually of 3 layers: 1. an innermost layer of slightly compressed cells 5.5–18 × 5.5–9 µ, the walls thin, with a combined thickness of c. 0.5 µm

thick or less, 2. a middle layer of tangentially compressed cells $4\text{--}12.5 \times 1.5\text{--}4\text{--}(6.5)$ μm , with thick walls with a combined thickness of $1.2\text{--}2.5$ μm thick, 3. an outermost layer of isodiametric or slightly flattened cells $3\text{--}5.5 \times 3\text{--}5$ μm , walls slightly thickened, with a combined thickness of $0.8\text{--}1.2$ μm thick. Exciple layers of variable thickness, the outer layer sometimes thin, and locally grading into a hyphal layer associated with the gonocysts, and sometimes enclosing free-living algae and debris; the innermost layer is present around the sides and base of the hymenium, but above gives rise to the periphyses; in the upper part of the exciple, middle layer with cells c. $6.5\text{--}9 \times 3\text{--}4$ μm , in rows, walls with a combined thickness of up to 2.5 μm ; these rows turn outwards towards the surface of the perithecium, where they grade into more or less isodiametric cells $2.5\text{--}6.5 \times 2.5\text{--}5$ μm . All cells walls in the exciple without pigment, but cells contain orange oil droplets, especially the innermost layer. Hamathecium of branched and anastomosing periphyses up to 110×1.5 μm , forming a lining to the neck canal; interascal filaments absent. Asci 8-spored; mature and healthy asci not seen. Ascospores colourless, 1-septate (rarely 3-septate when over-mature?), ellipsoid, $(10.5\text{--})11.5\text{--}12.5\text{--}13.5\text{--}(14.5) \times 5.5\text{--}6.0\text{--}6.5\text{--}(7)$ μm , length/width ratio $(1.6\text{--})1.9\text{--}2.1\text{--}2.3\text{--}(2.5)$ [39/2], smooth, thin-walled, without perispore

In thin crusts of lichens and acocarpous mosses growing over more or less calcareous substrata including calcareous stones, concrete blocks, and a tarmac garden path; rare or overlooked. Wales, England.

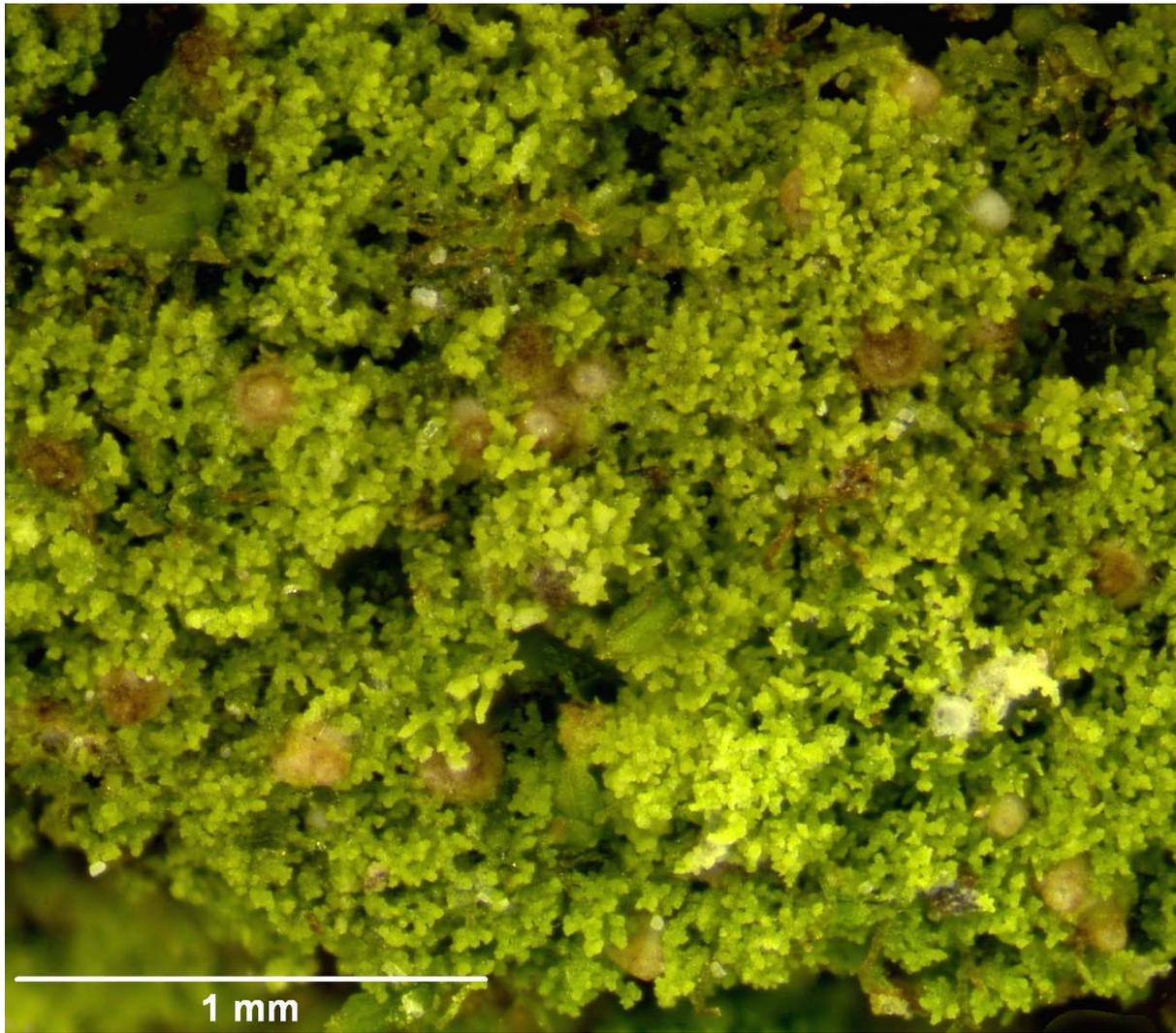
Psoroglaena stigonemoides (Orange) Henssen (1995)

Macentina stigonemoides Orange (1989)

Thallus $50\text{--}400\text{--}(600)$ μm tall, minutely fruticose, densely branched, branches $12\text{--}35$ μm wide, cylindrical, \pm prostrate or more frequently ascending; cortical cells with papillae c. 1 μm high; thallus locally disintegrating into soredia-like granules $15\text{--}40$ μm diam., the superficial cells often prominent and bearing one or more papillae. Perithecia $200\text{--}380$ μm wide, pale brown, ovoid or \pm obpyriform; exciple $30\text{--}80$ μm thick, the median layer of elongated cells, the outer layer of isodiametric cells. Asci fusiform-cylindrical. Ascospores $(13\text{--})16\text{--}21 \times (4\text{--})5\text{--}6$ μm , $3\text{--}4\text{--}(5)$ -septate.

On shaded bark in species-poor, bryophyte-dominated communities, mainly on *Sambucus* and *Ulmus*, in humid situations, frequent. Throughout British Isles. France.

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.



Literature:

Coppins, B.J. & Vězda, A. (1977) *Macentina*, a lichen genus new to Europe. *Lichenologist* **9**: 47-49.

Orange, A. (1989) *Macentina stigonemoides* (Verrucariaceae), a new lichenized species from Great Britain and Ireland. *Lichenologist* **21**: 229-236.

PYRENULA Ach. (1814) nom. cons.

Thallus crustose, immersed, or more rarely superficial, more or less continuous to sometimes areolate; pseudocyphellae sometimes present. **Photobiont** *Trentepohlia*, rarely apparently absent. **Ascomata** perithecia, immersed to erumpent, more or less globose to flattened, black. **Involucrellum** spreading laterally to developed around and closely adhering to the exciple, from which it is then not distinct, composed of filamentous hyphae interspersed with bark cells and often crystals. **Exciple** pigmented; pigment brown, K + darker brown (at least in British and Irish species), often containing colourless calcium oxalate crystals (insoluble in K, soluble in 10% HCl). **Ostiole** central or lateral. **Hymenium** with gel I – or + greenish blue in parts, sometimes densely interspersed with minute oil droplets, lateral parts sometimes with masses of orange-brown, K + purple-red pigment (anthraquinones). **Hamathecium** at first of branched and anastomosed, sparsely septate periphysoids; more or less unbranched paraphyses developing later and replacing the periphysoids; ostiole with paraphyses. **Asci** cylindrical, long-stalked, multilayered in structure, apex thickened, with an internal apical beak and a refractive subapical cap, I –, discharge fissitunicate, the different wall layers extending to different extents. **Ascospores** ellipsoid to narrowly ellipsoid or broadly fusiform, apices rounded to apiculate, 3-septate to muriform, very thick-walled, distoseptate, cell lumina appearing lenticular to angular; colourless to olivaceous or dark brown, smooth-walled, without a perispore. **Conidiomata** pycnidia, more or less globose, black (pigment like exciple), unilocular or divided into chambers. **Conidia** more or less thread-like to strongly curved, simple, colourless. **Chemistry**: lichexanthone, unidentified anthraquinones, other unidentified substances, or lichen substances absent. **Ecology**: on more or less smooth bark surfaces in humid situations.

Classification: Chaetothyriomycetidae, Pyrenulales, Pyrenulaceae.

A predominantly tropical genus of about 200 species, poorly represented in Europe. Features used to identify the British and Irish species include: presence of pseudocyphellae (appearing as small whitish dots on thallus surface), size of perithecia (in most species it is sufficient to measure the diameter of the blackish perithecia *in situ*), and presence of anthraquinones. Anthraquinones can be detected by mounting a section of perithecium and thallus in water, and drawing K under the coverslip; anthraquinones will give a purplish-red solution; this reaction is often strong enough to be also easily seen under the dissecting microscope.

LITERATURE: Harris (1995).

- 1 Ascospores (1–)3-septate; perithecia various, not in radial groups 2
Ascospores muriform; perithecia large, with lateral ostioles, often arranged in radial groups **hibernica**
- 2 Involucrellum not or slightly extended laterally, exciple pigmented throughout; ascospores often larger; photobiont present 3
Involucrellum much extended laterally; pigmented exciple not continuous below perithecial cavity; ascospores 10–17 µm long; photobiont probably absent **coryli**
- 3 Thallus immersed, UV – or + pale yellow or whitish (unidentified substances, lichexanthone absent); perithecia conspicuous, appearing black even when covered by a thin layer of bark 4
Thallus superficial, UV + yellow-orange (lichexanthone); perithecia immersed in thallus and visible only by the ostiole, sometimes exposed as black discs up to 0.38 mm diam. **dermatodes**
- 4 Perithecia 0.2–0.4 mm diam., forming at most low projections in the thallus 5
Perithecia 0.4–1.2 mm diam., forming distinct projections in the thallus 6
- 5 Hymenium at sides with masses of an orange-brown pigment, K + purple-red solution **nitidella**

- Hymenium K – **chlorospila**
- 6 Ostiole central 7
 Ostiole lateral; thallus without pseudocyphellae, all parts of perithecium lacking K + purple-red substances **acutispora**
- 7 Perithecium with K + purple-red substances on upper surface or within hymenium; hymenium densely inspersioned with oil droplets or not 8
 Perithecium lacking K + purple-red substances; hymenium not inspersioned 9
- 8 Hymenium with lateral parts containing an abundant orange-brown pigment which is K + purple-red going into solution; not inspersioned with oil droplets; thallus sometimes with pseudocyphellae **nitida**
 Hymenium without K + purple-red substances, but these present on outer surface of perithecial apex (sometimes sparse); inspersioned with oil droplets; pseudocyphellae absent **occidentalis**
- 9 Pseudocyphellae present; ascospores (24–)27–33(–36) μm long; perithecia not or scarcely flattened in section **macrospora**
 Pseudocyphellae absent; ascospores (14–)17–22(–26) μm long; perithecia often flattened in section **laevigata**

Pyrenula acutispora Kalb & Hafellner (1992)

Pyrenula microtheca auct.

Thallus immersed, pale yellow-grey; pseudocyphellae absent. Perithecia 0.54–0.8 mm diam., forming projections in thallus; ostiole excentric to lateral. Hymenium not inspersioned, anthraquinones absent (K –). Ascospores (17–)20–25(–27) × (7.5–)8–10.5(–11.5) μm, 3-septate. Thallus PD –, K –, C –, UV – (lichen substances absent). [?]

On smooth bark, rare. N. Wales (Merioneth), N.W. England, W. Scotland, S.W. Ireland. Distinguished from all British species except *P. hibernica* by the lateral ostioles.

Pyrenula chlorospila Arnold (1887)

Thallus olive-green to pale brown or fawn; pseudocyphellae 40–120 μm diam., white. Perithecia small, 0.2–0.4 mm diam., often rather densely arranged, forming very low projections in the thallus or not forming projections. Exciple containing colourless crystals. Hymenium not inspersioned with droplets [?], without anthraquinones. Ascospores (25–)28–32(–35) × (9–)11–13(–14) μm, 3-septate. Thallus PD + faintly yellow, K + yellow, KC –, C –, UV – or + whitish (unidentified substance).

On smooth, shaded bark of deciduous trees, often with *P. macrospora*; locally abundant. S. and W. British Isles. Denmark, Portugal, France, Italy, Greece.

Distinguished in the field by the small perithecia which scarcely project from the thallus. Most pre-1980 records of *P. nitidella* refer to this species.

Pyrenula coryli A. Massal. (1852)

Mycopyrenula coryli (A. Massal.) Vain. (1921)

Thallus pale grey; pseudocyphellae more or less absent; probably lichenized. Perithecia 0.2–0.3 mm diam. and c. 0.1 mm high, with a laterally extending involucrellum; pigmented exciple not continuous

below the perithecial cavity; anthraquinones absent. Ascospores $10\text{--}17 \times 4\text{--}6 \mu\text{m}$, 3-septate. Pycnidia scattered amongst the perithecia; conidia $20 \times 0.5 \mu\text{m}$, thread-like.

On *Corylus* bark, very rare. North Wales (Merioneth), N. and W. Scotland (Westernness, West Sutherland). C. and N. Europe, but rarely recorded this century.

In the field difficult to separate from species of *Arthopyrenia* and *Eopyrenula*. Sometimes treated in a separate genus due to the non-lichenized habit, but other characters are similar to other species of *Pyrenula*.

Pyrenula dermatodes (Borrer) Schaer. (1850)

Thallus superficial, yellowish green to more or less orange-rust coloured, fading to pale yellow-brown in the herbarium, continuous to finely cracked or areolate; pseudocyphellae absent. Perithecia 0.2–0.44 mm diam. (in section), completely immersed in thallus, forming at most very low projections, with only the grey ostiole *c.* $50\text{--}60 \mu\text{m}$ diam. visible from above, or sometimes perithecia becoming exposed as a black disc up to $380 \mu\text{m}$ diam. Hymenium not interspersed with oil droplets, without anthraquinones (K–). Ascospores $14\text{--}19 \times 6.5\text{--}7.5\text{--}(8.5) \mu\text{m}$, 3-septate. Conidia curved, *c.* $15 \mu\text{m}$ long. Thallus PD –, K ?+ orange-red in places, KC –, C –, UV + yellow-orange (lichexanthone).

On smooth bark of *Corylus*, *Crataegus*, *Fagus*, *Ilex* and *Sorbus* in oceanic woodlands, rarely on shaded siliceous rocks; very rare. N. Scotland (Knoydart in West Inverness), locally frequent in S.W. Ireland, extending north to Donegal; not known elsewhere in Europe. Macaronesia, India, China, South America.

Distinguished by the superficial, often cracked, thallus which is UV +, and by the (at least initially) very inconspicuous immersed perithecia.

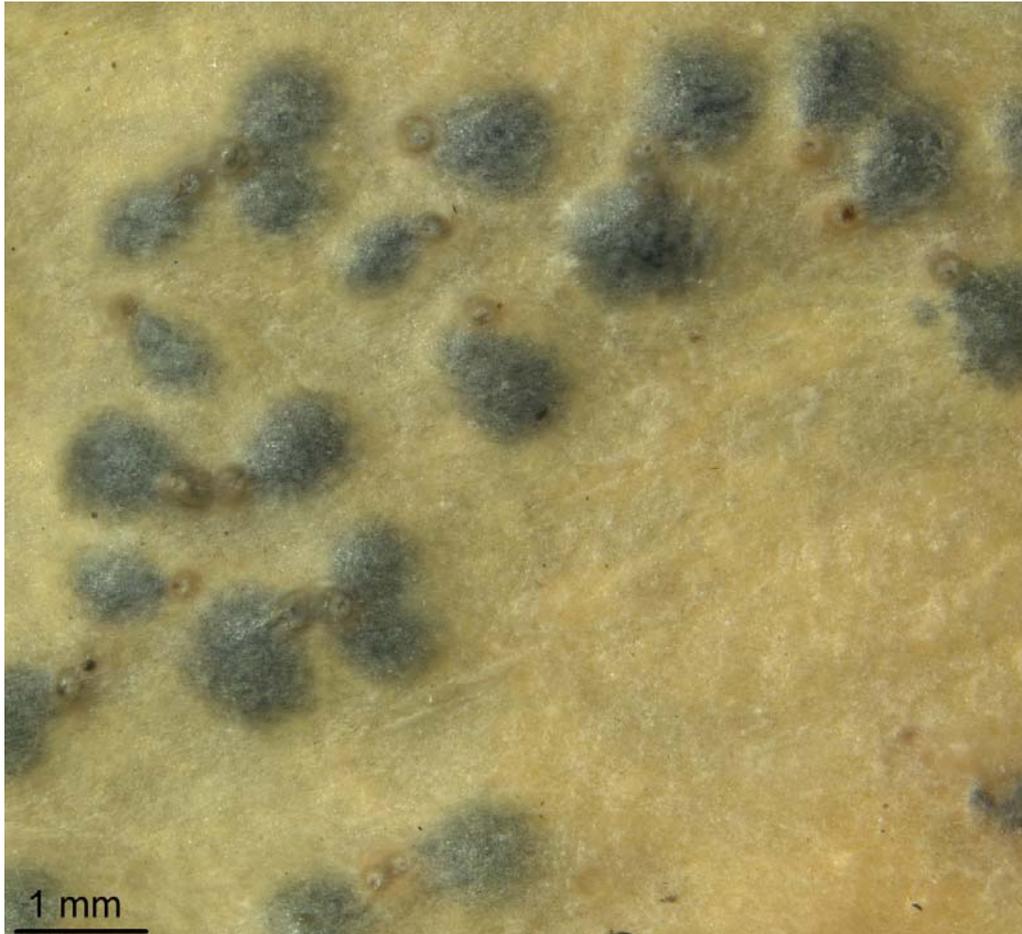
Pyrenula hibernica (Nyl.) Aptroot (2003)

Pyrenula chilensis auct., non (Fée) R.C. Harris (1989), *Parmentaria chilensis* auct., non Fée (1838)

Thallus immersed, pale olive-green or yellow-buff, sometimes with white dots, smooth, continuous; with age becoming rougher and rarely cracked. Perithecia 1–1.2 mm diam., black, arising 1–1.5 mm below the surface; only the pale ostiole visible at surface, or perithecia visible through translucent surface of thallus; occurring singly, or radially arranged in groups of 2 to 5; ostioles lateral, often joined, visible as a pale yellow- or orange-brown depression or disc at surface of thallus. Asci 4–8-spored. Ascospores muriform, brown when mature, $(57\text{--})70\text{--}135\text{--}(140) \times (24\text{--})26\text{--}47\text{--}(55) \mu\text{m}$, oblong to fusiform-ellipsoid. Pycnidia *c.* 2 mm dia., divided into chambers. Conidia $24\text{--}27 \times 1 \mu\text{m}$. Thallus PD –, K –, KC –, C –, UV + light yellow (lichen products not tested by TLC).

On smooth bark of *Corylus* and *Ilex* in very sheltered, moist ravines at *c.* 100 m altitude; very rare. N. Wales (Merioneth: Ceunant Llennyrch), W. Scotland (Westernness: Loch Sunart), S.W. Ireland (Kerry: Killarney). Canary Islands, Azores (erroneously reported from N. & S. America).

Distinguished by the large, immersed perithecia with lateral ostioles, arranged in groups, and the muriform ascospores. The perithecia are very striking when visible through the upper layers of the thallus, but sometimes they are very inconspicuous, detectable in surface view only by the pale ostioles.



Pyrenula hibernica.

***Pyrenula laevigata* (Pers.) Arnold (1885)**

Thallus immersed, silvery or cream to pale yellow-brown; pseudocyphellae absent. Perithecia 0.45–0.66 mm diam., forming projections in the thallus, somewhat flattened in section, with an involucrellum separable from the exciple and spreading somewhat. Hymenium not containing anthraquinones, K –. Ascospores (14–)17–22(–26) × (7–)8–9(–11) μm, 3-septate. Pycnidia black, up to c. 100 μm diam., scattered or in lines. Conidia 10–19 × c. 0.5 μm, curved. Thallus PD–, K + yellow [why?], KC –, C –, UV –.

On smooth bark, especially of *Corylus*, in oceanic woodlands; local. S.W. England (N. Devon), N. Wales (Cardigan, Merioneth), W. Scotland, S.W. Ireland (Clare, Kerry, Cork). Macaronesia (Canary Islands), Europe, E. North America.

This status of this taxon in the British Isles deserves closer study, as the species is primarily continental in distribution. A K + fleeting blue reaction has been reported in the hymenium of this species, but has not been detected in British or Irish material.

***Pyrenula macrospora* (Degel.) Coppins & P. James (1980)**

Thallus olivaceous or fawn to dark brown; pseudocyphellae 40–120 μm diam., white. Perithecia (0.4–)0.5–0.9(–1.2) mm, forming convex projections. Exciple containing numerous colourless crystals. Hymenium not containing anthraquinones. Ascospores (24–)27–33(–36) × (8–)10–13 μm, 3-septate. Pycnidia visible as dark dots 100–180 μm diam., frequent, mostly in young parts of thallus, often clustered along junctions between adjacent thalli. Conidia curved, 10–16 × 0.8 μm. Thallus PD + faintly yellow, K + yellow, KC –, C –, UV – or weak yellow (unidentified substance).

On smooth, more or less shaded bark of deciduous trees, locally common. Throughout south and west British Isles. Strongly oceanic; Macaronesia (Tenerife, Madeira), Europe from Scandinavia to Portugal, Turkey.

The commonest British species of the genus. Most pre-1980 records of *P. nitida* from Britain and Ireland region refer to this species. Distinguished in the field from most other species by the large perithecia and presence of pseudocyphellae. The rare *P. nitida* differs in the K + red substance flanking the inner exciple and the smaller ascospores. Often grows with *P. chlorospila*, which differs in the smaller perithecia which scarcely form projections in the thallus.

Pyrenula nitida (Weigel) Ach. (1814)

Thallus olive brown to dark brown or yellow-brown; pseudocyphellae often absent, but sometimes frequent, 50–75 µm diam., whitish. Perithecia 0.6–0.8(–1) mm diam. Exciple containing colourless crystals. Outer part of hymenium adjacent to exciple with orange-brown (by transmitted light) masses of anthraquinone, K + purple-red going into solution. Hymenium with oil drops sparse or absent. Ascospores (17–)19–24(–26) × 6–8(–9) µm, 3-septate. Conidia *c.* 16.5–19 × 0.8 µm, curved. Thallus PD –, K + orange-red, KC + reddish, C–, UV – (unidentified anthraquinones).

On smooth, dry, shaded bark of old deciduous trees, including *Carpinus* and *Fagus*; very rare. S. England (Buckingham, E. Kent, Hampshire, Sussex). Europe, avoiding highly oceanic areas.

Most pre-1980 British records of this species refer to *P. macrospora*. *P. nitida* is primarily a continental species, as reflected by its distribution in Britain.

Pyrenula nitidella (Flörke ex Schaer.) Müll. Arg. (1885)

Thallus olive-brown to fawn; pseudocyphellae 50–75 µm diam., often sparse, whitish. Perithecia 0.2–0.3(–0.35) mm diam. Hymenium not interspersed with oil droplets, at sides with K + purple-red material. Ascospores (20–)22–26(–28) × (8–)8.5–11(–12) µm, 3-septate. Thallus PD –, K + yellow to pale orange in parts, KC –, C –, UV – (unidentified anthraquinones).

On smooth bark of deciduous trees; extinct. Known from only two certain records; England (N.E. Yorkshire), Scotland (E. Perthshire). Europe. Most pre-1980 records of this species in Britain and Ireland refer to *P. chlorospila*, which differs in the lack of anthraquinones in the perithecia.

Pyrenula occidentalis (R.C. Harris) R.C. Harris (1987)

Pyrenula harrisii Hafellner & Kalb (1992)

Thallus immersed, yellow-brown to orange-brown; pseudocyphellae absent; surface K + purple-red in parts in section. Perithecia 0.4–0.8 mm diam., forming projections in the thallus. Exciple usually with K + purple-red pigment associated with the upper outside wall. Hymenium densely interspersed with minute oil droplets *c.* 0.5–2.5 µm diam., thus appearing cloudy; anthraquinones absent (K –). Ascospores (1–)3-septate, (17–)18–22 × (7–)8.5–10.5(–11) µm. Conidia *c.* 20 µm long, curved. Thallus PD + pale orange, K + yellowish to + purplish in parts, KC –, C –, UV – (unidentified anthraquinones).

On smooth bark, particularly of *Corylus*, *Ilex* and *Sorbus*, in more or less shaded, constantly humid woodland and sheltered stream valleys; local. Mid and N. Wales, W. Scotland, S.W. Ireland (Cork, Kerry). Norway, W. North America, South Africa.

Anthraquinones are responsible for the K + purple-red reaction in the thallus and on the outer surface of the exciple (but not the inner surface); small rusty patches of anthraquinone can sometimes be seen on the thallus surface under a dissecting microscope. This species has been much confused with *P. laevigata*, which differs in the paler thallus, absence of anthraquinones, and the hymenium which is not interspersed with droplets.

Literature:

Harris, R.C. (1995) *More Florida lichens, including a 10¢ tour of the Pyrenolichens*. New York: privately published.

SPORODICTYON A. Massal. (1852)

Thallus crustose, superficial, thin to thick, grey, greenish grey or brown. **Photobiont** a green alga, with *Nostoc* in cephalodia in some species; hymenial algae absent. **Ascomata** perithecia, forming projections, with thalline covering at least at below. **Involucrellum** 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** usually 8 per ascus, 39–84 × 19–47 µm, ellipsoid, muriform, colourless or medium to dark brown. **Conidiomata** unknown. **Chemistry**: lichen products absent. **Ecology**: on siliceous rock, often where calcareous or moist. **Distribution**: 5 species, Europe, North America, Australasia.

This genus has been recently reintroduced, largely on evidence from molecular data. Recent authors have treated the species under the genus *Polyblastia*; see the key under that genus. Cephalodia, when present, are usually easily identified as brown, verrucose, well-delimited structures on the surface of the thallus.

LITERATURE: Savić & Tibell (2008).

- 1 Mature ascospores colourless; cephalodia usually present *terrestris*
 Mature ascospores medium to dark brown; cephalodia present or not
 2
- 2(1) Perithecia forming projections 0.5–0.7 mm diam., with a typically smooth or slightly verrucose thalline covering; ascospores (47.5–)55–64.5(–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 (Körber) Körber (1863)

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

Thallus superficial, usually well-developed, 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 smooth or somewhat verrucose layer of thallus, or thallus layer partly lost, exposing the black perithecium. Ascospores muriform, medium brown when mature, occasionally dark brown but cell outlines rarely obscured, (47.5–)55–64.5(–75) × (24–)29–36(–42) µm, length/width ratio (1.4–)1.6–2.1(–2.5). 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, Scotland, Ireland. Europe, N. America, Australia (Tasmania), New Zealand.

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. schaeererianum*, which has darker and larger ascospores. *S. terrestris* differs in the colourless ascospores and usually the presence of cephalodia.

Sporodictyon schaeerianum A. Massal. (1852)

Polyblastia theleodes auct.p.p.

Thallus superficial, well-developed, often of areole-like convexities c. 0.1–0.3 mm wide, 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 more or less 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–)1.6–2.0(–2.2).

On damp calcareous rock on cliffs and below overhangs, mainly upland, occasional. S.W. and N. England, Wales. Scotland, Ireland. Scandinavia, C. Europe, Greenland, N. America.

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.

Sporodictyon terrestris (Th. Fr.) S. Savić & Tibell (2008)

Polyblastia terrestris Th. Fr. (1860)

Polyblastia inumbrata (Nyl.) Arnold (1870)

Thallus superficial, slightly uneven to usually verrucose, of indistinct areole-like units 0.08–0.3 mm wide, 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 brownish, with no colour visible in the cell walls except in withered and unhealthy spores, (39–)51–68(–81) × (22–)26–34(–40) μm, length/width ratio (1.5–)1.7–2.3(–3.0). On damp siliceous rocks, including mica schist and epidiorite, occasionally on soil, stones and bryophytes; upland, rare. N. Wales, Scotland, Ireland. Scandinavia, Novaya Zemlya, Greenland. Distinguished from *S. cruentum* and *S. schaeerianum* by the ascospores which are colourless when mature and healthy. *S. cruentum* also differs in the absence of cephalodia; the thallus of *S. cruentum* is often darker and smoother than in *S. terrestris*, but the two species overlap in these features.

Literature:

Savić, S., Tibell, L., Gueidan, C. and Lutzoni, F. (2008) Molecular phylogeny and systematics of *Polyblastia* (Verrucariaceae, Eurotiomycetes) and allied genera. *Mycological Research* **112**: 1307–1318.

STAUROTHELE Norman (1853)

Thallus crustose, immersed or superficial, grey, green or brown. **Cortex** ill-defined. **Medulla** poorly-defined or absent. **Prothallus** whitish or brown. **Photobiont** *Stichococcus*, ?*Diplosphaera*. **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** 1–8-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, ellipsoid to oblong. **Conidiomata** pycnidia, immersed in the thallus. **Conidia** rod-shaped. **Chemistry:** lichen substances not detected; brown, K + darker or + greenish brown acetone-insoluble pigments in thallus and ascomata. **Ecology:** on rock, especially calcareous rocks and damp siliceous rock, and on soil.

Classification: Chaetothyriomycetidae, Verrucariales, Verrucariaceae.

A genus found in all continents, with about 50 currently accepted species. The genus has been shown to be polyphyletic by recent molecular studies. The algae in the thallus may differ in shape from those in the hymenium, but they belong to the same taxon. *Stichococcus mirabilis* has been identified from one species, but there is an older report of '*Protococcus*' (= *Diplosphaera*?) from another. 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.

The genus is polyphyletic: *S. areolata*, *S. clopima*, *S. clopimoides*, *S. fissa*, and *S. frustulenta* belong to *Staurothele s.s.*

LITERATURE: Swinscow (1963).

- | | |
|------|---|
| 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 <i>S. bacilligera</i> ?), 2 or 8 per ascus 3 |
| 3(2) | Hymenial algal cells oblong to narrowly oblong in outline, 2–4 times as long as wide bacilligera
Hymenial algal cells isodiametric to shortly oblong or oblong-ellipsoid, 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 more or less sessile, without a thalline covering 7
Perithecia with a thalline covering at least below, 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 ellipsoid, thallus cream **rufa**
- 8(5) Perithecia forming distinct projections above the general level of the thallus, covered by thallus layer at least in lower half, but not immersed in swollen thalline warts; hymenial algal cells subglobose to oblong-ellipsoid, 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 oblong-ellipsoid, 1–1.4 times as long as wide **frustulenta**
- 10(5) Involucrellum absent; on soil 11
 Involucrellum present; on rock 12
- 11(10) Thallus of brown, goniocyst-like units; hymenial algal cells isodiametric to shortly oblong in outline, 1–2 times as long as wide; ascospores 34–36.5 µm long **geoica**
 Thallus of grey-green areoles; hymenial algal cells oblong to narrowly oblong in outline, 1.6–2.6 times as long as wide; ascospores 23–28 µm long **Staurothele sp.**
- 12(11) Thallus endolithic; base of perithecium often in a shallow pit in rock; hymenial algal cells oblong, 1.3–2.5 times as long as wide **hymenogonia**
 Thallus epilithic, of goniocyst-like units or convex areoles 13
- 13(12) Thallus of crowded, convex, cream to grey-green areoles; perithecia half to mostly immersed in areoles **rugulosa**
 Thallus of grey-green to brown, often lobed or branched, goniocyst-like units; perithecia usually prominent, 0.25–0.5 immersed in thallus **succedens**

Staurothele arctica Lynge (1937)

Thallus grey-brown, immersed or superficial and warty. Perithecia sessile, to 500 µm diam. Involucrellum present. Hymenial algal cells oblong to narrowly oblong in outline, 5–8(–12) × 4 µm. Asci 2-spored. Ascospores becoming dark brown, 32–48 × 12–18 µm.
 One record from a snowbed in western Scotland (Ben Nevis). Sweden, Greenland, Canada.

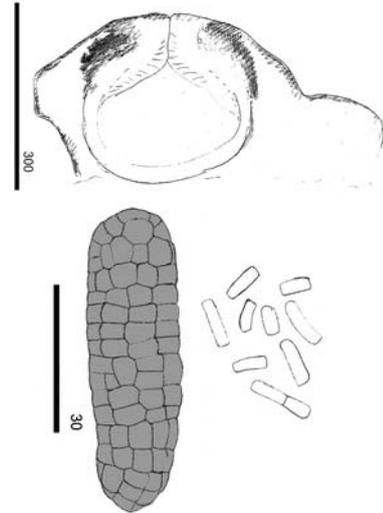
Staurothele areolata (Ach.) Lettau (1912)

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 apex of exciple. Hymenial algae oblong to narrowly oblong in side view, $5.7\text{--}8 \times 2.5\text{--}3 \mu\text{m}$, 2–4.3 times as long as wide. Asci 2-spored. Ascospores brown, oblong-ellipsoid to narrowly oblong-ellipsoid, $(43\text{--})45\text{--}53.6\text{--}62.5(-63.5) \times 14\text{--}17.4\text{--}22 \mu\text{m}$ [n = 4].

Reported from granite boulders in melt-water stream from a late snow patch, N. Scotland (Cairngorms, Cairn Toul); and there is a second record from W. Scotland. Mainly circumboreal, Norway, Sweden, Alps, N. America.

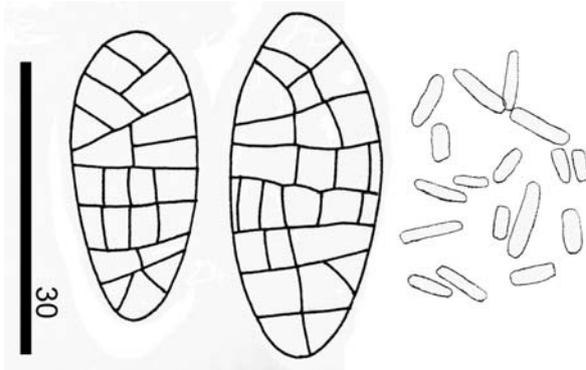
Illustrations: Thomson (1991) p. 353, Thomson (1997) p. 592 (same ill. as last).

Distinguished from *S. fissa* by the strongly convex areolae with immersed perithecia; *S. frustulenta* differs mainly in the short hymenial algae. The status of this species in Britain needs to be reviewed; the specimen from Cairn Toul is in very poor condition but it is not this species; possibly it is *S. clopima*.



Staurothele areolata, Iceland (16838).

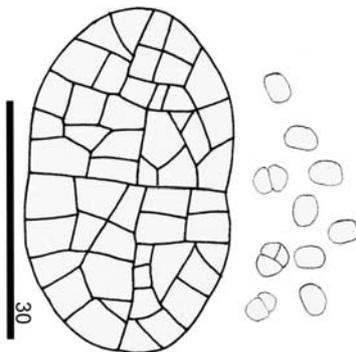
Staurothele bacilligera (Arnold) Arnold (1885)



Thallus endolithic, pale grey-brown (thallus units may be exposed at surface as minute brown specks). Perithecia 280–390 μm diam., immersed in well-defined pits in rock, occasionally projecting slightly when old; exciple brown, involucrellum absent. Hymenial algal cells 4–8 \times 1.5–2 μm , oblong to narrowly oblong in outline, 2–4 times as long as wide. Ascospores colourless (sometimes brown later?), 8 per ascus, (30–)32–**35**–37.5 \times (13–)14–**15.3**–16.5(–17) μm [15/3].

On unshaded limestone rocks, very local; N. England, C. and N. Scotland, W. Ireland. Sweden, Jura, Alps to Balkans. (including Italy).

Staurothele caesia (Arnold) Arnold (1885)



Thallus endolithic, rarely (in shade?) also with a thin epilithic layer; pale grey to brownish grey, thallus units sometimes exposed at surface as brown specks c. 30 μm diam; adjacent thalli sometimes separated by dark lines. Perithecia immersed in well-defined pits, 380–500 μm diam.; involucrellum absent. Hymenial algal cells 3–5 \times 3–3.5 μm , isodiametric to shortly oblong, 1–2 times as long as wide. Asci 8-spored. Ascospores colourless, to dilute brown when overmature, ellipsoid, (32.5–)35–**39.6**–44(–49) \times 20–**22.3**–24.5(–28) μm [30/4].

On mostly unshaded limestone, rarely on mortar, locally frequent; local in Great Britain, W. Ireland. Sweden, C. Europe to Balkans.

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

Staurothele clopima (Wahlenb.) Th. Fr. (1861)

S. fuscocuprea (Nyl.) Zschacke (1913)

Currently distinguished from *S. fissa* only by the elongate hymenial algae, but the taxonomy needs to be revised. Not yet certainly known from Great Britain.

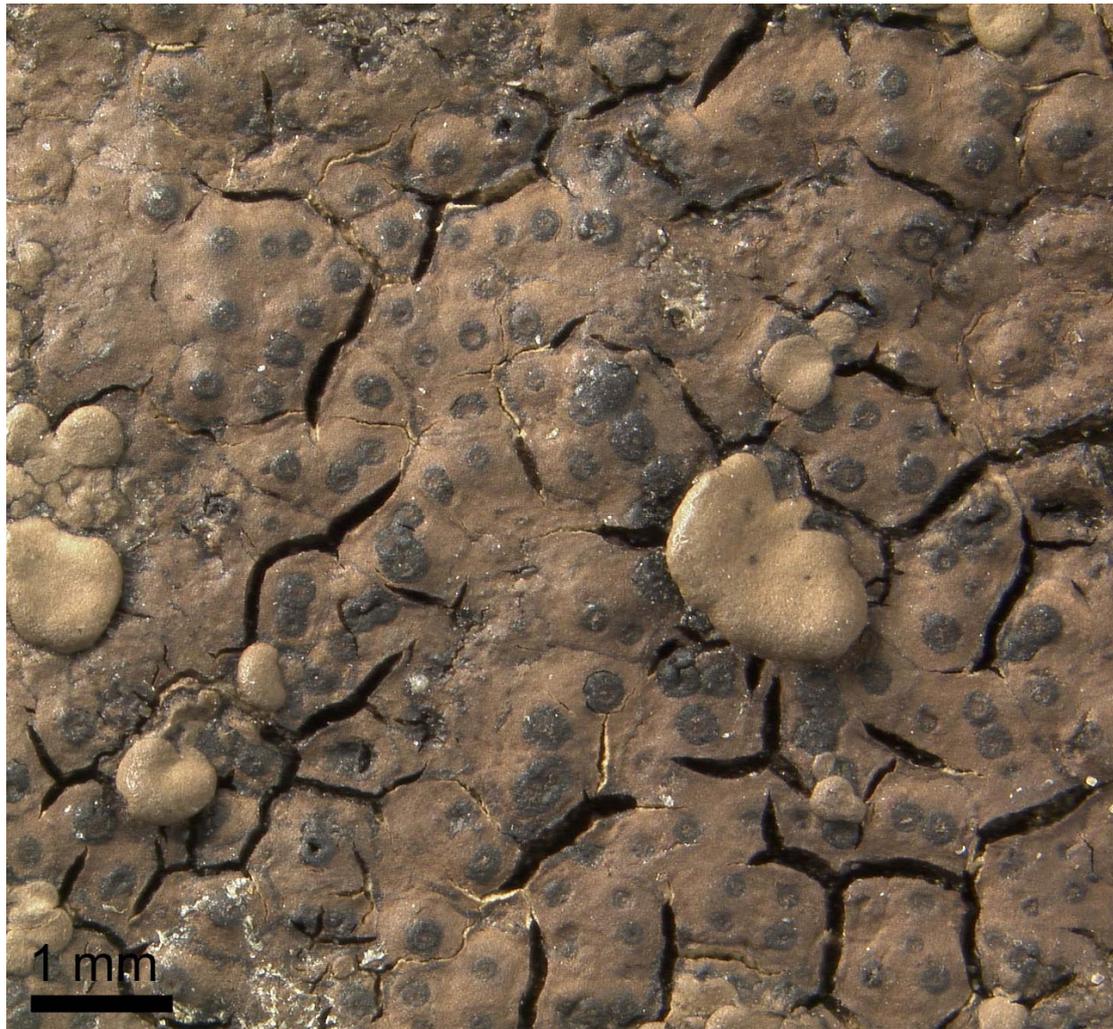


Staurothele clopima, Norway (19290).

Staurothele clopimoides (Anzi) J. Steiner (1907)

Thallus cracked (but not comprising convex areoles). Perithecia immersed. Hymenial algae rod-shaped. Ascospores brown, $38\text{--}50 \times 14\text{--}21 \mu\text{m}$.

On siliceous rocks in streams. Not reported for Great Britain. Norway, Sweden, Alps.



Staurothele clopimoides, Norway (8793).

Staurothele fissa (Taylor) Zwackh (1862)

Thallus superficial, continuous to (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 apical part of exciple, appressed to exciple or lightly divergent. Hymenial algal cells subglobose to oblong-ellipsoid, single cells $3.3\text{--}6.5 \times 3\text{--}5 \mu\text{m}$, 1–1.6 times as long as wide, but cells frequently in pairs or tetrads. Asci 2-spored. Ascospores oblong-ellipsoid to narrowly oblong, pale to mid brown (cell outlines never obscured), $(31\text{--})37\text{--}42.9\text{--}48.5\text{--}(55) \times (15\text{--})16\text{--}18.0\text{--}20\text{--}(25.5) \mu\text{m}$, (1.5–)2–2.4–3 times as long as wide [79/9]. Pycnidia frequent, Dermatocarpon-type. Conidia rod-shaped or slightly curved, $3\text{--}4 \times 1.2 \mu\text{m}$.

On frequently or permanently submerged siliceous rocks in unpolluted streams and lakes, avoiding the most acidic waters, locally frequent; north and west Britain, almost absent from C. and S.E. England, scattered records in Ireland. Norway, Sweden, to C. European mountains, Alps, Balkans, N. America, New Zealand.

Illustrations: Thomson (1991) p. 358, Thomson (1997) p. 596 (same ill. as last).

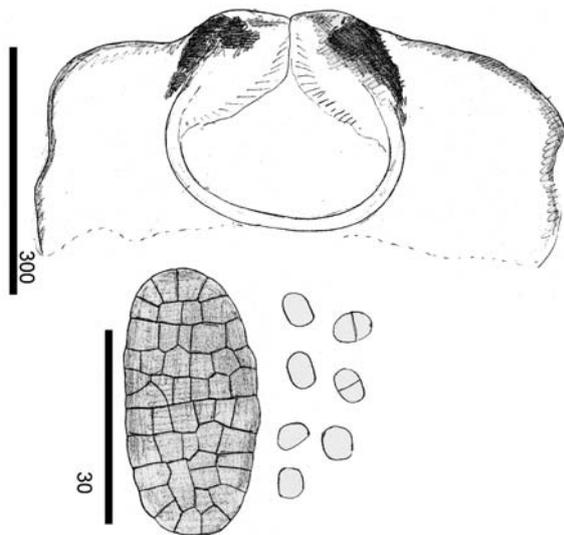
The perithecia are (at least partly) covered by a layer of thallus, but they form distinct mounds above the level of the rest of the thallus; in *S. areolata* and *S. frustulenta*, the perithecia are more or

less immersed in swollen areoles which are not as distinct from the sterile parts of the thallus. *S. clopima* is an arctic alpine species which could be found in Britain; it differs mainly in the hymenial algal cells which are oblong to narrowly oblong in outline (cells single or in pairs, never in tetrads?).



Staurothele fissa, a pale morph from a shady river, Wales (21210).

5. *Staurothele frustulenta* Vain. (1921)



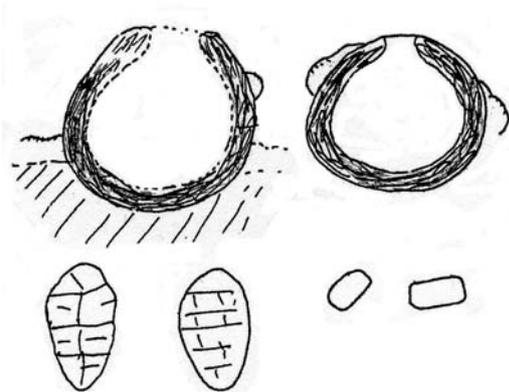
Thallus superficial, brown, areolate, areoles becoming strongly convex; fertile areoles larger than sterile, often constricted below; thallus secondarily cracked into single or small groups of areoles. Perithecia immersed in the thallus, mostly one per areole; either completely immersed and inconspicuous, or with the apex visible as a black disc, or projecting slightly as a low black mound. Involucrellum present, confined to apex of exciple or slightly spreading reaching to base-level of exciple. Hymenial algae almost isodiametric to shortly oblong-ellipsoid, $3.7\text{--}5.7 \times 3.3\text{--}4.5 \mu\text{m}$, 1.1–1.4 times as long as wide. Asci 2-spored. Ascospores brown, oblong-ellipsoid to rather narrowly oblong-ellipsoid, $(29\text{--})33.5\text{--}39.8\text{--}46(\text{--}48) \times (13\text{--})14.5\text{--}18\text{--}21 \mu\text{m}$ [7/1].

On dry and somewhat nutrient-enriched rocks, very rare; England (Devon, on concrete; Oxford, on tile roof). Ireland, Norway, Sweden, Germany.

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

6. *Staurothele geoica* Zschacke (1918)

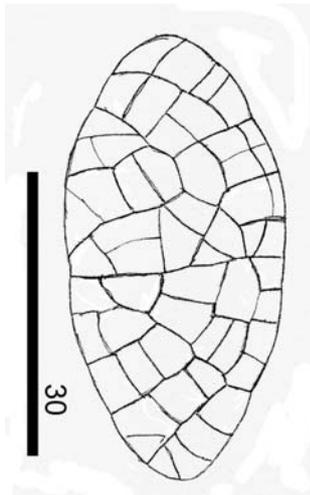
Thallus superficial, dark brown, thin, minutely roughened, comprising goniocyst-like units with brown pigment at surface. Perithecia forming projections 280–380 μm diam., 0.3–0.6 immersed in the thallus, mostly naked, but surface sometimes bearing small patches of thallus. Exciple 320–400 μm diam., pigmented throughout; involucrellum absent. Hymenial algal cells isodiametric to shortly oblong. Ascus 8-spored. Ascospores colourless, ellipsoid, 34–36.5 \times 17–17.5 μm [3/1].



On soil in montane sites, W. Scotland, Switzerland, Italy.

7. *Staurothele guestphalica* (Lahm ex Körb.) Arnold (1885)

Thallus endolithic, light grey, adjacent thalli often separated by dark lines. Perithecia immersed in well-defined pits in rock, 280–400 μm diam.; involucrellum absent. Hymenial algal cells 3–6 \times 3–5 μm , isodiametric to shortly oblong, 1–1.5 times as long as wide. Asci 2-spored when mature. Ascospores colourless, ellipsoid to rather narrowly ellipsoid, (33–)41–**45**–49(–50.5) \times (17–)19–**20.9**–23(–25.5) μm [30/5].

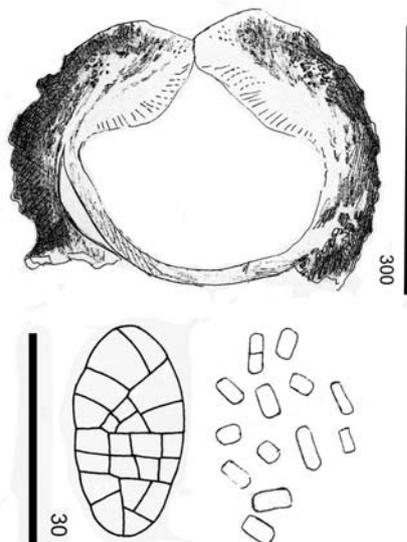


On limestone, rare; S.W. and N. England, S. Wales. Scotland, Ireland. France, C. Europe.

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

Illustration: Wirth (1995) p. 871.

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



Thallus endolithic, grey. Perithecia forming conical-hemispherical projections 300–600 μm diam., black (or dusted with rock fragments), surface often rough or radially fissured, ostiole plane 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 \times 2.5–3 μm , oblong, 1.3–2.5 times as long as wide. Asci 8-spored. Ascospores colourless, ellipsoid, (23–)25.5–**27.2**–29(–30) \times 12.5–**14.2**–16(–17) μm [16/5].

On limestone rocks and pebbles, locally common. Most records from England, also in N. Wales, Scotland, Ireland. Europe (report from N. America incorrect).

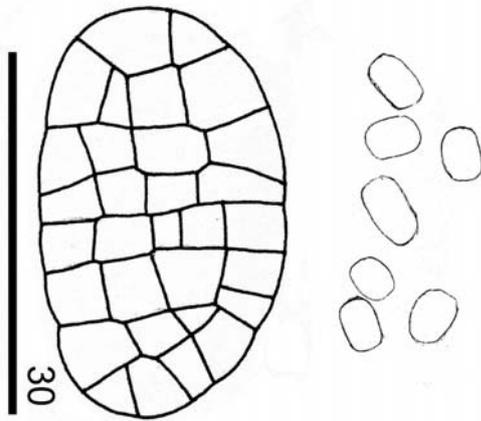
Illustration: Puntillo (1996) Tav. XXXVIII.

9. *Staurothele rufa* (A. Massal.) Zschacke (1913)

Thallus epilithic, pale cream, but thin and indistinct, to 40 µm thick. Perithecia forming black, conical-hemispherical projections 360–480 µm diam., without 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 × 2.5 µm, isodiametric to broadly ellipsoid, 1–1.5 times as long as wide. Asci 2-spored. Ascospores brown, oblong-ellipsoid, (34.5–)36–**38.2**–40.5(–42) × (11.5–)12–**15.1**–18(–20) µm 8/1].

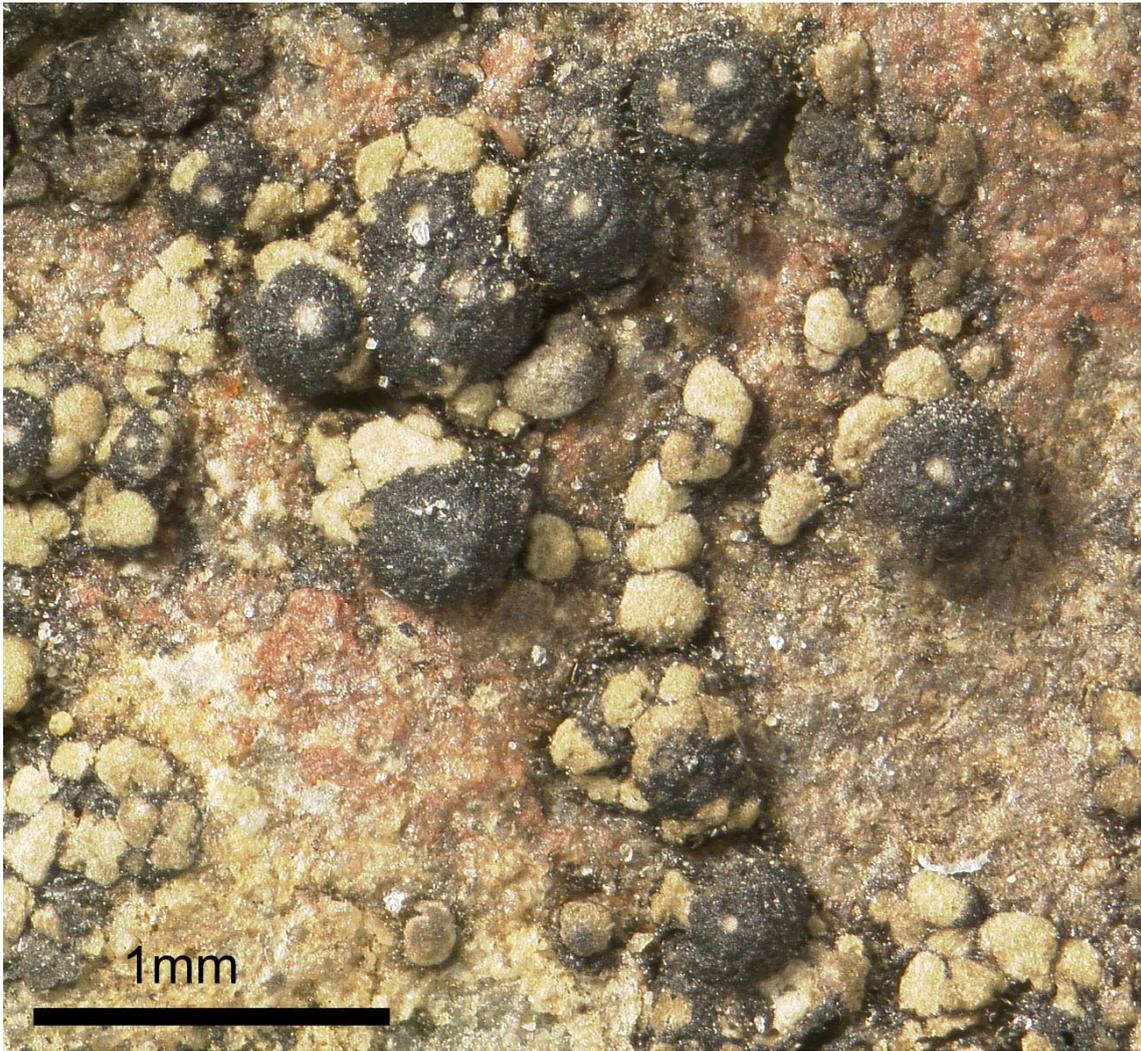
On Liassic limestone in disused coastal quarry near Porthkerry (South Wales). Europe, China. The single British specimen was collected in 1964, and the species has not been collected since, despite a recent search of likely sites.

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



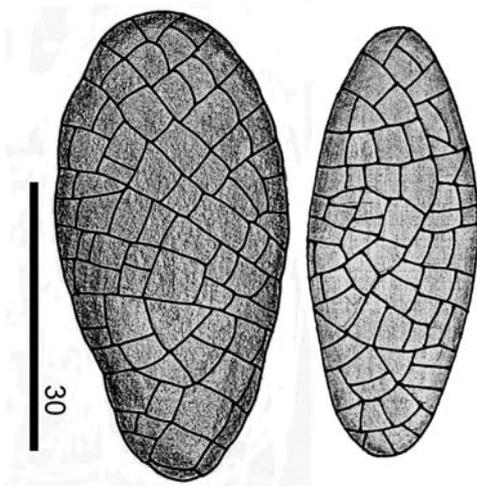
Thallus epilithic, well-developed, dirty cream or greenish grey; areoles strongly convex, crowded, thallus becoming secondarily cracked. Perithecia blackish, up to c. 500 µm diam. in situ, half to completely immersed amongst the areoles. Involucrellum present. Hymenial algal cells 3.3–5.7(–7) × 3 µm, 1.1–2(–2.4) times as long as wide. Asci 8-spored. Ascospores colourless, ellipsoid, 31–34.5 × 18–20.5 µm [13/2].

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



Staurothele rugulosa (15267).

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

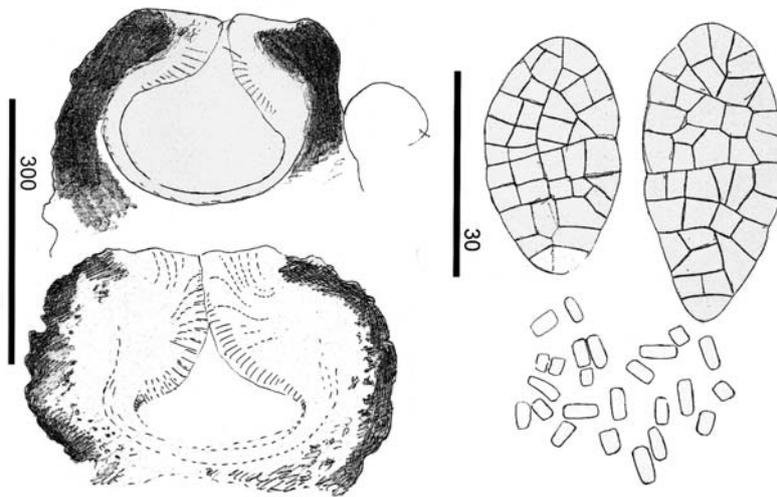


Thallus endolithic, light brownish grey, sometimes with minute brown specks. Perithecia immersed in well-defined pits in rock, 320–380 μm diam. [$n = 2$]; involucrellum absent. Hymenial algae isodiametric to shortly oblong, 3–4 \times 3 μm . Asci 4(–5)-spored. Ascospores ellipsoid to narrowly ellipsoid, brown, usually becoming opaque when mature, so that only cells at the apparent margin of the spore can be seen, (38.5–)44–**49.6**–55.5(–62) \times (18–)20–**22.6**–25(–27.5) μm [68/10].

On unshaded or slightly shaded limestone, typically on more or less north-facing or slightly damp (but not flushed) surfaces; locally frequent. Throughout British Isles. Europe from Norway and Sweden south to Italy, N. America.

12. *Staurothele succedens* (Rehm ex Arnold) Arnold (1880)

Thallus superficial, grey-green to brown (often growing with a black film of cyanobacteria), not cracked, surface roughened or with an almost microsquamulose appearance, composed of lobed and branched goniocyst-like units 350–500 µm wide. Perithecia 0.25–0.5 immersed in thallus, forming projections 300–520 µm diam., black, naked or with a few thallus granules, black, 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, ellipsoid to narrowly ellipsoid, (29.5–)34–**38.4**–42.5(–46) × (15–)17–**19.2**–21.5(–23) µm, (1.3–)1.5–**2.0**–2.5(–3.1) times as long as wide [23/4].

On damp calcareous rocks, including sandstone, limestone, mica-schist and epidiorite, sometimes on soft and unstable rock; local. N. & W. Britain, N.W. Ireland. Sweden, mountains of C. and

S. Europe.

13. *Staurothele* sp.

Thallus superficial, thin, grey-green, not cracked; areoles 80–200 µm diam., plane, soon confluent. Perithecia 0.7–0.9 immersed in substratum, apex black, not covered by thallus; exciple 300–375 µm diam., brown throughout. Involucrellum absent. Hymenial algal cells 3.3–5.7 × 2 µm, oblong to narrowly oblong in outline, 1.6–2.8 times as long as wide. Asci 8-spored. Ascospores colourless, 23–28 × 10–13 µm.

Calcareous soil in lowland grassland, S. Wales (Caerwent).

An unidentified species. *S. epigaea* Breuss & Etayo from soil in Spain has similar ascospores, but differs in the well-defined involucrellum.

Literature:

Swinscow, T.D.V. (1963) Pyrenocarpous Lichens: 4. Guide to the British species of *Staurothele*. *Lichenologist* **2**: 152–166.

Illustration references:

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STRIGULA Fr. (1823)

Discosiella H. Sydow & Sydow (1912) [anamorph]

Thallus crustose, superficial, immersed, or subcuticular on living leaves. **Photobiont** a member of the *Trentepohliaceae* (*Cephaleuros*, *Phycopeltis* or *Trentepohlia*). **Ascomata** perithecia, immersed in the substrate or projecting from the thallus. **Exciple** colourless or pigmented. **Involucrellum** absent or present, confined to the apex of the exciple or spreading. **Ostiole** central, rarely lateral.

Hamathecium of paraphysoids which are mostly simple, and only rarely branched and anastomosing, except where adjacent to the exciple. **Asci** cylindrical to narrowly clavate, bitunicate-fissitunicate, base shortly stalked with a more or less bilobed foot; apex thickened into a tholus, with an ocular chamber; I –. **Ascospores** 1-septate to multiseptate or muriform, in some species the 1-septate spores separating into two part-spores before or during dehiscence of the ascus; perispore present, surrounding the spore, rarely represented by gelatinous appendages at the spore apices. **Conidiomata** pycnidia, often of two types within the same species: micropycnidia 50–120 μ diam., and macropycnidia often a little larger. **Conidia** of two types: microconidia simple, fusiform to shortly cylindrical or cylindrical, 2–5 \times 1–2 μ m, often containing two oil droplets, lacking appendages, and borne on phialidic conidiogenous cells; macroconidia simple to several-septate, apices with a gelatinous appendage, or rarely the basal one absent; macroconidia laterally inserted on the conidiogenous cell, point of insertion thus subterminal and marked by a slight depression or more rarely a thickening of the wall. **Chemistry**: no lichen substances detected. **Ecology**: on siliceous and calcareous rocks, bark, and living leaves, usually in shaded and humid habitats.

Classification: Chaetothyriomycetidae, Strigulaceae.

Porina differs in the unthickened, unitunicate ascus and the lack of macroconidia, *Thelenella* differs in the trebouxoid photobiont.

The appendages of the macroconidia are best observed using phase-contrast microscopy, or in a solution of a stain such as Brilliant Cresyl Blue, when the appendages appear pale and unstained in contrast to the coloured solution.

LITERATURE: Aptroot & van den Boom (1995), Fryday & Coppins (2004), Harris (1995), Roux & Bricaud (1993), Roux & Sérusiaux (2004), Sérusiaux et al. (2005).

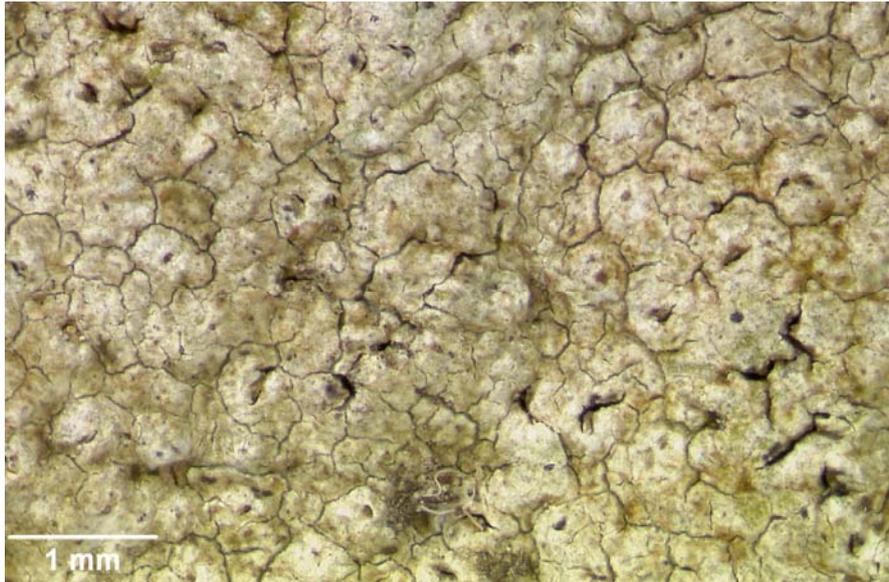
1	Ascomata present; macropycnidia present or not	2
	Ascomata absent; macroconidia present	11
2(1)	Ascospores muriform	3
	Ascospores transversely 3–(9)-septate, rarely with one longitudinal septum	4
3(2)	Ascospores (35–)40–58(–62) μ m long; ostiole central; on rock	confusa
	Ascospores (22–)24.5–30.5(–31.5) μ m long; ostiole usually lateral; on bark	tagananae
4(2)	Ascospores (3–)7(–9)-septate	stigmatella
	Ascospores 1- or 3-septate	5
5(4)	Ascospores 1-septate, sometimes separating into part-spores	6
	Ascospores 3-septate	8
6(5)	Ascospores (16–)19–24(–27) μ m long, separating into part-spores at ascus dehiscence or before; macroconidia 12.5–20 μ m long	taylorii
	Ascospores 6.5–14.5 μ m long, not separating into part-spores; macroconidia 6–11 μ m long	7

7(6)	Ascospores with a thin perispore 0.2–0.5(–1) µm thick; macroconidia (6–)7–8.5(–10) µm long	phaea	
	Ascospores without perispore; macroconidia (7.5–)8–11 µm long	Strigula sp.	
8(5)	Involucrellum absent, ascomatal wall colourless to orange or pale brown		9
	Involucrellum present, ascomatal wall dark brown; ostiolar region not elongated; ...		10
9(8)	On bark, ascospores (9.5–)10.5–13(–14.5) µm long, without perispore.....	thelopsidoides	
	On rock, ascospores 17-22 × 5.5-7 µm	calcarea	
10(8)	Ascomata 100–200 µm diam.; ascospores 13.5–16(–17.5) µm long	jamesii	
	Ascomata 200–300 µm diam; ascospores (17.5–)19–21 µm long	musciola	
11(1)	Macroconidia 5- to 11-septate, at least 20 µm long		11
	Macroconidia 1- to 3-septate, up to 20 µm long		12
11(10)	Macroconidia 5–7-septate, 20–30 µm long	stigmatella	
	Macroconidia (7–)11-septate, 36–44 µm long	tagananae	
12(10)	Macroconidia 3-septate		13
	Macroconidia (0–)1-septate		14
13(12)	Macropycnidia brown; macroconidia 13.5-16.5 µm; usually on bark	jamesii	
	Macropycnidia colourless; macroconidia 15-19.5 µm; on rock	calcarea	
14(12)	Macroconidia (6–)7–8.5(–10) µm long, the conidiogenous cells elongated, (4–)7–25 µm long	phaea	
	Macroconidia (7.5–)8–11 µm long, the conidiogenous cells 4.5–10 µm long	Strigula sp.	

Strigula calcarea Bricaud & Cl. Roux (1991)

Thallus endolithic. Perithecia 200-400 µm diameter, immersed in the substratum and thallus, exciple colourless except for brownish region near ostiole. Ascospores (15-)17-22(-23) × (4-)5.5-7(-8) µm, 3-septate. Macropycnidia 120-180 µm diameter. Macroconidia 15-19.5 × 4-5 µm. Microconidia 3-4 × 1-1.5 µm.

On vertical shaded limestone walls, Wales, England; rare but easily overlooked. France, Belgium.



Strigula calcarea.



Strigula calcarea, underside of scraping, showing bases of macropycnidia.

Strigula confusa Fryday, Coppins & Common (2004)

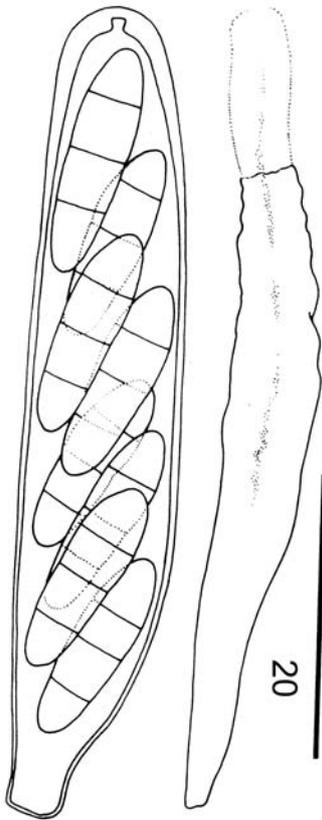
Thallus grey or whitish grey, continuous and fairly thin. Ascوماتа 300–500 µm diam., globose, at first almost completely immersed then half- to three-quarters immersed in the thallus, blackish or rarely whitish (on frequently submerged rocks). Involucrellum absent or not separable from the exciple. Exciple brown above, at first colourless below, then completely brown. Paraphysoids 1.5–2.5 µ wide. Asci (4–)6–8-spored. Ascospores (35–)40–**49.1**–58(–62) × (7–)8–12 µm, subfusiform or fusiform, muriform, with (6–)12–14(–17) transverse septa and 1–3 longitudinal septa per tier. Macropycnidia unknown. Micropycnidia 40–60 µm diam., largely immersed in the thallus. Microconidia 3.5–4.5 × 1–1.5 µm.

Over bryophytes on mildly basic rocks (including andesite, mica-schist and basalt), rarely directly on shaded mudstone. Hyperoceanic regions of W. Britain, in Wales, N.W. England, W. Scotland, Ireland.

Strigula jamesii (Swinscow) R.C. Harris (1980)

Thallus whitish or pale grey, very thin, largely immersed. Ascomata 100–200 µm diam., half-immersed in the substratum, upper part rounded or flattened, rarely conical. Involucrellum confined to the apical part of the exciple. Asci narrowly clavate. Ascospores 13.5–**14.9**–16(–17.5) × 4–**4.5**–5(–5.5) µm, subfusiform, 3-septate, lightly constricted at the septa, the two upper cells usually wider than the lower two, perispore 0.2–2.5 µm thick. Macropycnidia 50–100 µm diam., largely immersed, involucrellum present in upper part. Macroconidia (13–)13.5–**14.9**–16.5(–18) × (2–)2.5(–3) µm, narrowly oblong, 3-septate, not or scarcely constricted at the septa, each end with an appendage 1.5–3 × 1.5–2 µm. Microconidia 2.5–4 × 1–1.5 µm.

On bark, especially on *Ulmus* trunks, or on exposed roots in sheltered woodland, rarely over mosses on mortar, local; S. & N.E. England, Wales, S. & E. Scotland, S. Ireland. Sweden, Denmark, France, Belgium, Luxembourg, Germany, Austria, Switzerland, N. America.



< *Strigula jamesii*: ascus



Strigula jamesii.

Strigula muscicola F. Berger, Coppins, Cl. Roux & Sérus. (2005)

Thallus whitish or whitish grey, thin. Ascomata globose, hardly immersed in the thallus, single or usually in clusters of 2–4(–8). Involucrellum well-developed, extending almost to base of ascoma. Paraphysoids 1.5–2 μm wide, simple, or branched and anastomosed at their base. Ascospores 3-septate, (17.5–)19–21 × 4.5–6 μm. Conidiomata not seen.

On mosses on soil in crevice on boulder; very rare. C. Scotland (Braemar). Norway, Austria.

Strigula phaea (Ach.) R.C. Harris (1975)

Thallus grey-green or brownish, continuous, fairly thin but sometimes thicker and fairly swollen. Ascomata 200–350 μm diam., projecting, but mostly covered by a thin layer of thallus. Involucrellum reaching the base of the exciple. Exciple at first colourless, but soon dark brown. Paraphysoids up to (1–)1.5 μm wide. Asci cylindrical to more or less elongate-clavate. Ascospores (6.5–)9–**10.6**–12.5(–14.5) × (2–)2.5–**3.0**–3.5(–4.5) μm, fusiform, 1-septate, constricted at the septum but not separating into part-spores, cells often containing two oil-drops in herbarium material; perispore often visible, thin, 0.2–0.5(–1) μm thick. Macropycnidia 100–170 μm diam., globose, brown or blackish, projecting but covered by a thin thalline layer; covered by an involucrellum. Macroconidia (6–)7–**7.7**–8.5(–10) × (1.5–)2–2.2–2.5 μm, oblong, 1-septate, not or scarcely constricted at the septum, each end with a rather short and wide appendage 2–5 × 0.5–2 μm which is often curved, flexuose or helical; in the herbarium each cell often with two persistent oil droplets; conidiogenous cells elongated, (4–)7–25(–27) × 1–1.5 μm. Micropycnidia like the macropycnidia but 50–100 μm diam. Microconidia fusiform or subfusiform, 2.5–4 × 1–1.5 μm; conidiogenous cells very elongated, 5–21 × 1–1.5 μm.

On bark of *Fagus*, *Fraxinus*, *Quercus* and *Ulmus*, in areas of old woodland, very local. S. England (New Forest), Wales (Cardigan, Merioneth), W. Scotland, Ireland (Fermanagh, Kerry). France (Brittany, Pyrénées Atlantiques), Canary Islands (La Palma); widespread in Old and New World tropics.

Ascomata often absent, but specimens distinguished by the 1-septate macroconidia borne on a very elongated conidiogenous cell.

Strigula stigmatella (Ach.) R.C. Harris (1975)

Strigula alpestris (Vezda) Hafellner (2002), *S. stigmatella* var. *alpestris* (Vezda) Coppins (1980)

Thallus greenish or pale grey, usually continuous and partly immersed. Ascomata 300–400 µm diam., globose, one-quarter to half-immersed, partly covered by a thin thalline layer. Involucrellum distinct from the exciple when young, later not clearly distinct and usually appearing as a thickening of the upper part of the exciple. Exciple colourless to pale brown below. Ascospores (25–)26–**31.8**–36.5(–40.5) × (3.5–)5.5–**6.2**–7 µm, fusiform, (3–)7(–9)-septate, rarely also with a longitudinal septum, perispore absent. Macropycnidia c. 100 µm diam. Macroconidia 20–30 × 4–6 µm, oblong-fusiform, 5–7-septate, not or scarcely constricted at the septa, appendages not recorded but almost certainly present. Micropycnidia c. 50–100 µm diam. Microconidia 2.5–3 × 0.5–1.5 µm.

On bark of old broad-leaved trees, over mosses on tree bases or over mosses on calcareous upland rocks up to 800 m altitude, rare; S. England (Hampshire, ?extinct in Sussex), N. Wales, Scotland. Norway, France, Germany, Austria, Switzerland, Italy, Slovakia, N. America, Australia.

Strigula tagananae (Harm.) R.C. Harris (1995)

Strigula lateralis Aptroot & van den Boom (1995)

Thallus greenish to grey, continuous, largely immersed, usually inconspicuous. Ascomata 200–500 µm diam., circular or slightly elliptic in outline, flattened and scarcely projecting to projecting and hemispherical, solitary or often in groups of 2–7, often in lines, black and usually glossy, ostiole usually lateral. Ascospores subfusiform to fusiform, (22–)24.5–**27.2**–30.5(–31.5) × (6–)6.5–**7.6**–8.5(–9.5) µm, muriform, with (5–)6–7(–9) transverse septa and (0–)1–5 longitudinal septa. Macropycnidia 100–200 µm diam. Macroconidia cylindrical, (7–9–)11-septate, 36–44 × 4–5 µm, each end with an elongated appendage 10–30 × 1–4 µm. Microconidia 2.5–3 × 1 µm.

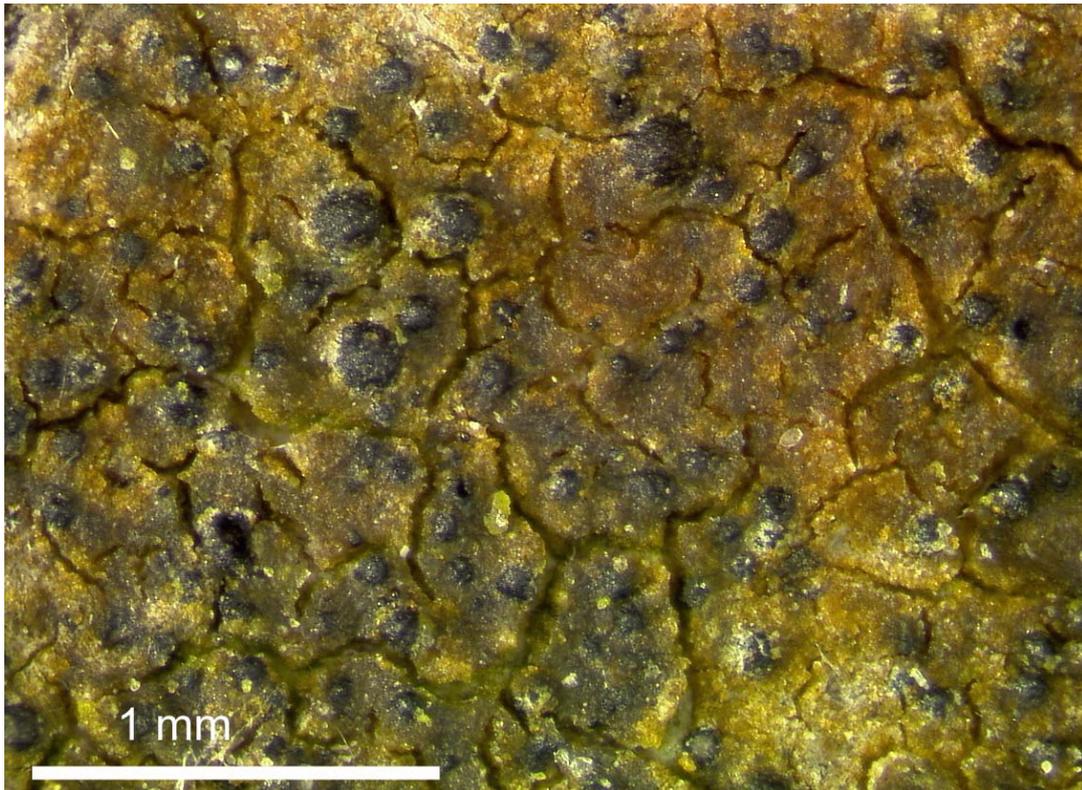
On *Corylus*, very rare; Ireland (Fermanagh). Spain (Catalonia), Portugal, Madeira, Canary Islands.

Strigula taylorii (Carroll ex Nyl.) R.C. Harris (1975)

Thallus brown, olive brown or dark brown, continuous or slightly cracked, thin, mostly endophloeodal. Ascomata 200–300 µm diam., projecting, immersed only in lower quarter, conical. Ascospores (16–)19–**21.7**–24(–27) × (3.5–)4–**4.3**–5 µm, 1-septate, separating into part-spores at ascus dehiscence or before, part-spores (8.5–)9.5–12.5(–14.5) × (3–)3.5–5(–5.5) µm. Macropycnidia semiglobose, 50–120 µm diam., with an involucrellum. Macroconidia (12.5–)13.5–**15.5**–17.5(–20) × (2–)2.5–**2.7**–3(–3.5) µm, (0–)1-septate, at each end with a poorly visible gelatinous appendage 1.5–4.5 × 1–2 µm; each cell containing (2–)3–4(–5) persistent oil droplets; conidiogenous cells 5–11.5 × 2–2.5 µm. Micropycnidia like the macropycnidia but 50–100 µm diam. Microconidia fusiform or subfusiform, 2.5–4 × 1–1.5 µm.

On usually ± smooth bark of mature trees (especially *Acer* and *Fraxinus*) in sheltered situations, or on limestone, local; S.W. England, Scotland, Ireland. S. and C. Europe (Spain, Portugal, France, Belgium, Luxembourg), Canary Islands.

Usually distinguished in the field from *Porina aenea* or *P. borreri* by the numerous pycnidia scattered among the larger, often ± conical perithecia.



Strigula taylorii (18337).

***Strigula thelopidoides* Coppins, Roux & Sérus. (2004)**

Thallus whitish or inconspicuous, immersed. Ascomata at first immersed in the substratum and elongated, later partially projecting, with a well-developed ostiolar canal lined with paraphysoids. Involucrellum absent. Exciple orange to pale brown, ostiolar region sometimes brown. Ascospores ellipsoid to subfusiform, 3-septate, not constricted at septa, (9.5–)10.5–**11.8**–13(–14.5) × 2.5–**3.2**–3.5(–4.5) μm, without a perispore. Macroconidia unknown. Microconidia immersed in the substratum, c. 100 μm diam., wall colourless. Microconidia 2–4 × 1–1.5 μm; conidiogenous cell 4–8.5 × 1–1.5(–2) μm.

On bark of *Fraxinus* and *Quercus*, rare; Scotland (Westernness, Mid Perthshire, Morvern, Dunbarton). Spain, France.

***Strigula* sp.**

Thallus very thin, whitish or inconspicuous. Ascomata 100–200 μm diam., projecting, globose. Ascospores 9.5–12(–13) × 2.5–3(–3.5) μm, fusiform or subfusiform, 1-septate, not separating into part-spores, without a distinct perispore. Macroconidia (7.5–)8–11 × 1.5–2.5 μm, 1-septate, each end with a short, poorly visible appendage 1.5–2 × 1 μm.

On *Ulmus* bark, calcareous rock, and on herbaceous stems (*Aubrieta*), rare; England, Scotland.

An unidentified species; the collections on rock and *Aubrieta* with macroconidia only. Similar to *S. phaea* but without a perispore, and with longer macroconidia.

Literature:

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THELENELLA Nyl. (1855)

Chromatochlamys Trevis. (1860)

Thallus crustose, membranous to verrucose or cracked, dirty whitish to pale grey or pale brown. **Photobiont** trebouxoid. **Ascomata** perithecia, thick-walled. **Exciple** of slender cells (*textura porrecta* to *textura intricata*), pigment homogeneous, lining the outer surface of the cells, or present throughout gel matrix, not appearing granular under high power. **Involucrellum** rarely present. **Hymenial gel** I –, K/I –. **Hamathecium** of paraphysoids which are delicate, branched and/or anastomosing, especially towards the base and apices; paraphysoids present at ostiole or absent. **Asci** 2-8-spored, fissitunicate, with two functional wall-layers, the inner wall thin and the outer thick, with ocular chamber, I –. **Ascospores** submuriform to strongly muriform, the outer wall scarcely thicker than the septa, colourless to brownish. **Conidiomata** pycnidia of *Roccella*-type; conidia simple, colourless, filiform. **Ecology**: on bark, leaves, bryophytes on leaves, rock and mossy soil. **Chemistry**: lichen substances not detected by TLC.

Classification: Ostropomycetidae, Thelenellaceae.

Characterized by the fissitunicate, thick-walled, I – asci, and the branched-anastomosing paraphysoids. *Protothelenella* differs in the amyloid tholus of the ascus; *Strigula* differs in the trentepohlioid photobiont and the different conidia.

LITERATURE: Fryday & Coppins (2004), Mayrhofer (1987), Mayrhofer & Poelt (1985).

- | | | |
|------|---|--------------------------------|
| 1 | Asci 2–4-spored, ascospores 60–110 µm long; over bryophytes on bark, rock and soil
..... | muscorum var. muscorum |
| | Asci 4–8-spored, ascospores 25–69 µm long | 2 |
| 2(1) | Ascospores 25–42 µm long; growing directly on bark | modesta |
| | Ascospores 44–69 µm long | 3 |
| 3(2) | Perithecia 150–200 µm diam.; growing directly on damp siliceous rock
..... | larbalestieri |
| | Perithecia 200–300 µm diam.; growing on bryophytes over trees, rocks or soil
..... | muscorum var. octospora |

Thelenella larbalestieri (A.L. Sm.) Coppins & Fryday (2004)

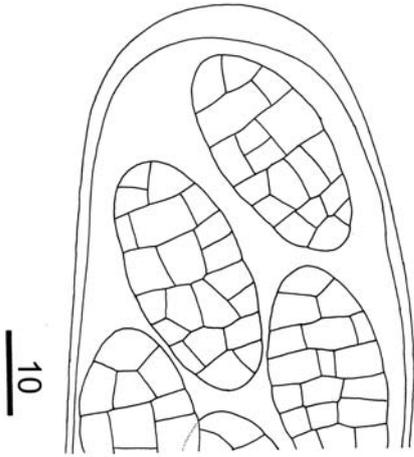
Chromatochlamys larbalestieri (A.L. Sm.) H. Mayrhofer & Poelt (1985)

Thallus thin to thickish, continuous or rimose, white to brown, sometimes growing epiphytically on other lichens. Perithecia black, three-quarters immersed, 150–200 µm diam., flattened vertically. Exciple pale brown, usually pigmented only in upper one-third or less, rarely more. Asci 8-spored. Ascospores 44–69 × 13–15 µm.

On damp siliceous rocks in woodland or beside streams, rare. W. Scotland, W. Ireland.
?Endemic.

Thelenella modesta (Nyl.) Nyl. (1855)

Thallus superficial, thin and membranous to thick and cracked or uneven-warted, yellow-grey to pink- or red-brown, fading to pale grey or grey in the herbarium. Perithecia 0.3–0.5 mm diam., rounded,



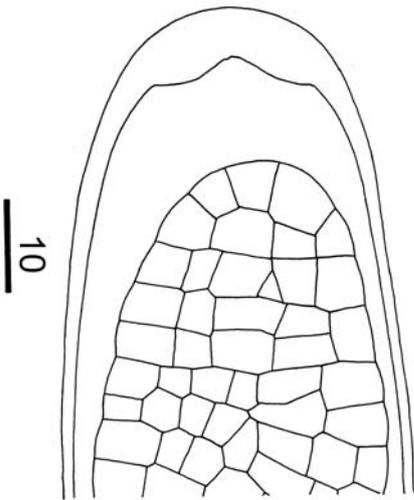
discrete or more or less aggregated, three-quarters- to fully immersed in thallus but forming prominent warts; exciple brownish above, pale or colourless below; ostiole dark brown. Asci 4–8-spored. Ascospores (20–)25–42 × (9–)11–17 μm. Conidia 11–14 μm long.

On more or less rough bark of wayside of parkland *Fraxinus*, very rare. N.E. Scotland (Angus, Glamis Village), also in 19th century in S.W. England (Gloucester, Barnsley Park). Europe (France, Germany, Greece, Italy, Poland, Portugal, Romania, Sweden, Switzerland), Africa.

Faded specimens in the herbarium superficially resemble *Pertusaria pertusa*.

Thelenella muscorum* (Fr.) Vain. (1899) var. *muscorum

Chromatochlamys muscorum (Fr.) H. Mayrhofer & Poelt (1985)



Thallus thin and membranous, or with convex to plane areoles 140–400 μm diam., often coalescing, whitish or pale brown; areoles with a colourless compact epinecral layer to 25 μm thick; cells of photobiont layer I + blue after treatment with K. Perithecia 0.3–0.6 mm diam., rounded or broadly pyriform, mostly immersed amongst the substrate with only the brown apex or the pale to brown ostiole evident; exciple 50–70 μm thick, pigmented above, brown, K – or almost, pale or colourless below. Paraphysoids 0.5–1.5 μm thick. Asci 2–4-spored, cylindrical, wall 3–6 μm thick. Ascospores 60–110 × 20–27 μm, colourless, becoming straw-coloured or brownish when old, strongly muriform, elongate-ellipsoid or subcylindrical.

Encrusting pleurocarpous mosses on basic-barked trees (especially *Ulmus*, *Fraxinus*, *Corylus* and *Acer*) in open situations, also on more or less calcareous dunes or

overgrowing mosses on limestones, serpentines, mica-schist, and epidiorite, often in exposed situations. Western British Isles, widespread. Europe (Austria, Bulgaria, Finland, France, Germany, Italy, Norway, Romania, Russia, Spain, Sweden, Switzerland, Yugoslavia), N. Africa (Tunisia), N. America.

A distinctive species with large muriform ascospores and branched paraphysoids; often only apparent as a thin, skin-like membrane with deeply immersed, rather pale perithecia. The I + blue reaction of the thallus (using 0.5% IKI) would assist in the identification of sterile material, but should not be confused with the I + violet reaction of the photobiont cell walls.

***Thelenella muscorum* var. *octospora* (Nyl.) Coppins & Fryday (2004)**

Thallus very thin, white, membranous. Perithecia pale brown to dark brown, three-quarters to completely immersed, 200–300 μm diam., rounded to broadly pyriform. Exciple pale brown above, colourless below. Asci 8-spored. Ascospores (50–)55–65 × 14.5–19 μm.

Over bryophytes, usually on trees, rarely on basic rocks or soil. N. England, Scotland, Germany.

Differs from *T. muscorum* var. *muscorum* in the 8-spored asci with smaller ascospores. *T. muscorum* var. *octospora* has been confused with *Strigula confusa*, which differs in the trentepohlioid

photobiont, the rounded to angular or elongate cells (*textura angularis*) of the exciple, and the granular rather than homogeneous exciple pigment.

Literature:

- Fryday, A.M. & Coppins, B.J. (2004) A reassessment of the genera *Chromatochlamys* and *Thelenella*, and a new species of *Strigula* from the British Isles. *Lichenologist* **36**: 89–95.
- Mayrhofer, H. (1987) Monographie der Flechtengattung *Thelenella*. *Bibliotheca Lichenologica* **26**: 1–106.
- Mayrhofer, H. & Poelt, J. (1985) Die Flechtengattung *Microglæna* sensu Zahlbruckner in Europa. *Herzogia* **7**: 13–79 (1985).

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 ellipsoid to clavate, I –, fissitunicate, wall thickened above, ocular chamber usually present; dehiscence by extrusion of a delicate endotunica as a long rostrum. **Ascospores** 8 per ascus, 1–3(–7)-septate (occasionally a small proportion of ascospores with 1–2 longitudinal septa), colourless, broadly to narrowly ellipsoid or oblong-ellipsoid, 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 either damp or calcareous, including freshwater habitats; occasionally on soil.

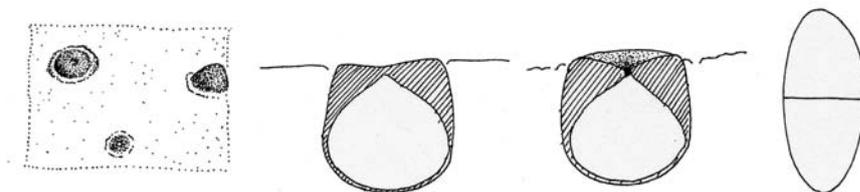
Classification: Chaetothyriomycetidae, Verrucariales, Verrucariaceae.

Verrucaria differs in the simple ascospores, and *Polyblastia* differs in the consistently submuriform to muriform ascospores, but a proportion of spores in some *Thelidium* species can have some longitudinal septa. The genus is unnatural.

- | | | |
|------|--|-------------------|
| 1 | Perithecia immersed in pits in calcareous rock, involucrellum absent, thallus endolithic | 2 |
| | Perithecia prominent, or immersed in 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– 31.2 –35(–47) μm long; exciple 160–340 μm diam.; a yellow, K + violet pigment often present in thallus | fontigenum |
| | Ascospores (28.5–)36– 41.0 –46(–54) μm long, exciple (170–)260–520(–660) μm diam.; yellow, K + violet pigment absent | incavatium |
| 4(1) | Involucrellum absent | 5 |
| | Involucrellum present | 7 |
| 5(4) | Ascospores 1-septate | 6 |
| | Ascospores 3-septate | zwackhii |
| 6(5) | Photobiont cells irregularly arranged, ascospores 20–30 \times 8–15 μm , involucrellum absent or fused with the exciple and visible as a slight thickening in the upper part of the perithecium; on sandstone | rehmii |
| | Photobiont cells arranged in small groups, ascospores 13–31 \times 4–15 μm , involucrellum absent or thin, indistinctly separated from the exciple and reaching the thallus base; on various substrata | minutulium |
| 7(4) | Ascospores 1-septate | 8 |
| | Ascospores 3(–5) septate | 13 |
| 8(7) | Ascospores (9–)11– 12.5 –14.5(–15.5) μm long; thallus endolithic | impressum |
| | 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 involucrellum reddish-brown, K + dark grey-brown; ascospores (24–)25.5–**28.1**–30.5(–34) μm long **fumidum**
 Involucrella not confluent; pigment in involucrellum brown, K – or + darker brown 10
- 10(9) Perithecia forming projections which are covered except at the apex by a layer of thallus; ascospores (19.5–)24–**26.8**–30(–37) μm **pluvium**
 Perithecial projections not covered by thallus 11
- 11(10) Ascospores (16.5–)21–**24.8**–28.5(–36.5) μm long, thallus usually white or grey, rarely brownish **pyrenophorum**
 Ascospores 26–46 μm long, thallus usually light grey-brown to dark brown 12
- 12(11) Perithecia (430–) 500 (–1600) μm diameter, ascospores (26–) 34 (–46) μm long **methorium**
 Perithecia (250–) 361 (–510) μm diameter, ascospores (26–) 28 (–39) μm long **submethorium**
- 13(7) Ascospores (20–)27.5–**31.2**–35(–47) μm long; perithecial projections 100–360 μm diam.; a yellow, K + violet pigment often present in thallus **fontigenum**
 Ascospores (27–)36.5–**42.8**–49.5(–65) μm long; perithecial projections (360–)400–800(–880) μm diam.; yellow, K + violet pigment absent **papulare**

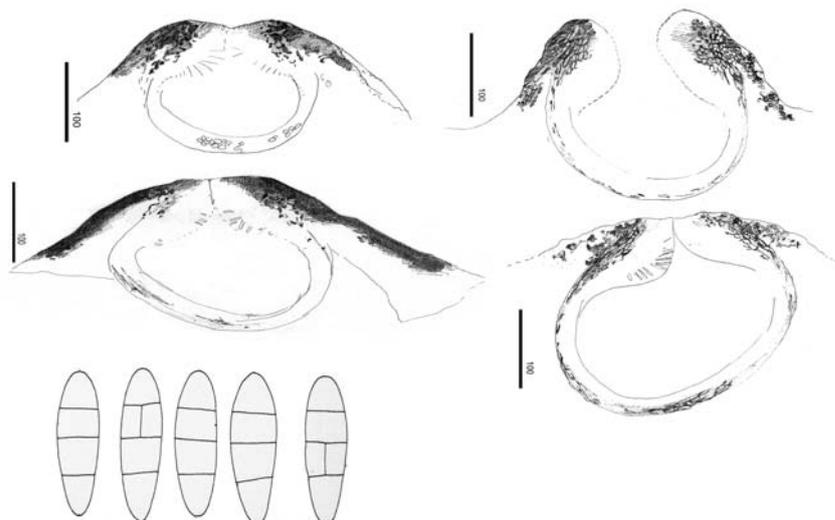
Thelidium decipiens (Nyl.) Kremp. (1861)



Thallus endolithic, white, grey or cream, or discoloured brown. Perithecia immersed in well-defined pits in rock, apex occasionally

projecting when old, apex usually separated from surrounding rock by a thin crack; ostiole inconspicuous. Involucrellum absent. Exciple 200–400 μm diameter, wall 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–**28.8**–32.5(–41) \times (9.5–)11.5–**12.9**–14.5(–19) μm , length/width ratio (1.5–)1.9–**2.2**–2.6(–3.2) [245/24]. On limestone, mortar, and calcareous sandstone; frequent. Widespread in Britain and Ireland. Widespread in Europe; Tajikistan.

Thelidium fontigenum A. Massal. (1856)



Thelidium microbolum (Tuck. in Drummond) Hasse (1913)

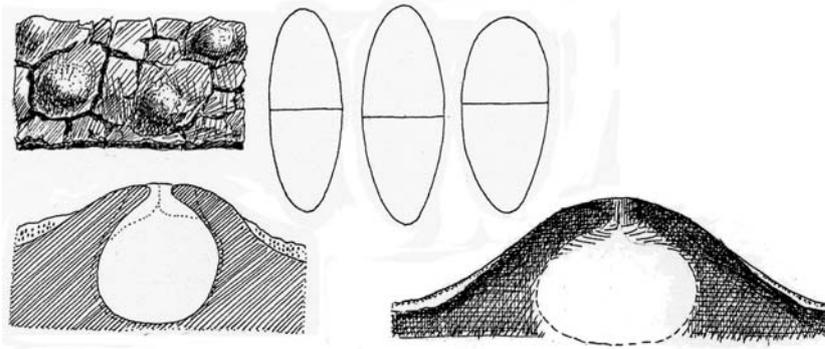
Thallus immersed, or superficial, thin, continuous or in small flecks; white, grey, dark brown, orange-yellow or purple-red;

often with flecks or extensive patches of a yellow, K + violet pigment. Perithecia immersed in pits in rock, or forming projections 100–360 μm wide. Involucrellum absent, or developed around the apex of the exciple in immersed perithecia; or thin, spreading from exciple below, and often reaching down to substratum in projecting perithecia. Exciple 160–340 μm wide, colourless to brown below. Ascospores 3-septate, (20–)27.5–**31.2**–35–47) \times (9–)11–**12.5**–14(–17) μm , length/width ratio (1.8–)2.2–**2.5**–2.8–4) [234/38]. Thallus (yellow areas) K + purple (quinone-like pigment).

On limestone, mortar, tufa, and on siliceous stones, especially where damp; local. Widespread in Britain and Ireland. Norway, Sweden, Germany, Switzerland. N. America.

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

Thelidium fumidum (Nyl.) Hazsl. (1884)



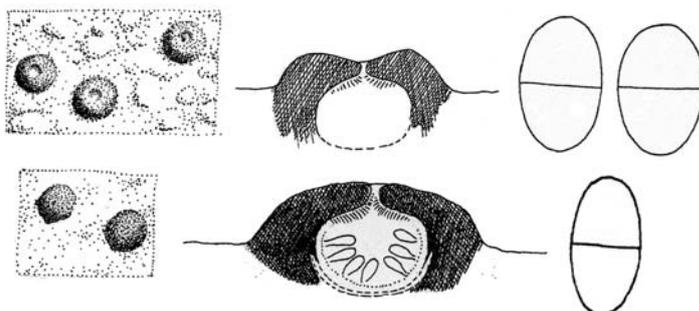
Thallus superficial, dark brown to blackish brown, to 210 μm thick, cracked, with a thick dark basal layer. Perithecia partly immersed in the thallus, forming low to moderate projections 260–635 μm wide, covered by a layer of thallus below but free above. Involucrellum thick, enclosing exciple, upper margin spreading

sideways and downwards, continuous with basal layer of thallus, pigment dark reddish brown, K + dark grey-brown. Exciple 180–365 μm wide. Ascospores 1-septate, (24–)25.5–**28.1**–30.5(–34) \times (9–)10–**11.1**–12.5(–15) μm , (1.7–)2.2–**2.6**–2.9(–3.8) times as long as wide [84/6].

On damp, slightly calcareous mica-schist rocks above 550 m altitude; rare. Scottish Highlands. France (Pyrenees), Austria, Romania.

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 except *T. impressum*. 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 may not be the same species.

Thelidium impressum (Stizenb.) Zschacke (1920)



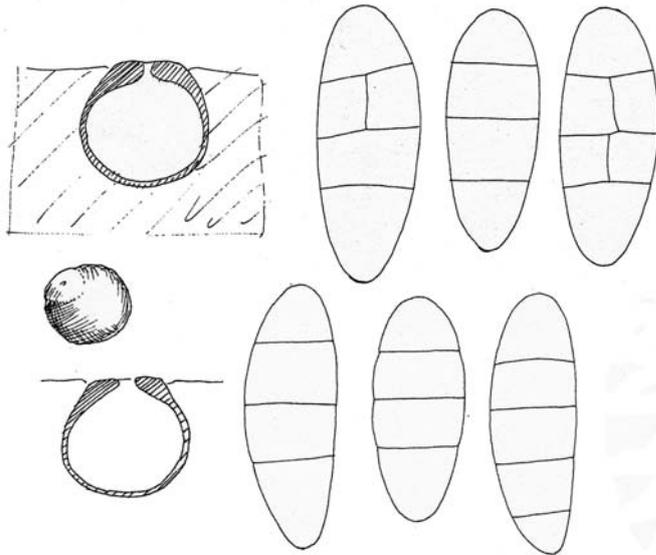
Thallus endolithic, pale grey to grey-brown, rarely epilithic. Perithecia approximately half-immersed in rock, sometimes leaving shallow pits, forming black projections 200–480 μm wide, sometimes flattened above; ostiole sometimes in a shallow depression. Involucrellum well-developed,

clasping exciple and often reaching to base-level of exciple, pigment dark reddish-brown, K + dark grey-brown. Exciple 155–280 μm wide. Ascospores 1-septate, (9–)11–**12.5**–14.5(–15.5) \times (6–)6.5–**7.5**–8.5(–9) μm , length/width ratio (1.4–)1.5–**1.7**–1.9(–2.1) [58/11].

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

Distinguished from other species in the genus by the small, 1-septate ascospores. Probably belongs in *Parabagliettoa*.

Thelidium incavatum Mudd (1861)

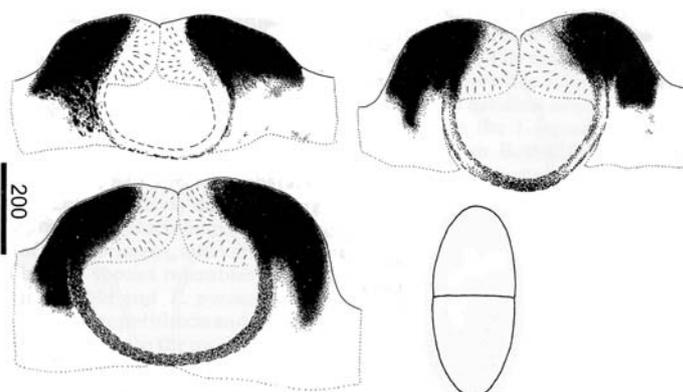


Thallus endolithic, white, grey or discoloured brown. Perithecia immersed in well-defined pits in rock, occasionally the apex projecting. Involucrellum absent. Exciple (170–)260–520(–660) μm diameter, wall brown throughout (blackish in thick section, translucent brown in squash preparation), K – to K + slightly darker brown or greenish-brown. Ascospores 3(–5)-septate, occasionally with 1(–2) longitudinal septa, (28.5–)36–**41.0**–46(–54) \times (11–)13.5–**15.1**–16.5(–20) μm , length/width ratio (1.8–)2.5–**2.7**–3.0(–3.9) [549/62]. On limestone and other calcareous rocks; frequent. Throughout Britain and Ireland. Widespread in Europe; N. America, South Orkney Islands.

Characterised 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.

Thelidium methorium (Nyl.) Hellb. (1875)

T. aeneovinosum (Anzi) Arnold (1868)

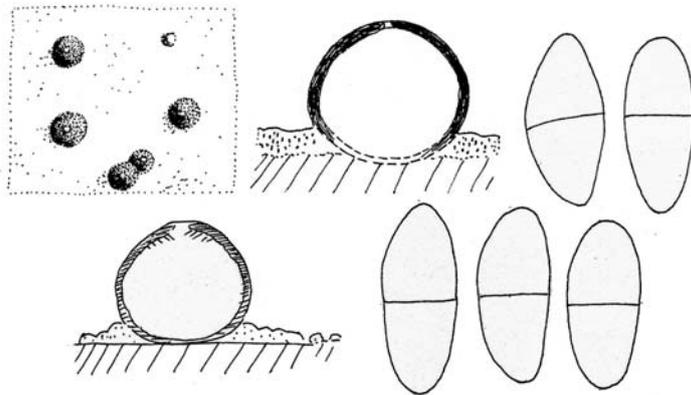


Thallus epilithic, light grey-brown to dark brown (rarely greenish-grey in shade), usually rimose, 85–240 μm thick. Perithecia forming projections (300–)400–700(–740) μm diameter, black, sometimes appearing grey or brown due to very thin pale surface layer; not covered by thallus; ostiole inconspicuous or visible as a pale dot, depressed or not. Involucrellum

well-developed, sometimes reaching to level of base of exciple. Exciple 28–500 μm diameter, (almost colourless to) dilute brown to brown or green-brown (dark in thick section), K + greenish brown to green. Ascospores 1-septate, (25–)30–**34.1**–38(–49) \times (10–)13–**14.7**–16.5(–20), length/width ratio (1.6–)2.0–**2.3**–2.7(–3.5) [405/68]. On mica-schist, one collection beside a stream; very rare. C. Scotland. Northern and montane Europe, N. America.

The description applies mainly to material from outside the British Isles; in parts of N. Europe this is a conspicuous species of wet siliceous rocks. Usually easily identified by the brown, epilithic thallus, large perithecia, and the large, 1-septate ascospores, but there is a gradation to a minority of specimens which have smaller perithecia and a spore length which falls in part below 30 μm . *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)**



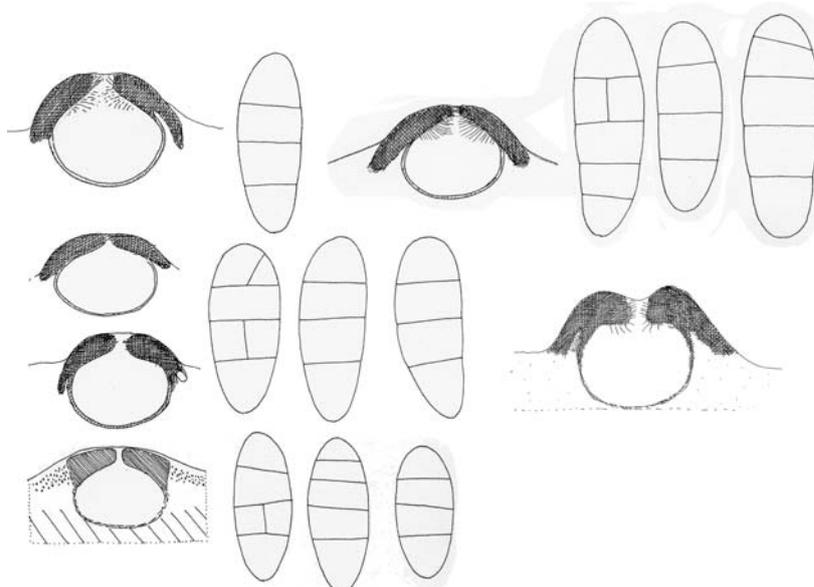
Thallus superficial, pale grey-green to dark brown, in numerous small patches or continuous, usually not cracked, thin, 30–160 μm thick. Perithecia very prominent or up to half-immersed in thallus, (85–)100–260(–340) μm diameter. Ostiole inconspicuous. Involucrellum absent. Exciple brown above, K – or K + slightly darker brown or greenish brown, usually colourless at base.

Ascospores 1-septate, (12–)19–**22.0**–25(–30.5) \times (5–)8.5–**9.6**–

10.5(–13) μm , length/width ratio (1.2–)2.1–**2.3**–2.6(–3.3) [405/40]. 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. Widespread in Europe.

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) f. *papulare



Thallus immersed to superficial, white, grey or brown, superficial thallus 50–150(–200) μm thick. Perithecia forming projections (360–)400–800(–880) μm diameter, blackish or appearing grey or brown due to very thin pale surface layer, not covered by thallus. Ostiole often visible as a pale dot, sometimes lightly depressed. Involucrellum well-developed. Exciple

(220–)250–550(–620) μm diameter, wall brown, K – or + slightly darker brown or greenish brown. Ascospores 3(–5)-septate, occasionally with 1 or more longitudinal septa, comprising 4(–7) cells in total, (27–)36.5–**42.8**–49.5(–65) \times (10.5–)14–**16.4**–18.5(–23) μm , length/width ratio (1.7–)2.3–**2.6**–3.0(–3.9) [581/124].

On limestone, mica-schist, calcareous sandstone and mudstone; often on damp rocks, locally frequent. Widespread in Britain and Ireland. Widespread in Europe. N. Africa, N. America, Australia, New Zealand.

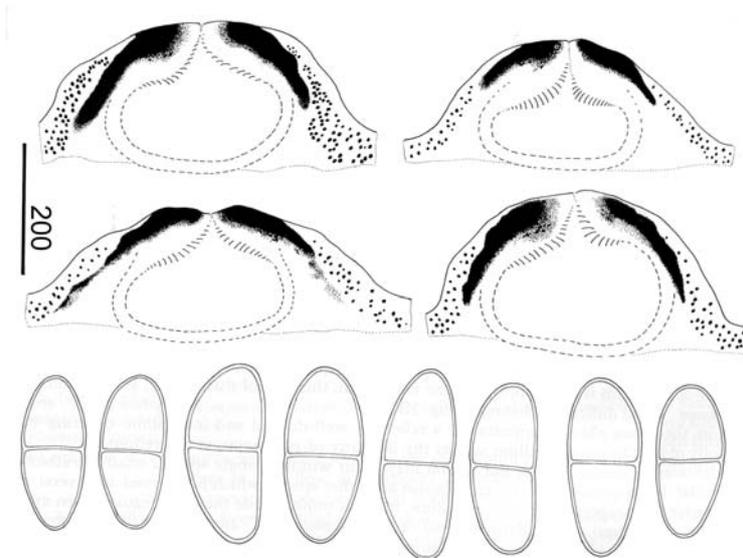
Characterised by the relatively large perithecia, well-developed involucrellum and 3(–5)-septate ascospores. Specimens from limestone, with an immersed thallus, tend to have smaller ascospores with fewer septa than specimens from siliceous rocks which have a superficial thallus. *T. methorium* and *T.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

***Thelidium papulare* f. *sorediatum* Coppins (1991)**

Thallus grey-brown to mid brown, cracked; soralia present, mainly scattered and irregularly linear, developing along cracks in the thallus, brown, abrading dull pale green. Perithecia as in f. *papulare*.

On slightly calcareous schist or on limestone, at altitudes of 120–900 m; rare. N.W. and C. Scotland, Outer Hebrides (Lewis).

***Thelidium pluvium* Orange (1991)**



Thallus epilithic, pale grey-green to dark brown, continuous to lightly rimose, 3–85 μm thick. Perithecia forming conical-hemispherical projections 240–450(–500) μm diameter, covered except at apex by a layer of thallus, black at apex. Ostiole inconspicuous, not depressed. Involucrellum relatively thin and weakly developed, present only in upper half of exciple and scarcely spreading, or spreading sideways and downwards and nearly reaching to base-level of

exciple, brown, K – or K + darker brown or greenish-brown. Exciple 200–350 μm diameter, brown at apex, colourless below. Ascospores 1-septate, (19.5–)24–**26.8**–30(–37) \times (7–)10.5–**12.3**–14(–18) μm , length/width ratio (1.7–)1.9–**2.2**–2.5(–3.1) [242/24]

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

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

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

Thallus superficial, white or grey, rarely brownish, or immersed, cracked or not. Perithecia forming projections (240–)300–700(–860) μm diameter, not covered by thallus, black or sometimes grey due to superficial colourless layer. Ostiole inconspicuous or somewhat depressed. Involucrellum well-

developed. Exciple colourless to brown below. Ascospores 1-septate, $(16.5-21-24.8-28.5(-36.5) \times (7.5-10-11.7-13.5(-16.5) \mu\text{m}$, length/width ratio $(1.5-1.9-2.1-2.4(-3.3)$ [474/58].

On limestone, mortar, mica-schist, and basic siliceous rocks; occasional. Widespread in Britain and Ireland. Widely distributed in Europe; N. America.

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.

***Thelidium rehmi* Zschacke**

Very similar to *T. minutulum* but thallus often more even (less granular), and the photobiont cells not in aggregated groups. The two differ in ITS sequence.

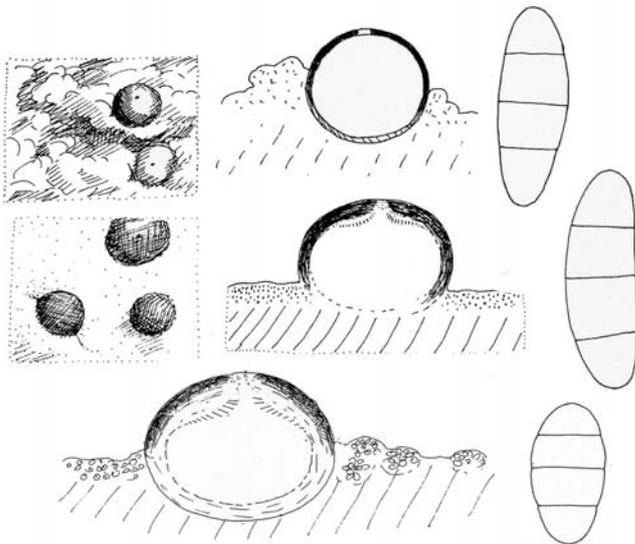
Not reported from Great Britain. Germany.

***Thelidium submethorium* (Vain.) Zahlbr.**

Differs from *T. methorium* in the smaller perithecia and ascospores.

Not reported from Great Britain. Finland, Germany, Italy.

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



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 $20-45 \mu\text{m}$ in section, often with brown pigment in surface cells. Perithecia prominent or half-immersed in thallus, $100-290 \mu\text{m}$ wide, sometimes collapsing into a concave shape when dry. Involucrellum absent. Exciple $140-300 \mu\text{m}$ wide (moist sections), brown above, usually colourless at base. Ascospores $(20-26.5-29.8-33(-39) \times (8.5-10.5-11.7-13(-15) \mu\text{m}$, length/width ratio $(1.8-2.3-2.6-2.8(-3.5)$ times as long as wide [466/55].

On limestone, chalk, and siliceous rocks, usually on small stones, and on soil; in moist situations, apparently a rapid coloniser of short-lived niches; in woodland, waste ground and by streams; frequent. Widespread in Britain. Widespread in Europe.

Distinguished by the small, prominent perithecia without an involucrellum, and the 3-septate ascospores. *Thelidium fontigenum* differs in the perithecia being either immersed in pits, or with an involucrellum; *T. minutulum* differs in the 1-septate ascospores.

Literature:

H. Thüs and J. Nascimbene 2008: Contributions toward a new taxonomy of Central European freshwater species of the lichen genus *Thelidium* (Verrucariales, Ascomycota). - *Lichenologist* **40(6)**: 499-521.

THELOCARPON Nyl. (1853)

Thallus present, typically surrounding the ascoma as a sheath, the whole forming a thalline verruca, or thallus absent. **Photobiont** green or absent. **Ascomata** perithecioid and then globose to flask-shaped, or apothecioid, cylindrical to disc-shaped, with the hymenium exposed as a narrow or broad disc; sessile, immersed in thalline verrucae, or immersed in the substratum; ascomata often yellow-pruinose. **Exciple** colourless or pale brownish, lacking dark pigments. **Hamathecium** of simple, branched, or branched and anastomosing paraphyses, or of periphysoids and periphyses. **Hymenial gel** I –, or hemiamyloid: I + red, (but I + yellow or blue at low concentrations of iodine), K/I + blue. **Asci** flask-shaped to cylindrical, wall I – to + blue or dull reddish, uniformly thin, or thickened, sometimes thickened at apex into a tholus; apical apparatus absent, or present as an I + darker blue plate or ring-structure; asci multispored, with 12–300 spores. **Ascospores** small, 3–13 µm long, simple, rarely 1-septate, spherical to cylindrical, often with 2 oil-droplets, colourless. **Conidiomata** pycnidia, flask-shaped, sessile, or immersed with ascomata in thalline verrucae. **Conidiogenous** cells simple, acrogenous, elongated. **Conidia** oblong-ellipsoid to shortly cylindrical, simple, or a proportion to 2-septate, 3–8 × 1–2 µm. **Chemistry:** pulvinic acid derivatives (including vulpinic acid, pulvinic dilactone and pulvinic acid) in many species; when present, forming a superficial yellow pruina, or rarely enclosed within the upper exciple. **Ecology:** on rock, soil, wood, leather, and on decaying lichens; short-lived species, often found on substrata recently made available for colonisation, such as disturbed soil, burnt ground, exposed stones beside tracks, and stones on bonfire sites.

Classification: Lecanoromycetidae, Lecanorales, Thelocarpaceae.

Species of this genus are easily overlooked, as the ascomata are very small, and they are short-lived. The iodine reactions of the hymenium are useful in identification, but should be used with caution as they vary somewhat with the concentration of iodine in the reagent, and authors have not always specified the formula used. A solution with 0.5% iodine or less is the most useful.

LITERATURE: Magnusson, A.H. (1936), Salisbury (1966), Poelt & Hafellner (1975), Poelt & Vezda (1977), Kocourková-Horáková (1998).

- | | |
|------|--|
| 1 | Paraphyses absent; periphyses and periphysoids lining ascomatal cavity 2
Paraphyses present; periphyses and periphysoids absent 7 |
| 2(1) | Lichenized, with a well-defined algal sheath surrounding each ascoma 3
Not lichenized, algal sheath absent (but free-living algae may be associated with base of ascoma) 5 |
| 3(2) | Thalline verrucae bright yellow, with a yellow pruinose surface; ascospores (2–)2.5
3.5(–4) × 1.5–2 µm olivaceum
Thalline verrucae almost colourless to brown or pale yellowish, without pruina;
yellow pruina absent or confined to apex of ascoma 4 |
| 4(3) | Ascospores oblong, slightly constricted, 3.5–4.5(–5) × 1.2–2 µm; yellow pruina
completely absent magnussonii
Ascospores oblong-ellipsoid, (6–)7–9(–10) × 3.5 µ; yellow pruina sometimes present
on apex of ascoma pallidum |
| 5(2) | Ascomata bright yellow, the surface with yellow pruina; ascomata prominent,
immersed only at base 6
Ascomata brown, with the apex yellow-green when moist, yellow pigment confined
to inner part of upper exciple; ascomata immersed in the substratum, with only the
apex projecting opertum |

6(5)	Asci I + pale blue; ascospores 3–4(–5) × 1–1.5 µm	intermediellum	
	Asci I –; ascospores 4–7 × 2–3 µm	saxicola	
7(1)	Hymenial gel I – or absent		8
	Hymenial gel I + red		10
8(7)	Ascomata perithecioid, conical to globose; asci flask-shaped, tapered to apex	epibolum	
	Ascomata apothecioid; cylindrical to obconical or dish-shaped; asci cylindrical		9
9(8)	Ascomata shortly cylindrical, obconical or dish-shaped, (80–)100–200 µm diam., (0.5–)0.9–2.9 times as wide as high	lichenicola	
	Ascomata obconical-cylindrical, c. 100 µm diam., c. 0.4–0.5 times as wide as high	strasseri	
10(7)	Lichenized, with a well-defined algal sheath surrounding each ascoma; paraphyses branched and anastomosing		11
	Not lichenized, algal sheath absent (but free-living algae may be associated with base of ascoma); paraphyses simple or mostly so		12
11(10)	Thalline verrucae with well-defined margins, yellow, covered by yellow pruina	laureri	
	Thalline verrucae with irregular margins, grey-green or brownish, yellow pruina confined to ostiolar region of exciple	robustum	
12(10)	Ascomata perithecioid, conical or globose	superellum	
	Ascomata more or less apothecioid, truncate above, with a narrowly exposed hymenial disc		13
13(12)	Ascospores oblong, 6–8.5(–11) × 4–5 µm; ascomata 160–200(–370) µm diam.	impressellum	
	Ascospores spherical, 4.5–6 µm; ascomata 150–200 µm diam.	sphaerosporum	

Thelocarpon epibolum Nyl (1866)

Perithecia immersed only at base, ovoid or conical, 100–170 µm diam., 150–200 µm high, yellow-pruinose; algal sheath absent. Perithecial wall 15–30 µm thick, colourless. Paraphyses simple, as long as asci. Asci flask-shaped, narrowed to apex, wall I –, apex unthickened, sometimes in young asci containing a thin, I + blue structure. Hymenial gel I + red, (+ blue at low concentrations of iodine), K/I + blue. Ascospores oblong, not or slightly constricted, 4–6 × 1.7–2 µm (var. *epibolum*) or (6–)8–10(–12) µ × 3 µm (var. *epithallinum* (Leight.) G. Salisb. (1953)). Pycnidia flask-shaped, 75–105 µm high, 40–60 µm diam., yellow-pruinose above. Conidia simple to 2-septate, 4–7 × 1.2–1.6 µm.

Illustration: Wirth (1995) p. 901.

On the thallus of *Baeomyces rufus*, *Lichenomphalia hudsoniana*, *Solorina* and *Peltigera*, and on soil and rotten wood. Throughout Britain. Europe (widespread), N. America.

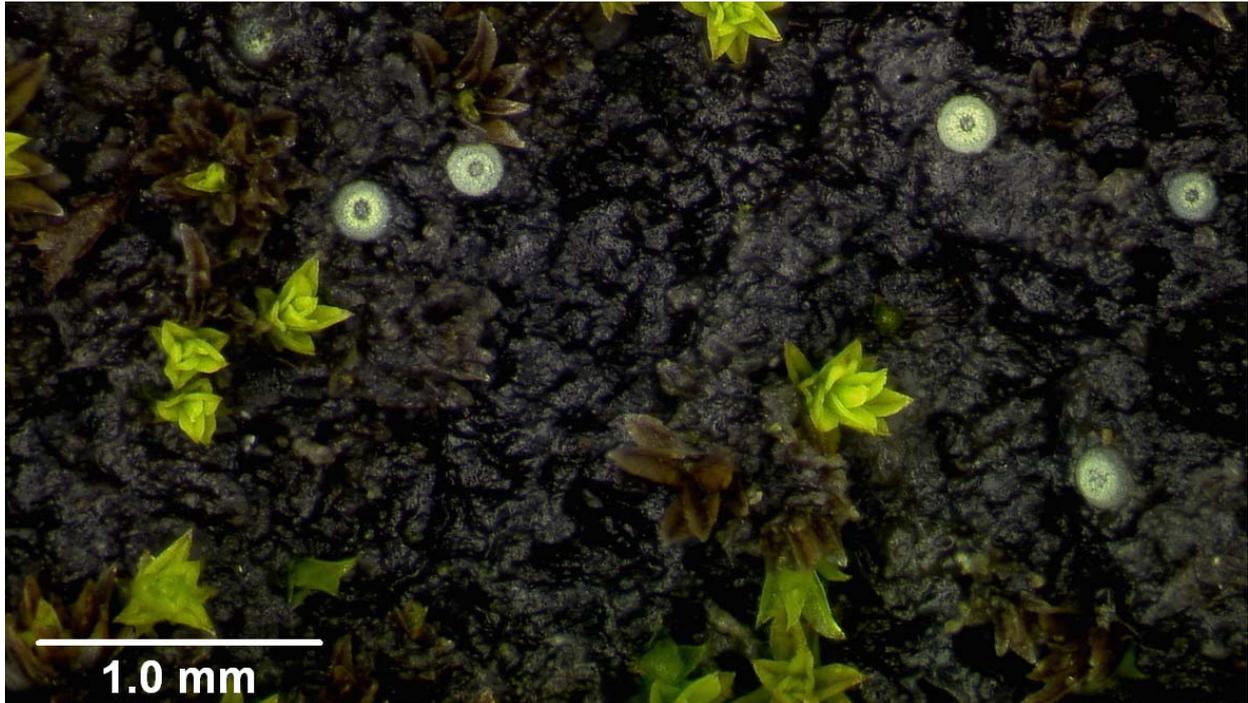
Thelocarpon impressellum Nyl. (1867)

Ascomata, globose, 160–200(–370) µm diam., up to 200 µm high, more or less apothecioid; apex truncate, hymenium exposed as a minute disc; apex of ascoma yellow-pruinose, sides less pruinose; algal sheath absent. Exciple 30–50 µm below, expanded to 40–70 µm at apex, colourless. Hymenial

gel I + red (+ faint dull bluish at low concentrations of iodine, soon yellow, then orange, with increasing concentration), K/I + blue. Paraphyses mostly simple, sometimes a few also branched and anastomosing, exceeding the asci, apices pressed together to form an epithecium. Asci spindle-shaped, wall I – or I + pale blue in upper part, the apex thickened into a tholus with a darker-staining ring-shaped structure within. Ascospores oblong, $6-8.5(-11) \times 4-5 \mu\text{m}$, simple, often with 1-2 oil droplets.

On soil, rock or humus, especially in calcareous dunes, rare. N. & W. British Isles. Europe (widespread, from Norway to Czech Republic). N. America.

The hymenial gel is a dense red in 0.5% IKI; the shade of red is similar to that in *T. opertum*, and is perhaps denser and more orange than in the other species.



Thelocarpon impressellum

Thelocarpon intermediellum Nyl. (1865)

Perithecia immersed only at base, globose, $150-250(-300) \mu\text{m}$ diam., yellow-pruinose; algal sheath absent. Perithecial wall $30-45 \mu\text{m}$ thick above, $15-25 \mu\text{m}$ below. Periphyses lining apex and sides of hymenial cavity, $20-25 \mu\text{m}$ long, branched, easily detached. Paraphyses absent. Hymenial gel I + red. Asci flask-shaped, tapering to apex, $(80-100-160(-220) \mu\text{m}$ long, I + pale blue; ascus apex unthickened, I –. Ascospores oblong, slightly constricted, $3-4(-5) \times 1-1.5 \mu\text{m}$, simple, sometimes with two oil-droplets. Pycnidia flask-shaped, colourless or pale yellow, $105-165 \mu\text{m}$ high, $45-80 \mu\text{m}$ diam. Conidia simple to 2-septate, $4.5-6.5 \times 1.1-1.8(-2.1) \mu\text{m}$.

On rotten wood, old leather, moist rocks, generally associated with algae; rare. Throughout British Isles. Europe (widespread), Siberia, N. America.

Thelocarpon laureri (Flot.) Nyl. (1855)

Thallus comprising an algal sheath $25-60(-100) \mu\text{m}$ thick surrounding the perithecium, forming gently convex to hemispherical or globose verrucae $150-300 \mu\text{m}$ diam., yellow-pruinose, sometimes with a darker centre denoting the perithecial apex. Hyphae branched, $2 \mu\text{m}$ wide, photobiont cells not reaching the surface, leaving a colourless cortex $8-15 \mu\text{m}$ thick and formed of vertically arranged gelatinized hyphae. Hymenial gel I + red (+ blue at very low concentrations of iodine), but very

scanty, occasionally not discernible. Paraphyses branched and anastomosing, as long as asci. Asci flask-shaped, tapering to apex, 75–150(–170) μm long, wall I + pale dull blue at least in upper part (in reagents with 0.5% I concentration). Ascus apex slightly thickened, with a darker staining I + blue structure within. Subhymenium I + blue. Ascospores subglobose to ellipsoid, 1.5–4(–6) \times 1.5–2 (mostly 3 \times 2) μm , simple, often with 1-2 oil droplets.

Illustration: Wirth (1995) p. 901.

On recently exposed or burnt stones, wood, burnt ground, brick and leather; occasional. Throughout British Isles. C. & N. Europe, Canary Isles, N. America.

Distinguished from other species, except *T. robustum*, by the long, branched and anastomosed paraphyses.

Thelocarpon lichenicola (Fuckel) Poelt & Hafellner (1975)

Non-lichenized. Ascomata sessile, apothecioid; shortly cylindrical, obconical or dish-shaped; (80–)100–200 μm diam. (to 300 μm when moist), 70–120(–160) μm high, diameter/height ratio (0.5–)0.9–2.9, yellow; hymenium exposed as a disc which is more or less plane or deeply sunken (dry); algal sheath absent; disc and sides of ascoma with yellow pruina. Hymenial gel absent. Paraphyses sparingly dichotomously branched, apices unthickened, forming an epithecium. Asci cylindrical-clavate, 65–85 \times 11–14(–17) μm , wall thickened, I + strongly blue at low concentrations of iodine (0.1% IKI), but dark bluish brown at 0.5%IKI and above, K/I + dark bluish brown; with a darker-staining, shallowly convex cap within the apex. Ascospores simple, (4–)5–7.5 \times 1.5–2.5 μm . Pycnidia flask-shaped, sessile, 75–120 μm high, 50–85 μm diam., yellow-pruinose above. Conidia simple or rarely 1-septate, 6.5–8 \times 1.8–2.1 μm .

On soil, siliceous and dolomite stones, wood, and on *Baeomyces rufus*; often associated with a thin layer of algae; in woodland or beside woodland tracks; frequent. S., W. & N.W. England, Wales, Scotland, Norway, Sweden, France, Netherlands, Austria, Italy, Slovakia, Russia.

Distinguished by the exposed hymenium and cylindrical asci. *T. strasseri* is said to differ in the small ascomata that are twice as tall as wide. Young ascomata of *T. lichenicola* are cylindrical to top-shaped, but are still typically no taller than wide; however, one collection had some ascomata resembling *T. strasseri* in size and shape, but others up to 150 μm diam. and 100 μm high.

Thelocarpon magnussonii G. Salisb. (1953)

Thallus mostly comprising an algal sheath 20–35 μm thick surrounding the perithecium, forming hemispherical verrucae 140–250 μm diam., also continuing as a very thin layer on the substratum; verrucae almost colourless to brown-green when moist, pale brown to almost black when dry, without pruina. Hyphae gelatinized, no distinct cortex formed, the photobiont cells reaching the surface. Perithecia seated on the substratum, globose, 130–180 μm diam., wall 15–18 μm thick, colourless. Paraphyses absent. Periphyses 6–10 μm long, sparingly branched. Asci flask-shaped, (90–)120–150 \times 30–40 μm , the apices often projecting through the ostiole, I –. Hymenial gel I + red, K/I + blue. Ascospores oblong, slightly constricted, 3.5–4.5(–5) \times 1.2–2 μm , simple, often with 2 oil droplets.

On siliceous stones in woodland, beside streams, rabbit burrows, and on bonfire sites; or on old leather; occasional, overlooked. N. & W. England, Wales, N.W. Scotland, Austria.

Completely without yellow pruina, and thus very inconspicuous when dry.

Thelocarpon olivaceum de Lesd. (1914)

Thallus comprising an algal sheath around the perithecium, forming hemispherical verrucae which are 150–270 μm diam. and 120–170 μm high, yellow-pruinose, or grey to discoloured brown and yellow-pruinose only at the apex; hyphae branched, gelatinized; photobiont cells absent near surface, leaving an uneven cortical zone 6–12 μm thick. Perithecia globose, 100–150 μm diam., immersed within a thalline verruca, wall 6–12 μm thick, colourless. Periphyses lining the sides and apex of perithecial

cavity, branched, 20–25 µm long. Paraphyses absent. Hymenial gel I + red, K/I + blue. Asci flask-shaped, tapering to apex, 70–120 µm long, I – or + pale blue. Ascospores simple, oblong-ellipsoid, sometimes nearly spherical, not constricted, (2–)2.5–3.5(–4) × 1.5–2 µm. Conidiomata rare, *c.* 35 µm diam., colourless, immersed in thalline verrucae; conidia 4.5–5 × 1 µm.

On recently exposed stones and thin soil, on old leather and brick, rare. W. England (Shropshire, West Gloucestershire), N.W. England (S. Lancashire), Wales (Pembrokeshire). C. Europe.

Thelocarpon opertum J.C. David & Coppins (1997)

Thallus inconspicuous, associated with various cyanobacteria, but a true photobiont absent. Ascomata perithecioid, globose to slightly conical, immersed in the algal mass, slightly protruding when dry, the exposed part pale brownish to brown; sometimes the ostiolar region faintly greenish when dry, yellow-green when moist. Exciple *c.* 250–290 µm diam., the wall 30–40 µm thick, colourless on the outside, dilute brown within, inner exciple near ostiole with a patch of yellow crystalline material; algal sheath absent. Paraphyses absent. Periphyses present in upper part of exciple, up to 70 µm long, sparingly branched. Hymenial gel I + red (+ yellow at very low concentrations of iodine), K/I + strongly blue. Asci cylindrical, narrowed to apex, thin-walled, 130–170 × 14–21 µm, I –, K/I –. Ascospores more or less spherical, 3–5.5 µm diam., simple.

In crusts of cyanobacteria (including *Nostoc*, *Oscillatoria* or coccoid species) on calcareous dunes and over limestone; local, probably overlooked. S.W. England, S. Wales, N.W. Scotland.

In the field, detected by the greenish apices of the moist ascomata within crusts of cyanobacteria; this green colour is caused by the small patch of yellowish crystals (presumably pulvinic acid derivatives) enclosed within the exciple. When dry the green colour is scarcely evident, and the ascomata are inconspicuous. The ‘hemiamyloid’ reaction of the hymenial gel differs from that in many other ascomycetes, as very low but increasing concentrations of iodine first cause a yellow to orange reaction, proceeding to red with increasing iodine concentration, but without a blue stage. The periphysoids are partly appressed to the exciple, and longer than they at first appear; they could be mistaken for paraphyses in a squash preparation.

Thelocarpon pallidum G. Salisb. (1953)

Thallus comprising an algal sheath 35–40 µm thick around the perithecium, forming verrucae 200–300(–400) µm diam., colourless or pale yellowish translucent when moist, but inapparent when dry, sometimes yellow-pruinose on exposed apex of exciple. Hyphae gelatinized, photobiont cells not reaching surface, leaving a cortical zone *c.* 20 µm thick. Paraphyses absent. Periphyses 6–20 µm long, branched. Hymenial gel I + red. Asci flask-shaped, tapering to apex, 110–180 × 25–30 µm, I + pale blue. Ascospores oblong-ellipsoid, (6–)7–9(–10) × 3.5 µm, simple, sometimes with 1–2 oil droplets.

On brick, chalk, and damp mortar. England (S. Lancashire, Sussex), Wales (Cardigan). Endemic.

Thelocarpon robustum Eitner (1900)

Thallus forming more or less plane to convex verrucae 200–300 µm diam., the margins irregular, sometimes divided by cracks from similar verrucae; verrucae green-grey, somewhat cartilaginous in appearance, without pruina. Cortex 30–40 µm thick, colourless, strongly gelatinized. Perithecia immersed in thallus, 1(–2) per verruca, the ostiole visible as a yellow-green disc 30–50 µm diam.; apex of perithecium with yellow pruina which is partly covered by the thallus cortex. Paraphyses long, branched and anastomosing. Hymenial gel I + red (+ blue at low concentrations of iodine). Asci flask-shaped, tapering to apex, wall uniformly thin, I + dull red, K/I + blue. Ascospores oblong-ellipsoid, simple, 3.7 × 2.1 µm, with two oil-droplets.

On siliceous stones which are recently disturbed or exposed to fire. Wales (Montgomeryshire), W. Scotland (Isle of Skye). Poland.

Differs from *T. laureri* in the poorly delimited verrucae which lack pruina, and in the thicker, strongly gelatinized cortex. *Myriospora heppii* differs in the apothecioid ascomata (sometimes with yellow pruina) and the strongly thickened ascus apex.

Thelocarpon saxicola (Zahlbr.) H. Magn. (1935)

Non-lichenized. Ascomata perithecioid, immersed only at base, globose, 120–180 µm diam., rather coarsely yellow-pruinose; algal sheath absent. Perithecial wall *c.* 25 µm thick above, 10–15 µm thick below, colourless. Paraphyses absent. Periphyses 20–25 µm long, slightly branched. Asci flask-shaped, tapering to apex, (70–)90–125 × 12–15 µm, I –. Hymenial gel very viscous, I + yellow then yellow-red, K/I + blue. Subhymenium I + pale blue. Ascospores oblong-ellipsoid, sometimes slightly curved, 4–7 × 2–3 µm, simple, ellipsoid, rarely with a weak septum visible in K.

On shaded stones in woodland, C. Wales (Breconshire). Spain Austria, Poland.

Thelocarpon sphaerosporum H. Magn. (1935)

Non-lichenized. Ascomata more or less apothecioid, with a narrowly exposed hymenial disc; 150–200 µm diam., yellow-pruinose. Hymenial gel I + red, K/I + blue. Asci flask-shaped, tapering to apex. Paraphyses simple. Ascospores spherical, 4.5–6 µm diam. Pycnidia minute, flask-shaped, pale yellow; conidia 4–6 µm long.

On a cyanobacterial film on calcareous schist; rare. Scotland (Aberdeenshire). Norway, Sweden, Netherlands, Austria, Italy (Tirol), N. America.

Similar to *T. impressellum*, but differing in the smaller ascomata and spherical ascospores.

Thelocarpon strasseri Zahlbr. (1902)

Non-lichenized. Ascomata apothecioid, stalked, obconical-cylindrical, *c.* 100 µm diam., 200–240 µm high, greenish yellow. Paraphyses simple or often dichotomously branched, apices somewhat widened, forming a yellow-granular epithecium. Asci 80–90 × 10–15 µm, wall I + blue. Ascospores 5–7 × 1.7–3 µm.

On decaying wood, rare. S. England (New Forest). Belgium, Netherlands, Austria.

Similar to *T. lichenicola*, but with ascomata taller than wide.

Thelocarpon superellum Nyl. (1866)

Thallus absent. Perithecia immersed only at base, conical or globose, 200–300(–380) µm diam., 250–350(–500) µm high, yellow-pruinose; algal sheath absent. Perithecial wall 35–60 µm thick, colourless. Paraphyses simple, as long as asci, up to 1 µm thick. Asci flask-shaped, tapering to a narrow apex, 150–250(–300) µm long, wall I + dull blue to dull reddish (in 0.5% I; + blue in 0.1% I), K/I + blue; apex unthickened, in K/I staining slightly darker than rest of wall. Hymenial gel I –. Ascospores oblong, (6–)8–13 × (2.5–)3.5–5(–6) µm, simple, usually with a pseudoseptum, with two oil drops in I.

On acidic to calcareous soil and on stones, sometimes associated with a layer of algae; rare. North Wales, Scotland. C. & N. Europe, N. America, S.E. Asia (Hong Kong).

Thelocarpon citrum (Wallr.) Rossman (1999) is not recorded from the region, but should be looked out for; it differs in the smaller perithecia and the slightly smaller ascospores, 4.5–10 × 2–3.5 µm, without pseudosepta.

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Illustration references:

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THELOPSIS Nyl. (1855)

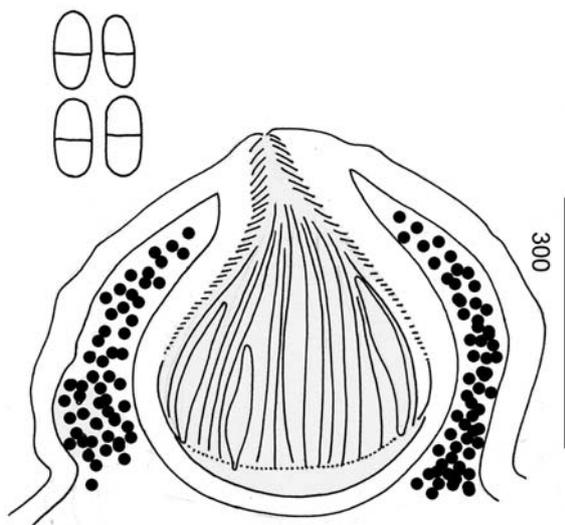
Thallus crustose, immersed to superficial, rarely byssoid; grey, greenish, or orange-red. **Prothallus** present and whitish, or absent. **Photobiont** trentepohlioid. **Ascomata** perithecia, immersed, sessile, or enclosed in thalline warts; colourless to reddish brown or black. **Involucrellum** absent. **Exciple** of compressed cells or of distinctly filamentous hyphae, colourless to brownish black, sometimes layered. **Hymenial gel** I-, K/I-. **Hamathecium** of thread-like unbranched paraphyses (a few anastomoses sometimes present), and of periphyses. **Asci** multispored, cylindrical to oblong, I+ blue or (blue at low concentration) dull greyish or dull red, K/I+ blue; walls uniformly thin, without an apical apparatus. **Ascospores** 0-3(-5)-septate, often with a perispore. **Conidiomata** pycnidia, pale, in one species divided into several locules. **Conidia** simple, colourless, ellipsoid to ovoid (or also thread-like?). **Chemistry**: lichen products not detected by t.l.c. **Ecology**: on bark and rock. **Distribution**: c. ten species, cosmopolitan.

Characterized by its trentepohlioid photobiont, and thin-walled, multispored asci containing simple to few-septate ascospores. In at least some species, the I+ reactions of the hymenium are situated in the ascus walls, the hymenial gel itself is I-. The paraphyses occupy a broad zone around the ostiole, becoming gradually very short below; they are very distinct in size and point of origin from the paraphyses.

LITERATURE: Vězda (1968b).

- 1** Ascospores 1-septate; ascomata enclosed in a thalline wart; exciple unpigmented *isiaca*
 Ascospores 3-septate; ascomata sometimes immersed in thallus or clothed below with thallus fragments, but not enclosed by a well-defined thalline wart; exciple orange-brown in outer part **2**
- 2(1)** Ascomata pale brown to red-brown, sometimes blackish at the apex, surface smooth; thallus grey-green to pale brownish when fresh; on bark of native trees, lowland *rubella*
 Ascomata black, surface wrinkled or striate; thallus orange-red to red-brown when fresh; on mosses on rocks, upland *melathelia*

Thelopsis isiaca Stizenb. (1895)



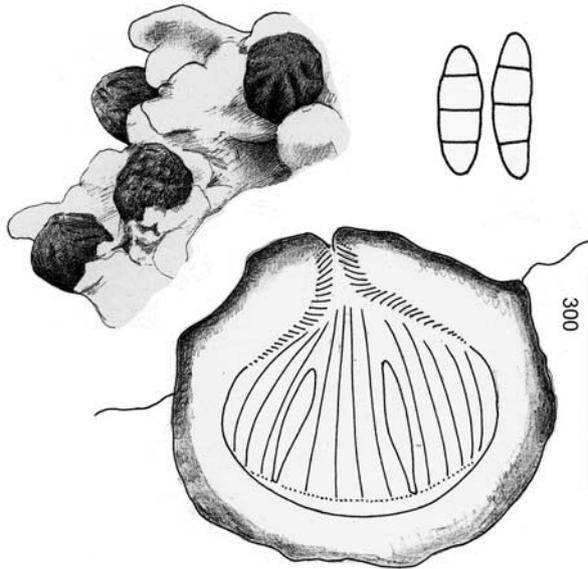
Thallus immersed, or superficial and cracked or areolate, grey; cortex of hyphae with gelatinized walls. Ascumata 0.4-0.5 mm diam., enclosed in thalline verrucae 0.46-0.74 mm diam. Exciple

unpigmented, of compressed cells. Ascospores 1-septate. Conidia ellipsoid to ovoid, *c.* 3-5 × 1-1.5 μm, or thread-like, 18-20 × 1 μm.

On mortar and shale on walls, rare; S. England (N. and S. Devon). S. Europe, N. Africa, N. America, Asia, Australia.

The description is based largely on extra-British material. The existence of long, thread-like conidia needs confirmation.

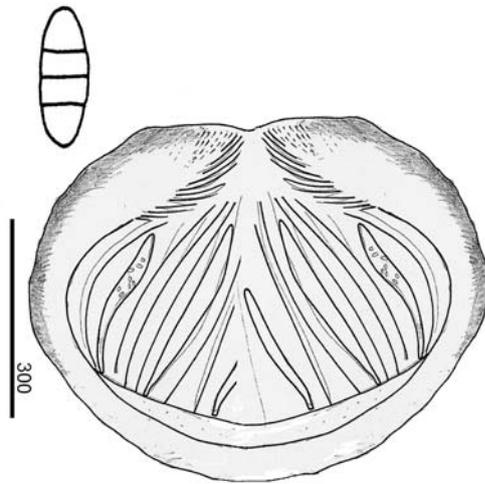
Thelopsis melathelia Nyl. (1864)



Thallus superficial, normally orange-red to red-brown when fresh, becoming grey-green in the herbarium. Ascomata black, half-immersed, 0.5-0.8 mm diam., surface wrinkled. Exciple two-layered, inner layer colourless, outer layer dark orange-brown. Asci 200-250 × 15-25 μm; ascospores 11-20 × 4-7 μm, with a thickened perispore.

Overgrowing bryophytes and plant detritus, often ± in sheltered crevices in basic schistose rocks and epidiorite on upland crags; very rare. N. Scotland (Highlands, Breadalbane Mountains). Norway, C. European mountains, Slovenia, N. America.

***Thelopsis rubella* Nyl. (1855)**



Thallus superficial, thin, grey to grey-green or pale brownish, often wide-spreading and diffuse. Perithecia scattered, discrete, at first \pm immersed, later half- to three-quarters immersed, 0.4-0.6 mm diam., sometimes lower part covered with a ring or with patches of thallus fragments, but without a well-defined thalline layer; pale pink-brown, red-brown to dark brown. Exciple distinctly hyphal, of intertwined hyphae with thick gelatinized walls, innermost layer of exciple of \pm thin-walled hyphae; exciple colourless within, outer part orange-brown, K \pm slightly darkening. Hymenial gel I-, K/I-. Periphyses simple or sparingly branched, up to 65 μ m long. Asci (100-)150-200 \times (16-)18-25 μ m, 100-150-spored, wall I+ dull grey to dull red, K/I+ blue. Ascospores (10-)12-16(-18) \times 4-8 μ m, ellipsoid-oblong, ends rounded, (1-)3-septate, without a distinct perispore.

On trunks of mature, broad-leaved trees, particularly *Quercus*, *Fagus* and *Fraxinus*, with bark of pH >5.0; mostly in the *Lobarion* in ancient woodlands or parklands, where it is an important indicator species; often in furrows or intermittent rain tracks in association with *Metzgeria furcata*; local. Throughout Britain, from S. England (E. Sussex to Cornwall) to Scotland (West Ross, Skye and Nairn), absent from most of C. and E. England and E. Scotland. Europe, Azores, N. America.

References:

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THROMBIUM Wallr. (1831)

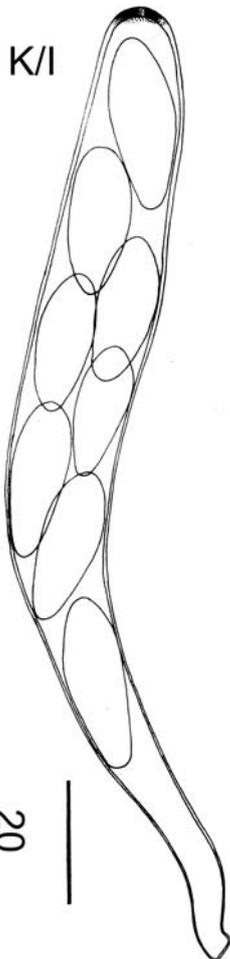
Thallus crustose, membranous, subgelatinous when wet, indeterminate. **Photobiont** *Leptosira* (Trebouxiophyceae). **Ascomata** perithecia, immersed. **Involucrellum** absent. **Exciple** brown, widened towards the ostiole. Hamathecium of thin, unbranched paraphyses; paraphyses absent. **Asci** elongate-cylindrical or narrowly clavate, thin-walled, with a well-defined K/I + blue apical cap; tholus K/I + blue with narrow, cylindrical axial mass; 8-spored. **Ascospores** simple, colourless, thin-walled, without a distinct perispore. **Conidiomata** not known. **Chemistry**: lichens products not detected by TLC. **Ecology**: on soil.

Classification: Ostropomycetidae, Protothelenellaceae.

Distinguished by the combination of lack of involucrellum, colourless, simple ascospores, and presence of paraphyses. *Verrucaria* differs in the absence of interascal filaments.

LITERATURE: Swinscow (1964).

Thrombium epigaeum (Pers.) Wallr. (1831)



Thallus wide-spreading, a yellow-green or grey-green film, smooth or slightly uneven, subgelatinous when wet, or indistinct. Perithecia immersed in the substratum, 250–400 μm diam, visible only by the grey to black ostiole. Exciple pale to dark brown, the wall 20–30 μm thick, becoming 50–100 μm thick towards the ostiole. Paraphyses few to abundant, c. 1 μm thick, unbranched. Asci 130–170 μm long, cylindrical, \pm clavate at apices, thin-walled (Fig. 35b). Ascospores (15–)18–25(–30) \times 5–10(–12) μm , ellipsoid or longly ellipsoid, often somewhat clavate, containing numerous oil droplets.

On recently disturbed, consolidated, neutral to acidic soil of sheltered cuttings and earth banks by roadsides, especially in well-wooded sites, also on cliff tops; very local. W. British Isles. Azores, Chile.

The thallus is host to the lichenicolous fungus *Leightonimyces phillipsii*.

Literature:

Swinscow, T.D. V. (1964) Pyrenocarpous lichens: 6. The genus *Thrombium* in the British Isles. Species of *Belonia* in Britain. *Lichenologist* **2**: 276–283.

TRIMMATOTHELE Norman ex Zahlbr. (1903)

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

Classification: Chaetothyriomycetidae, Verrucariales, Verrucariaceae.

Similar to *Verrucaria* except for the multispored asci. A little-known genus, with two European species, and much in need of revision.

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

Thallus to 120 µm thick, brownish or brown (but often overgrown by a blackish cyanobacterium), matt, cracked and secondarily areolate. Photobiont cells 5–10 × 5–8 µm, dividing by binary fission. Perithecia c. 300 µm diam., half- to three-quarters immersed in thallus. Involucrellum absent. Exciple dark brown throughout, wall 70–80 µm thick above, 50–60 µm thick at sides and base. Periphyses to 30 µm long, c. 1.5 µm wide. Asci 50–65 × 13–17 µm, c. 65-spored, cylindrical-clavate. Ascospores 6–9 × 2–3.5 µm, ellipsoid to oblong-ellipsoid.

On crystalline limestone at c. 1000 m, very rare. N. Scotland (E. Inverness: Ben Alder; Argyll: Ben Sgulaire). N. Scandinavia, Alps.

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

VERRUCARIA Schrad. (1794)

Thallus crustose, immersed or superficial, white, green, grey, brown, black or purple; 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** usually green (including *Dilabifilum incrustans* [Ulvophyceae] and ?*Trebouxia* sp. [Trebouxiophyceae]), very rarely Phaeophyceae (*Petroderma maculiforme*), occasionally absent. **Ascomata** perithecia, black (except rare albino morphs); 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 –, fissitunicate, 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, simple, colourless (very rarely brown), broadly to narrowly ellipsoid or oblong-ellipsoid, smooth, wall thin or only slightly thickened, perispore often present, or very rarely spores 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 1. brown, K + darkening, 2. reddish brown, K + dark grey-brown, 3. dull green, K –. **Ecology**: mostly on rock, including limestone and (often damp) siliceous rock, including freshwater and maritime habitats, one species truly marine; occasionally on soil or bark, or parasitic on lichens.

Classification: Chaetothyriomycetidae, Verrucariales, Verrucariaceae.

A difficult artificial genus with *c.* 200 currently accepted species. There are few clear-cut morphological characters to assist identification, and these are rather variable in response to environment. It is recommended that each specimen is carefully examined and the structure understood before identification is attempted. Despite this, most species can be recognized 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 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, very smooth when dry, and uncracked (but fine cracks can develop in the herbarium), 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. 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. 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 hyaline material, but these are often ephemeral.

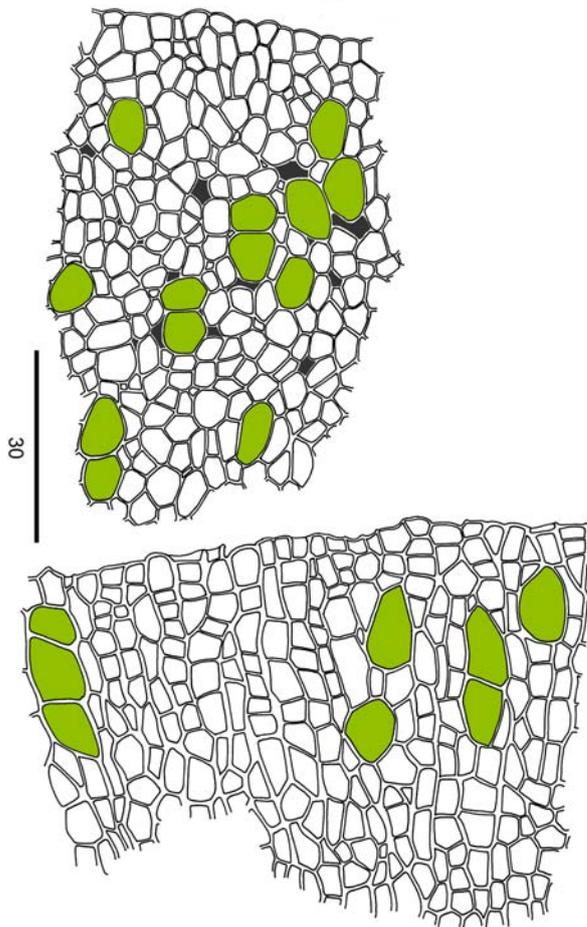
Vegetative propagules (blastidia) currently known in the region only in *V. macrostoma* and *V. nigrescens*.

In the descriptions the spore size range is given as average in bold, plus and minus one standard deviation, with extreme measurements in parentheses; the number of spores/specimens measured to give this figure is given in square brackets. 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.

The account below must be regarded as provisional, as numerous unidentified collections remain. Molecular work suggests that cryptic or near-cryptic species may be frequent.

The phylogenetic relationships of species with the genus are becoming better understood, and it is probable that most species currently in *Verrucaria* will eventually be transferred to other genera. *Heteroplacidium*, *Hydropunctaria* and *Placopyrenium* are treated in separate accounts, but the species

are included in the key below. Other recently accepted genera are here retained in *Verrucaria* for the time being, purely for ease of identification. These include *Bagliettoa*, *Parabagliettoa* and *Wahlenbergiella*.



< Thallus structure in epilitic species:

Upper: non-gelatinous thallus. Cells not in regular columns, small spaces often present between cells (shown as dark grey) (*Verrucaria cernaensis*).

Lower: subgelatinous thallus. Cells typically in columns, no spaces between cells (*Verrucaria funckii*).

LITERATURE: *Maritime*: Fletcher (1975), Lamb (1948), Renobales & Noya (1991), Orange (2012), Santesson (1939). *Freshwater*: Orange (2004b, 2013), Thüs & Schultz (2009). *Terrestrial*: Halda (2003), McCarthy (1988a, b), McCarthy & Mitchell (1988), Orange (1991, 2004a). *Lichenicolous*: McCarthy (1988b), Navarro-Rosinés *et al.* (2007), Orange (2002), Zehetleitner (1978).

- 1 Ascospore wall brown; involucrellum absent, parasitic on calcicolous lichens *phaeosperma*
- Ascospore wall colourless (at most overmature spores faintly brownish in one species, or overmature spore contents brown) 2
- 2(1) 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 3
- Thallus mostly superficial (although sometimes thin), at most the lower part immersed, or thallus absent (when parasitic on lichens) 12
- 3(2) Involucrellum absent; exciple more or less pigmented throughout (usually thickened above, but without a distinct involucrellum)4

	Involucrellum present; in section clearly distinct from exciple (but sometimes small and developed only around apex of exciple)	5
4(3)	Ascospores (25–)29–34.5(–41.5) μm long, exciple 375–700 μm wide; thallus usually without cracks	<i>hochstetteri</i>
	Ascospores (21–)23–27(–29) μm long, exciple 240–420 μm wide; thallus often with cracks radiating from the perithecium	<i>calciseda</i>
5(3)	Involucrellum in the form of a small disc, attached only to apex of exciple, in surface view with minute cracks radiating from ostiole ($\times 20$ lens)	6
	Involucrellum not disc-shaped, in surface view without cracks	7
6(5)	Thallus white to pale grey (or greenish in shade), usually matt; involucrellum 200–300 μm wide	<i>baldensis</i>
	Thallus grey to grey-green or blue-grey, glossy; involucrellum 150–220 μm wide	<i>parmigerella</i>
7(5)	Ascospores 7.5–11 μm long	<i>knowlesiae</i>
	Ascospores larger	8
8(7)	Ascospores (24–)27–33(–41) μm long	<i>viridula</i>
	Ascospores at most (17–)19.5–24(–26) μm long, and often much shorter	9
9(8)	Perithecia forming small projections 120–300 μm diam.	10
	Perithecia forming larger projections 240–500 μm diam.	11
10(9)	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 \pm immersed in substratum	<i>cyanea</i>
	Thalli not forming mosaics; ascospores (14.5–)18–24(–28.5) μm long; perithecia forming moderate to prominent projections, base not immersed in substratum	<i>murina</i>
11(9)	Apex of perithecium flat to depressed; ascospores (15.5–)16.5–20(–23.5) μm long, oblong to ellipsoid, length/width ratio (1.9–)2.0–2.7(–3.4); pycnidia frequent	<i>dufourii</i>
	Apex of perithecium rounded to slightly flattened, rarely shallowly depressed; ascospores (17–)20–24(–27) μm long, ellipsoid, length/width ratio (1.4–)1.7–2.3(–3.1); pycnidia apparently rare or absent	<i>muralis</i>
12(2)	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; ascospores less than 20 μm long; species of freshwater or maritime habitats, never lichenicolous	13
	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	19
13(12)	Species of freshwater habitats; thallus often with dots but no ridges in surface view	14
	Species of maritime habitats; thallus often with dots, or ridges, or both	15
14(13)	Thallus with green pigment in cortex (or pigment absent); ascospores (11–)14–17.5(–21.5) μm long; exciple <i>c.</i> 275–290 μm wide; medulla dilute to densely pigmented	<i>Hydropunctaria scabra</i>
	Thallus with brown pigment in cortex (or pigment absent); ascospores (8.5–)11–14.5(–16) μm long; exciple <i>c.</i> 110–210 μm wide; medulla colourless or with dilute pigment	<i>Hydropunctaria rheitrophila</i>
15(13)	Ascospores 13–19.5 μm long	16
	Ascospores 7–10 μm long	17
16(15)	Actively growing thallus with dark ridges 40–400 \times 40–50 μm perpendicular to thallus margin; length/width ratio of ascospores (2.1–)2.4–3.1(–3.5)	<i>Hydropunctaria amphibia</i>
	Actively growing thallus margin with dark dots or very short ridges; length/width ratio of ascospores (1.5–)1.7–2.1(–2.3)	<i>Hydropunctaria maura</i> group
17(15)	Thallus cracked into areolae, these bordered by dark ridges	<i>degelii</i>
	Thallus not cracked (but new cracks can appear after collection)	18
18(17)	Thallus with black ridges up to 100–200 μm wide	<i>striatula</i>

	Thallus with small dark dots or short irregular ridges 10–100 × 10–60 µm	<i>ditmarsica</i>	
19(12)	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	<i>ceuthocarpa</i>	
	Not this combination of characters		20
20(19)	Thallus well-developed, often pruinose, non-gelatinous, cracked, the cracks with blackish sides; perithecia immersed in thallus, involucrellum absent		21
	Thallus various, if with dark-sided cracks then involucrellum present		25
21(20)	Perispore present, ascospores (14–)17.5–26.5(–30.5) µm long; young thallus initially parasitic on <i>Aspicilia</i> species, later independent		22
	Perispore absent or present but indistinct, ascospores (10.5–)12.5–21(–25.5) µm long; young thallus independent, or sometimes on <i>Staurothele</i> or <i>Verrucaria</i> species		23
22(21)	Ascospores (18.5–)21.5–26.5(–30.5) µm long, thallus initially parasitic on <i>Aspicilia calcarea</i>	<i>Placopyrenium canellum</i>	
	Ascospores (14–)17.5–22.5(–27) µm long, thallus initially parasitic on <i>Aspicilia aquatica</i>	<i>Placopyrenium formosum</i>	
23(21)	Thallus margin thin, prothallus often apparent; perithecia arising between photosynthetic units on the thallus surface, in surface view often appearing as if connected by dark lines.....	<i>polysticta</i>	
	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		24
24(23)	Ascospores (13–)16–18.5–21.0(–25.5) × (5.5–)6.5–7.2–8.0(–9.5) µm, length/width ratio (1.9–)2.2–2.6–2.9(–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 <i>Staurothele fissa</i>	<i>Placopyrenium cinereoatratum</i>	
	Ascospores (11.5–)13–15.1–17(–20.5) × (4.5–)5–5.7–6(–7.5) µm, length/width ratio (1.9–)2.3–2.7–3(–3.7); upper surface of areoles typically divided by dark lines; on calcareous rocks in terrestrial habitats, sometimes parasitic on <i>Verrucaria</i> spp.	<i>Placopyrenium fuscillum</i>	
25(21)	Parasitic on lichens, a lichenized thallus present or not		26
	Not parasitic on lichens		28
26(23)	Lichenized thallus absent; growing on <i>Ionaspis</i>	<i>conturmatula</i>	
	Lichenized thallus present; growing on other lichens		27
27(26)	Growing on <i>Caloplaca</i> , <i>Diplotomma</i> and <i>Lecanora</i>	<i>latericola</i>	
	Growing on <i>Aspicilia calcarea</i>	<i>Heteroplacidium fuscillum</i>	
28(25)	Average ascospore length in the range 8–10 µm, extreme lengths in range 7–12 µm		29
	Average ascospore length higher, at least 12 µm, extreme lengths as low as 9 µm		36
29(28)	Maritime species, thallus subgelatinous		30
	Freshwater or terrestrial species		31
30(29)	Perithecia completely immersed in the thallus	<i>mucosa</i>	
	Perithecia forming projections (compare also smooth morphs of <i>V. ditmarsica</i> and <i>V. striatula</i>)	<i>halizoa</i>	
31(29)	Involucrellum absent		32
	Involucrellum present (but may be appressed to exciple)		33
32(31)	Thallus very thin, perithecia 80-130 µm, ascospores 6-10.5 × 3.5-5.5 µm	<i>simplex</i>	

- Thallus well-developed, lumpy, perithecia 200-300 μm , ascospores $9-12 \times 7.5-10 \mu\text{m}$
..... *sphaerospora*
- 33(31)** Perithecia 100–150 μm diam; involucrellum appressed except at base, scarcely spreading; on stones in terrestrial habitats *bulgarica*
Perithecia 120–300 μm diam. 34
- 34(33)** Thallus semi-immersed and inconspicuous, or superficial, thin, and brownish grey; perithecia without a thalline covering *knowlesiae*
Thallus superficial, brown to blackish; perithecia sometimes with a thin, partial thalline covering 35
- 35(34)** In freshwater habitats; thallus uncracked or cracks few; perithecia forming projections 120–240 μm diam. *aquatilis*
In terrestrial habitats; thallus cracked; perithecia forming projections 200–300 μm diam.
..... *aranensis*
- 36(28)** Involucrellum absent; on rock, soil or mosses 37
Involucrellum present, at least as a small dark structure at apex of exciple; **or** if involucrellum present then growing on rock 39
- 37(36)** Ascospores narrowly ellipsoid, $(15-)19-25(-29) \times (5-)6-7(-8) \mu\text{m}$, often truncate at the ends and with small gelatinous appendages; thallus without pigment *bryoctona*
Ascospores ellipsoid, $(13.5-)16.5-21(-27) \times (5.5-)6.5-8(-10) \mu\text{m}$, without appendages ... 38
- 38(37)** On soil *xyloxena*
On rock *consociata*
- 39(36)** Ascospores narrowly ellipsoid, $12-14 \times 2-3 \mu\text{m}$; maritime *sandstedei*
Ascospores more than 3 μm wide (often much more) 40
- 40(39)** Thallus subgelatinous, uncracked (fine cracks may appear in old herbarium specimens); growing in freshwater habitats 41
Thallus non-gelatinous; habitats various 47
- 41(40)** Ascospores 9–14 μm long; asci (3–)4(–5)-spored *madida*
Ascospores 15–27 μm long; asci 8-spored 42
- 42(41)** Perithecia often completely immersed in thallus, rarely some projecting; thallus with dull green or brown pigment in cortex when well-lit; ascospores $(15-)16-22(-23.5) \mu\text{m}$ long
..... *pachyderma*
Perithecia forming at least low projections; pigment if present brown; ascospores usually larger 43
- 43(42)** Ascospores broadly ellipsoid, $(17-)20-24(-27.5) \times (11-)12-13.5(-15.5) \mu\text{m}$, length/width ratio $(1.2-)1.5-1.9(-2.3)$; on limestone in calcareous streams *elaomelaena s.l.*
Ascospores narrower in shape 44
- 44(42)** Perithecial projections shallow and poorly defined; thallus variable but usually rather thick, $(20-)80-160(-240) \mu\text{m}$; involucrella often widespreading and partly joined to form a dark basal layer to the thallus; ascospores $(19-)22.5-26(-30) \times (8-)9-11(-13) \mu\text{m}$
..... *funckii*
Perithecial projections usually distinct; thallus thin, 20–50 μm ; involucrella rarely joined
..... 45
- 45(44)** Ascospores relatively small, $(15-)19.5-21.1-23 (-26) \times (6.5-)8-8.9-9.5(-11) \mu\text{m}$, perithecia relatively small, forming projections 240–400 μm wide, exciple 240–400 μm wide; perithecia rather dense, 29-42-64 in an area of 25 mm^2 *hydrophila*
Ascospores and perithecia larger; perithecia 13-26 in an area of 25 mm^2 46
- 46(45)** Ascospores $(19-)21.5-24.0-26.5(-30.5) \times (8-)9-9.9-10.5(-12) \mu\text{m}$ *placida*
Ascospores $(19-)23-25.2-27(-32) \times (9.5-)11.5-12.4-13.5(-16.5) \mu\text{m}$ *elaomelaena s.l.p.p.*

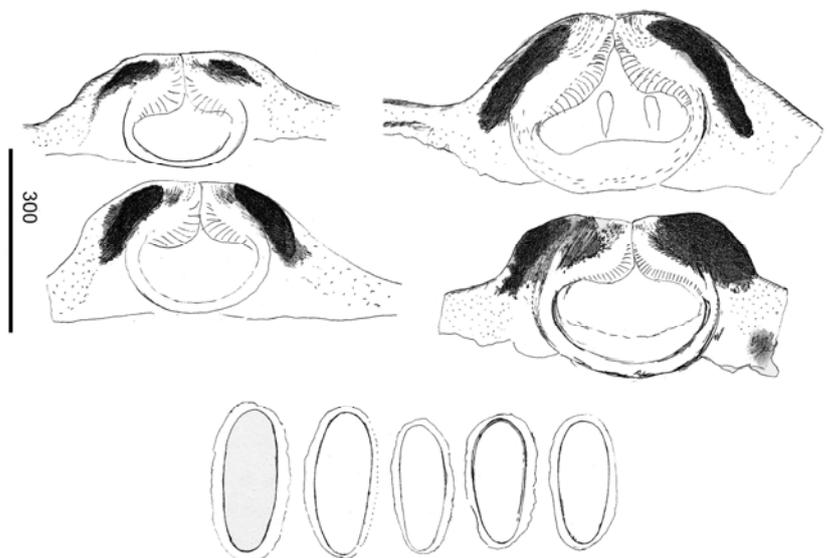
- 47(40) Thallus in section composed of more or less distinct goniocyst-like units (thallus varying from minute flecks to a cracked crust; ascospores in the range (13–)15–26.5(–28.5) μm long, average length in individual specimens less than 27 μm) 48
 Thallus in section not composed of goniocysts 51
- 48(47) Ascospores (12.5–)15–18(–21.5) μm long; involucrellum often more or less conical, diverging from exciple below *indet. sp.*
 Ascospores larger (but there is a broad overlap) 49
- 49(48) Thallus thin, without obvious patches of new growth *murina*
 Thallus often well-developed, sometimes with patches of younger, paler thallus overgrowing older layers 50
- 50(49) Thallus of relatively coarse units, in section divided into units 30–325 μm wide.. *nodosa*
 Thallus of somewhat finer and more crenulate units, in section divided into units 30–50 μm wide *rosula*
 (Typical *V. rosula* is distinctive in appearance, but *V. nodosa* is variable and should be confirmed by sequencing).
- 51(47) Ascospores in the range (19–)24–34.5(–41.5) μm long, average length in individual specimens in the range 23–33 μm 52
 Ascospores smaller, in the range (10.5–)11.5–25(–30) μm long, average length in individual specimens 19.5–24 μm 57
 (There is a small overlap here, but most specimens should key out correctly; if the specimen is from siliceous rock in a freshwater habitat and has a distinct perispore, take the first option in the couplet).
- 52(51) On calcareous rocks in terrestrial habitats (epinecral layer or blastidia occasionally present) 53
 On calcareous or siliceous rocks in freshwater habitats (epinecral layer and blastidia always absent) 55
- 53(52) Perithecia partly immersed in the substratum, often produced into a beak at apex; involucrellum weakly developed, to well-developed around upper half of exciple (thallus variable, more or less immersed to well-developed and cracked, never blastidiate; pycnidia rather frequent) *viridula*
 Perithecia not immersed in substratum, not much produced; involucrellum well-developed, often reaching to base-level of exciple (thallus well-developed, occasionally blastidiate) 54
- 54(53) Initial areoles discrete, with a rather smooth outline *squamulosa*
 Initial areoles less discrete, soon crenulate *macrostoma*
 (Provisional couplet).
- 55(52) Involucrellum conical *margacea*
 Involucrellum mainly developed around apex or in upper half of exciple, or absent, not distinctly conical 56
- 56(55) Involucrellum absent, perithecia immersed to somewhat projecting *anziana*
 Involucrellum present, perithecia usually projecting *aethiobola*
- 57(51) Perithecia immersed in the thallus, involucrellum absent; ascospores 16–26 μm long *ochrostoma*
 Perithecia not immersed, or an involucrellum is present 58
- 58(57) Thallus usually very thin, often with a waxy appearance under the dissecting microscope; perithecia large, up to 800 μm wide, prominent, with thick involucrellum; ascospores (10.5–)11.5–14(–16) μm , usually distinctly oblong; on maritime rocks *prominula*
 Thallus various; perithecia smaller; terrestrial or freshwater habitats 59
- 59(58) Ascospores (12–)12–20(–24.5) μm long 60
 Ascospores (15–)17.5–25(–30) μm long 63
- 60(59) Thallus pale grey to dull grey-brown, closely and finely cracked, with an epinecral layer; perithecia three-quarters to completely immersed *caerulea*

- Thallus various, but epinecral layer absent 61
- 61(60)** Involucrellum well-developed, thick in upper part and often appressed to exciple below; ascospores often oblong or oblong-ellipsoid *pinguicula*
 Involucrellum not conspicuously thick in upper part, sometimes conical, or poorly developed; ascospores more or less ellipsoid or tapering below 62
- 62(61)** Perithecia immersed in thallus, involucrellum rather poorly developed, often confined to apex of exciple; in streams or rivers *sublobulata*
 Perithecia prominent, involucrellum well-developed, often conical; in terrestrial habitats *dolosa*
- 63(59)** Perithecia immersed in thallus, at most forming very ill-defined projections; involucrellum more or less conical, becoming joined with others to form a dark basal layer; freshwater habitats *praetermissa*
 Perithecia often forming projections; involucrellum various 64
- 64(63)** 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 thallus surface *cernaensis*
 In terrestrial habitats; thallus various; ascospores often slightly larger or more narrowly ellipsoid 65
- 65(64)** Thallus regularly cracked into discrete areoles, mid to dark brown, the sides of the areoles often pigmented 66
 Thallus various; whitish, grey-green to light brown 67
- 66(65)** Perithecial projections low to rather prominent, prothallus often conspicuous, dark brown; on siliceous rocks, often near the coast *fusconigrescens*
 Perithecial projections very low to moderate, prothallus less conspicuous; on calcareous rocks *nigrescens*
- 67(65)** Ascospores rather narrowly ellipsoid, (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 *elaeina*
 Ascospores ellipsoid, (7.5–)9–12.5(–14) μm wide, length/width ratio (1.4–)1.7–2.5(–3.2); thallus whitish to light brown; apex of perithecium not irregular 68
- 68(67)** Thallus superficial, whitish or brownish white, usually well-developed; on siliceous rocks in the supralittoral of sea shores *internigrescens*
 Thallus immersed to superficial, but rarely well-developed; on limestone, rarely siliceous rocks, not maritime *muralis*

Verrucaria aethiobola Wahlenb. (1803)

Verrucaria latebrosa Körb. (1855)

Thallus 35–200 μm thick, grey-green, light brown or dark brown, cracks few to numerous (few or absent in very thin thalli); thallus surface smooth, matt to slightly glossy; 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 rather strong projections 220–480(–600) μm , sometimes covered by thallus, but usually with the black convex apex of the perithecium exposed. Ostiolar region often conspicuous as a pale spot 20–110 μm wide, plane or depressed. Exciple 190–300 μm diam., colourless below or only locally and thinly with brown pigment. Involucrellum present, developed only around the apex of the exciple, or well-developed and spreading outwards and downwards, but only rarely more or less conical. Ascospores (21.5–)24–**26.6**–29(–35) \times (8.5–)10.5–**11.4**–12.5(–14.5) μm , length width ratio (1.7–)2.1–**2.3**–2.6(–3.1) [283/34]. Pycnidia not detected.

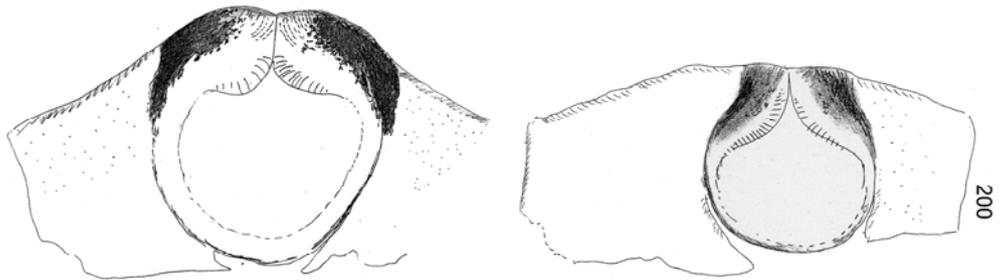
On unshaded or shaded rocks by streams and lakes; occasional to frequent in upland Britain, in Wales, N. England and Scotland. Specimens confirmed from Norway, Faroe Islands and Ireland.

Notes. The perithecia typically form mounds on a relatively thin thallus; the black apex of the perithecia often projects and has a 'button-like' appearance, and the ostiolar region is often rather conspicuous as a pale dot. *Verrucaria anziana* differs in the thicker thallus and scarcely developed involucrellum. Some specimens of *V. margacea* are difficult to distinguish, but in that species the perithecia are typically covered by a layer of thallus and the involucrellum is typically conical; *V. margacea* differs markedly in its ITS sequence. This is probably a collective species.



Verrucaria aethiobola (Norway, 19311)

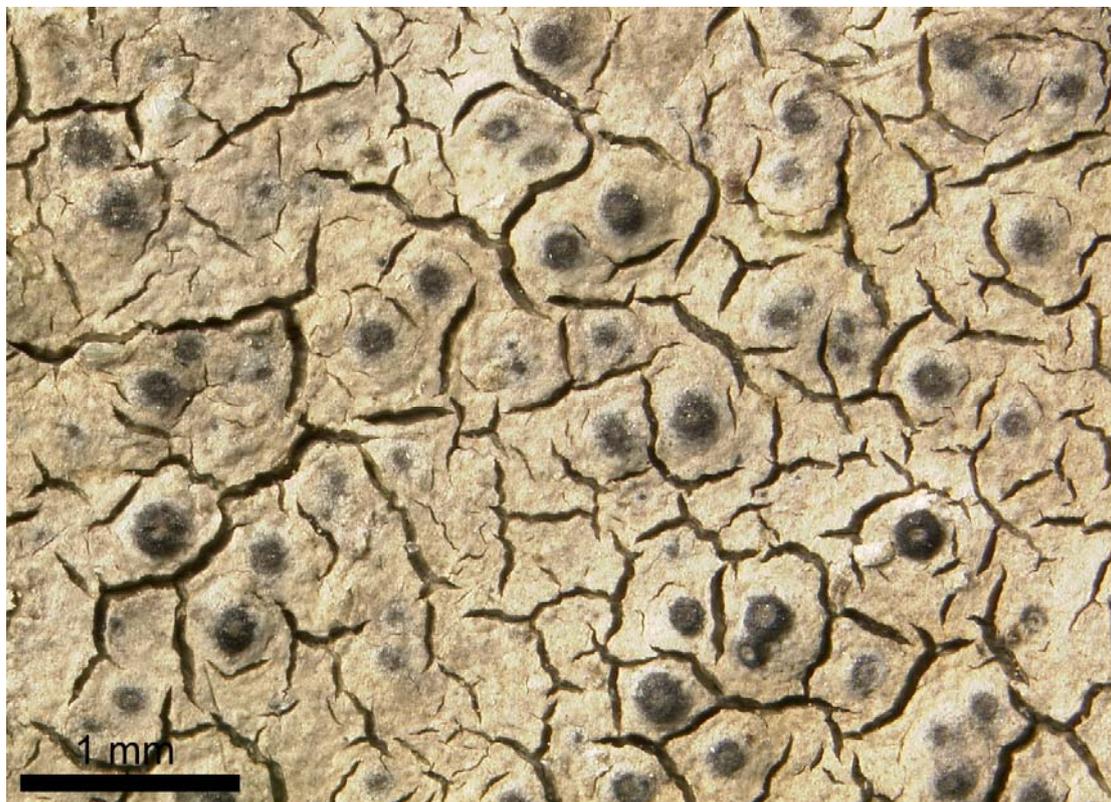
Verrucaria anziana Garov. (1865)



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). Exciple 210–380 μm diam., brown throughout or colourless below. Involucrellum absent or very weakly developed around the apex of the exciple, not spreading. Ascospores (23–)25.5–**28.4**–31(–36.5) \times (10.5–)11.5–**12.1**–13(–14.5) μm , length/width ratio (1.9–)2.1–**2.3**–2.6(–3.0) [96/9], perispore often distinct, 0.8–2.5 μm thick. Pycnidia not detected.

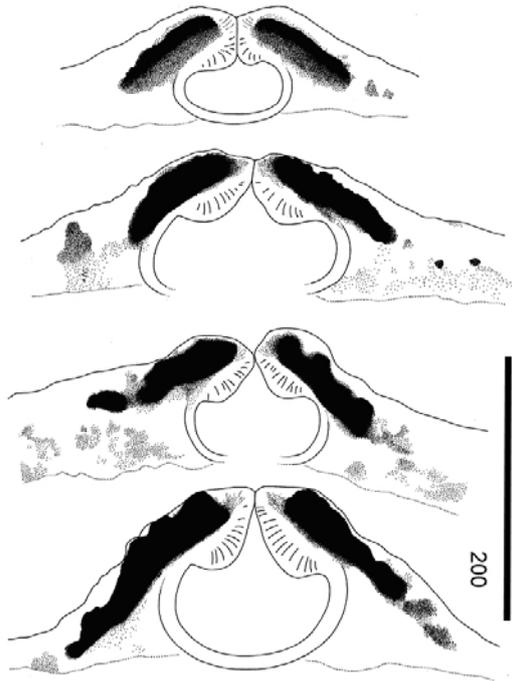
On rocks in unshaded streams, rivers and lakes, usually on siliceous rock, one record on limestone, recorded at 100–715 m; occasional in upland Britain, including North Wales, N. England and C. and W. Scotland. Specimens have been confirmed from Norway, Sweden, Faroe Islands, Switzerland, Italy, Bulgaria.

Distinguished from *V. aethiobola* by the often thicker, often paler thallus, more usually immersed perithecia, and the absence or very weak development of an involucrellum. When the thallus is rather thin, the perithecia project, but an involucrellum is still absent. *V. anziana* is more often attacked by lichenicolous fungi than *V. aethiobola*.



Verrucaria anziana (17501)

Verrucaria aquatilis Mudd (1861)

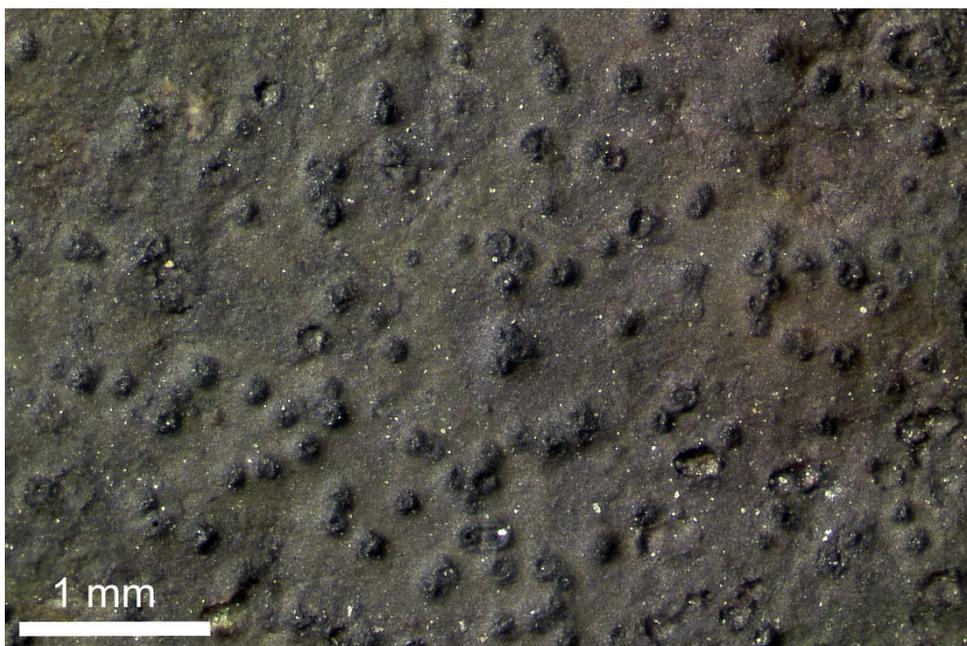


Prothallus very inconspicuous, perhaps brown. Thallus thin, 20–55 µm thick, diffuse, dark greyish brown or dark greenish brown to brownish black (blackish with the unaided eye), uncracked or cracks very few, surface smooth or slightly roughened; upper layer of thallus (and sometimes also elsewhere) with 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 thallus. Perithecia forming low to moderate conical-hemispherical projections 100–240 µm diam., more or less concolorous with thallus, covered at least when young by a layer of thallus; ostiole inconspicuous, sometimes visible as a minute pit up to 20 µm wide. Exciple 120–160 µm, colourless at sides and base, ostiole often dull blue-grey or blue-green. Involucrellum conical, often not reaching base of thallus, but sometimes merging into pigment in lower part of thallus; pigment in involucrellum red-brown, K + grey. Ascospores broadly ellipsoid, without perispore, (6.5–)7.5–

8.2–9(–10) × (4.5–)5.5–6.2–6.5(–8) µm, (1.1–)1.2–1.3–1.5(–1.8) times as long as wide [n = 134/13]. Conidiomata not detected.

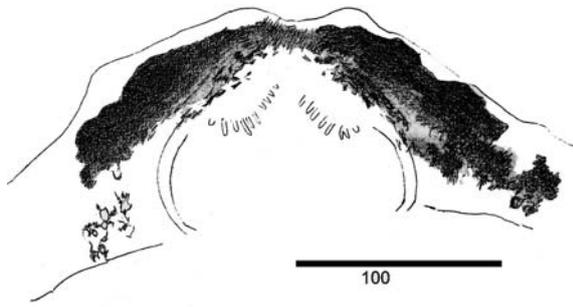
On long-submerged rocks, widespread in N. and W. Britain and Ireland, very local in C. and S.E. England. Throughout Europe; Himalayas, Siberia.

Usually easily distinguished from other freshwater species by the thin blackish thallus and the very small, broadly ellipsoid ascospores. *Verrucaria 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.



Verrucaria aquatilis.

Verrucaria aranensis P.M. McCarthy (1988)

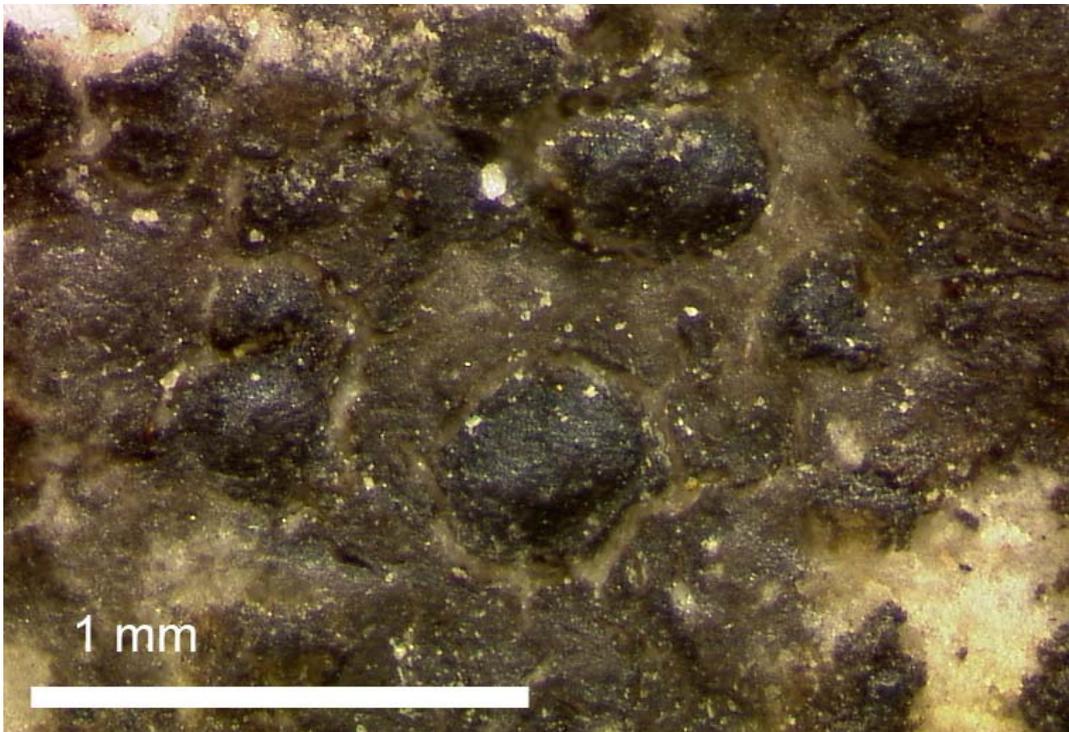


Thallus superficial, brown to blackish, mostly thin, 40(–120) μm thick, with sparse to numerous cracks. Perithecia semi-immersed in thallus, forming projections 200–300 μm diam., partly covered by a thin thalline layer. Involucrellum more or less semicircular in section or somewhat spreading, 200–300 μm wide. Exciple 150–200 μm diam., brown. Ascospores ellipsoid to subglobose, (7–)9.8(–11) \times (5.5–)6.3(–7) μm [33/1].

Shaded limestone at base of wall. W.

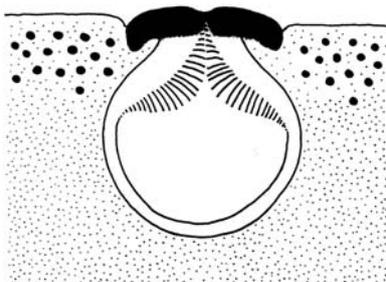
Ireland (Aran Islands).

Known from a single collection. Differs from *V. aquatilis* in the slightly larger perithecia, cracked thallus, and habitat.



Verrucaria aranensis (holotype).

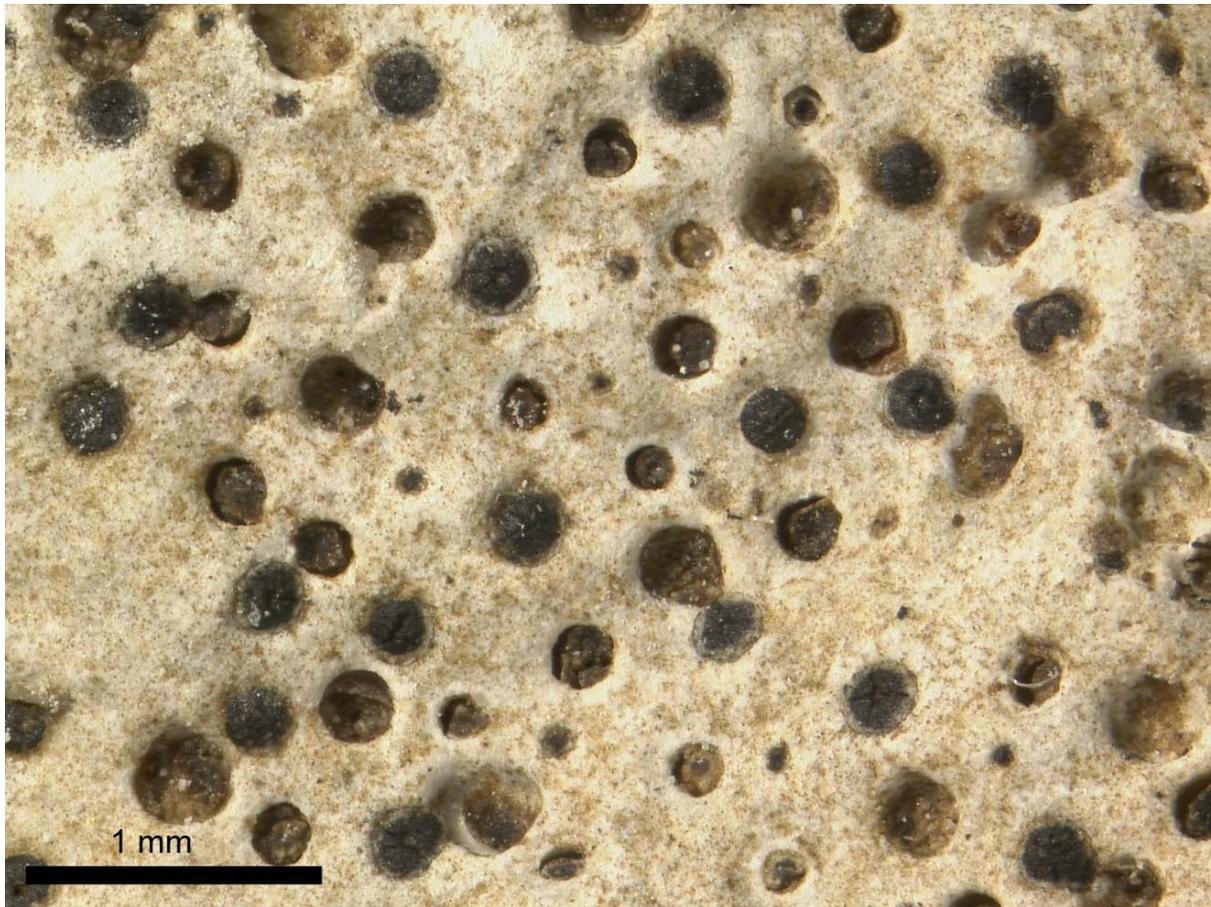
Verrucaria baldensis A. Massal. (1852)



Thallus immersed, white to pale grey, sometimes greenish in shade, not cracked, usually matt; often with dark lines between contiguous thalli. Perithecia almost completely immersed, in well-defined pits in rock; exciple colourless to brown, 200–400 μm ; involucrellum disc-shaped, spreading sideways but scarcely downwards, 200–300 μm diam., flat to slightly convex, in surface view with 3–6 fine cracks radiating from the ostiole, perithecia apex often surrounded by a fine crack. Ascospores (18.5–)21–25.1–29.5(–32) \times (10–)10.5–11.7–13(–14.5) μm [35/4].

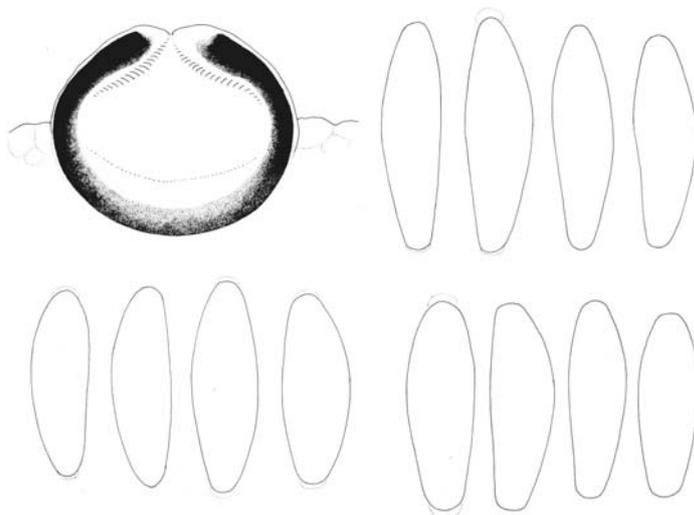
On hard limestones, also on mortar, often abundant. Throughout Britain and Ireland. Sweden, C. & S. Europe, Australia, New Zealand.

The whitish thallus with rather densely crowded (but not contiguous) perithecia is often conspicuous in the field; the cracks in the disc-like involucrellum can be seen with a $\times 20$ lens in the field. One of the commoner *Verrucaria* species of sunny limestone rocks. This species belongs in *Bagliettoa*, as *B. baldensis* (A. Massal.) Vězda (1981).



Verrucaria baldensis (15815).

***Verrucaria bryoctona* (Th. Fr.) Orange (1991)**

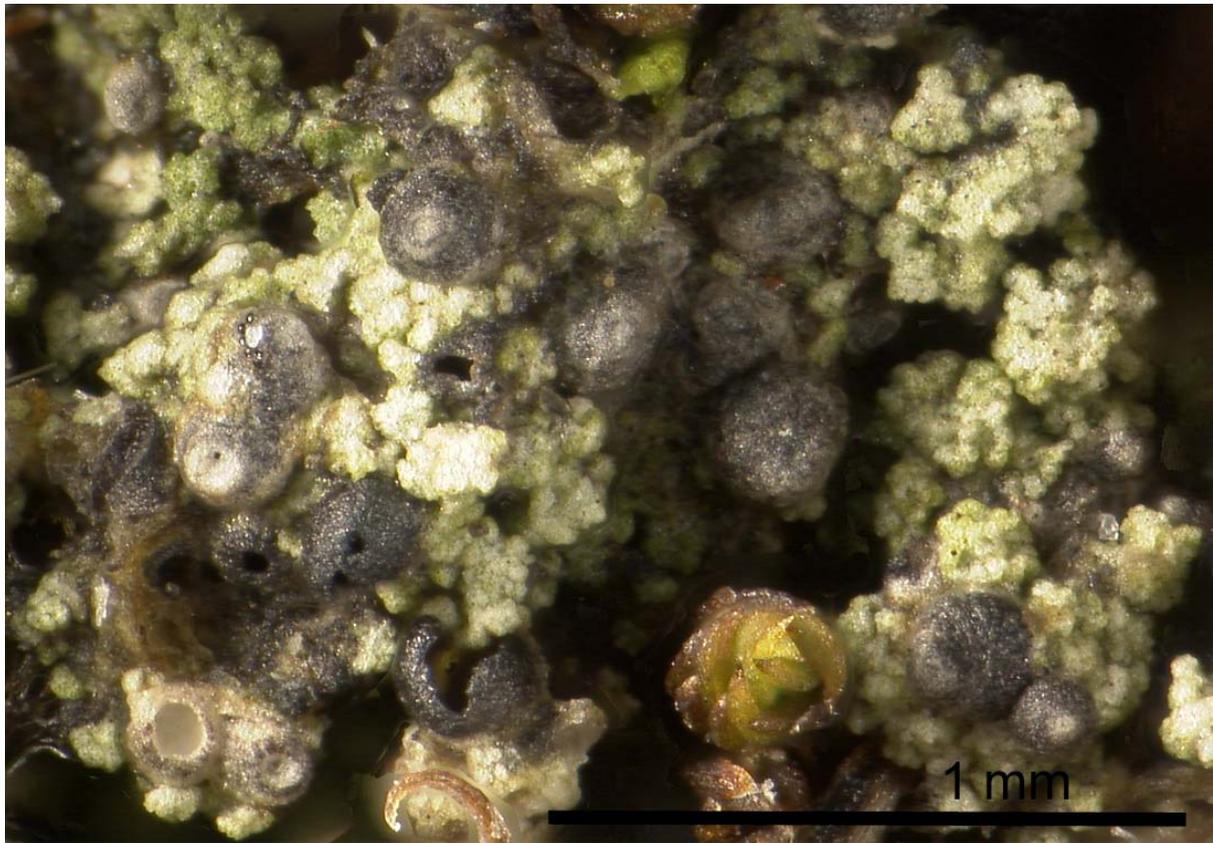


Thallus superficial, grey-green, granular-verrucose, composed of goniocyst-like units 15–40 μm diam., without pigment in cell walls. Perithecia (0.3–)0.5(–0.75)-immersed in substratum, 110–310 μm diam., black or grey; exciple pigmented throughout, pigment brown to reddish brown, K + dark greyish brown; involucrellum absent. Ascospores narrowly ellipsoid, simple but often 1(–3)-septate when overmature, (15–)19.5–22.0–24.5(–29) \times (5–)6–6.4–7(–8) μm , length/width ratio (1.9–

)3.0–3.4–3.9(–4.5) [124/14], apices rounded or narrowly truncate, frequently with a small gelatinous appendage 2–3.5 μm wide and 1 μm long. Pycnidia not detected.

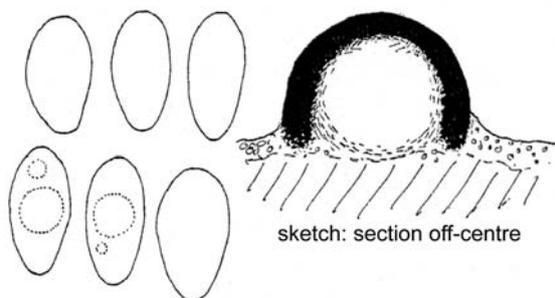
On more or less basic soil, usually with acrocarpous mosses, in dunes, dry grassland, waste ground, spoil heaps and wall tops; occasional. Widespread in Britain and Ireland. Finland, Sweden.

The only British species to have gelatinous appendages on the ascospores (other species may have a perispore surrounding the whole spore). *V. xyloxena* differs in the less elongated spores without appendages, and the presence of brown pigment in the thallus.



Verrucaria bryoctona (18392)

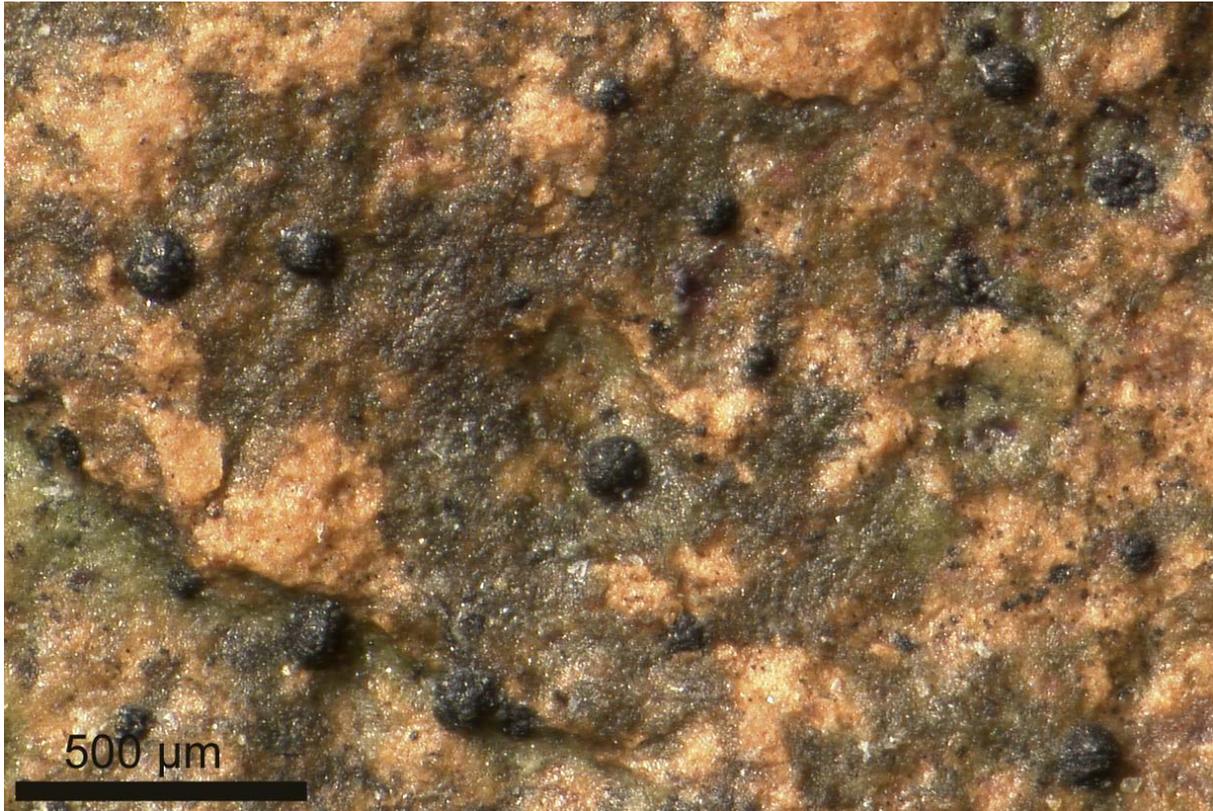
***Verrucaria bulgarica* Szatala (1930)**



Thallus thin or very thin, uncracked, greenish to dark brown. Perithecia forming hemispherical to prominent projections 60–140 μm diam., black, not covered by thallus layer. Involucrellum appressed to exciple except at base, not spreading, reaching to base-level of exciple. Ascospores (7–)8–8.6–9.5(–10) \times 4.5–4.8–5(–5.5) μm , length/width ratio (1.5–)1.6–1.8–2.0(–2.2) [12/3].

On fragments of limestone, mortar or brick, lying on the ground in woodland, in a garden and a churchyard; rare but overlooked. Wales, E. England. Bulgaria.

A minute species with small ascospores; *V. simplex* differs in the lack of an involucrellum, but the distinction is not always easy to make.



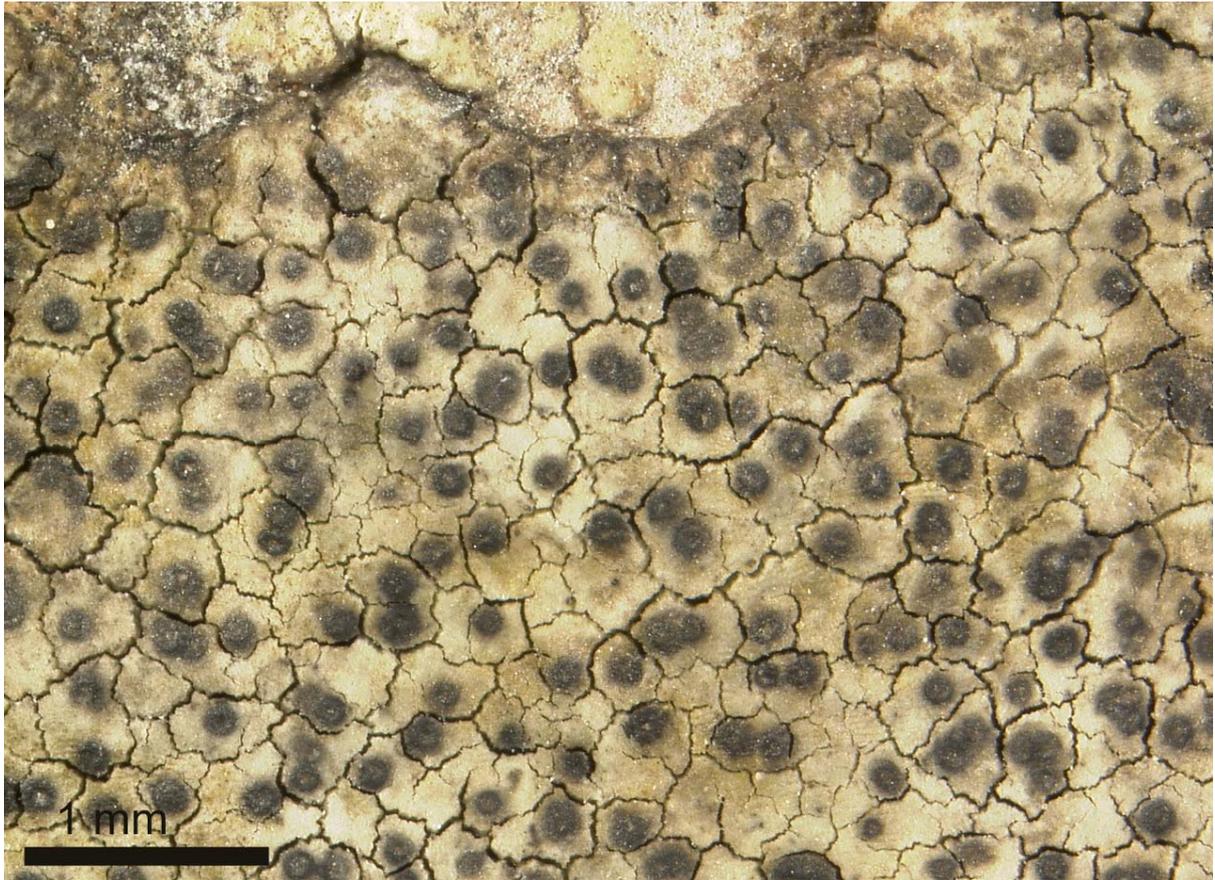
Verrucaria bulgarica (10941)

***Verrucaria caerulea* DC. (1805)**

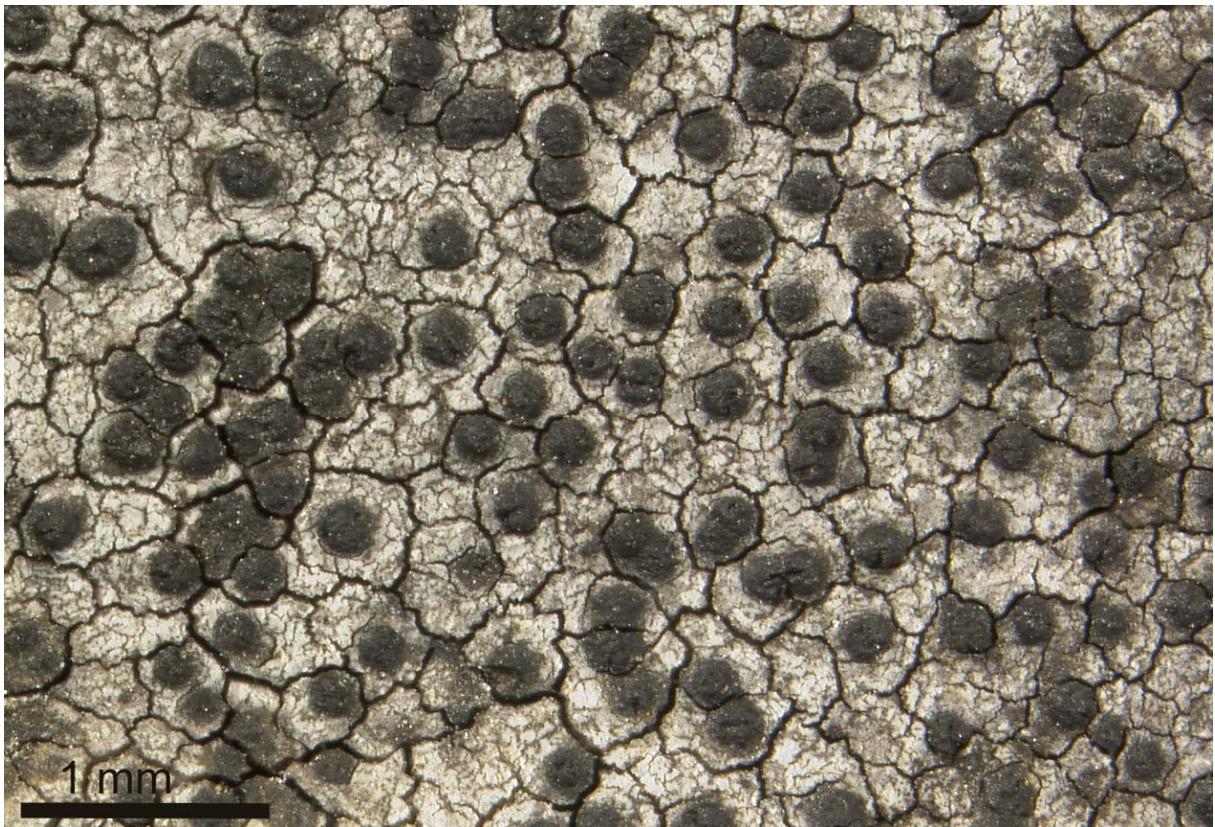
Thallus superficial, 100–300 µm thick, or also partly immersed at base, often raised above adjacent endolithic species or bare rock, pale grey to dull grey-brown, closely and finely cracked, often into discrete areoles, sides of cracks not or little pigmented; surface of areoles with a slightly translucent appearance or often with a whitish compact pruina. Epinecral layer present, cortex with dilute brown pigment when well-lit, without a dark basal layer. Perithecia three-quarters immersed to completely immersed in thallus, apex black, plane or appearing as a shallowly convex projection 120–220 µm diam. Exciple *c.* 150–195 µm wide, colourless or lightly pigmented below. Involucellum appressed to exciple, in upper half or extending to base. Ascospores (12–)13–**15.0**–17.5(–23.5) × (5–)5.5–**6.2**–7(–9.5) µm, length/width ratio (1.9–)2.2–**2.5**–2.7(–3.4) [68/7].

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. *V. pinguicula* differs in the more projecting and larger perithecia.



Verrucaria caerulea (18351)



Verrucaria caerulea (15152)

Verrucaria calciseda DC. (1805)

Thallus endolithic, whitish or pale grey, surface smooth or with a few long cracks radiating from some of the perithecia; surface apparently composed of redeposited calcite. Perithecia immersed in well-defined pits in rock, 240–420 µm wide. Exciple pigmented throughout, pigment dark reddish brown, K + dark grey-brown. Involucrellum absent. Ascospores ellipsoid, (21–)23–**24.9**–27(–29) × (8.5–)10–**11.4**–13(–15) µm, length/width ratio (1.7–)2.0–**2.2**–2.5(–2.8), perispore absent [60/4]; ascospores sometimes with dull grey-brown contents. Conidiomata not seen.

On limestone rocks; frequent but under-recorded. Wales, England, Ireland.

In the field the often white thallus and the radiating cracks running from the perithecial pits are distinctive, but the cracks not always present; ascospores and asci often (when over-mature or unhealthy?) with dark contents, which are very distinctive for this species.

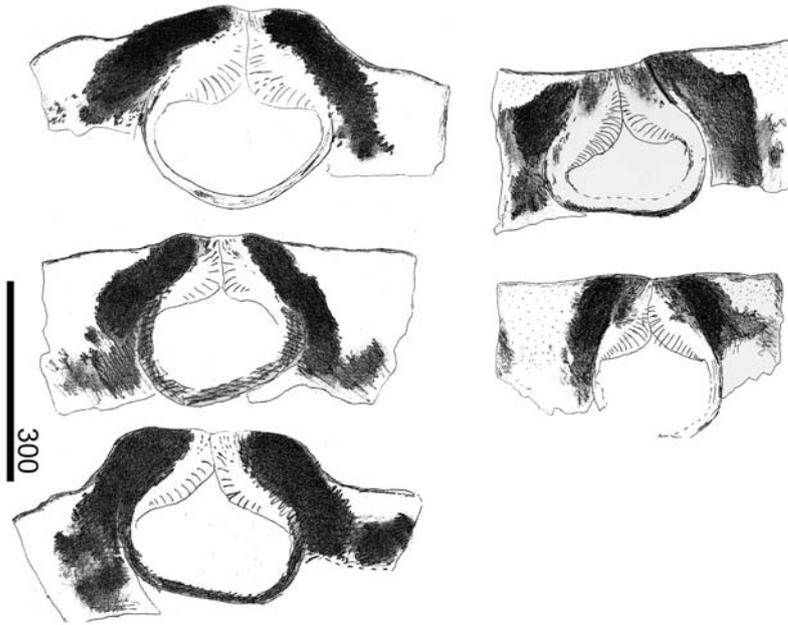


Verrucaria calciseda (15800).

Verrucaria cernaensis Zsch. (1927)

Verrucaria aethiobola auct. brit., *Verrucaria 'cernaensis'*

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 immersed to completely immersed in thallus, not projecting or forming low to moderate projections 120–360 µm diam. when measurable, apex blackish. Exciple 220–320 µm wide. Involucrellum usually well-developed,



sometimes mainly apical, but often reaching to base of exciple; often more or less appressed to exciple and the sides steeply conical or even vertical. Pigment dark brown, K + darker brown or greyish brown. Ascospores (15-)18-**19.8**-22(-27) × (7.5-)9.5-**10.6**-11.5(-14) μm, length/width ratio (1.5-)1.7-**1.9**-2.1(-2.4) [169/16]; perispore absent. Pycnidia often

present, scattered, visible as brown dots 40-60 μm wide, conidia straight or slightly curved, 4-8 × c. 1 μm.

On frequently submerged rocks beside lakes and rivers, and on seeping 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. Europe, India, Kashmir, mainland N. America and Greenland.

Detected in the field by the brown, regularly cracked thallus and little-projecting perithecia. Some specimens of *V. aethiobola* are similar, but differ in the larger spores with a perispore.



Verrucaria cernaensis. Morph with typical thick thallus and only gently projecting perithecia (16308).



Verrucaria cernaensis (21407) Morph with a relatively thin thallus, growing adjacent to a thicker thallus with an identical ITS sequence.

***Verrucaria ceuthocarpa* Wahlenb. in Ach. (1803)**

Prothallus absent or forming a very narrow white border to thallus. Thallus often thinning rapidly to a well-defined margin; epilithic, thin to usually thick, up to 400 μm thick; surface matt, greyish brown or greenish brown to dark brown; deeply cracked to margin, often into discrete areoles, areoles often separated by wide cracks; sides of areoles black when mature; surface of areoles plane to gently convex, edge of areoles 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 thallus, occasionally slightly projecting. Ascospores $8.5\text{--}10.5 \times 6\text{--}7.5 \mu\text{m}$.

On siliceous rocks on the sea shore. N. Scotland (very rare; Outer Hebrides: Rona; East Lothian). N. Europe, Novaya Zemlya, N.E. Siberia, N. America, Antarctica.



Verrucaria ceuthocarpa, Norway. (19323).



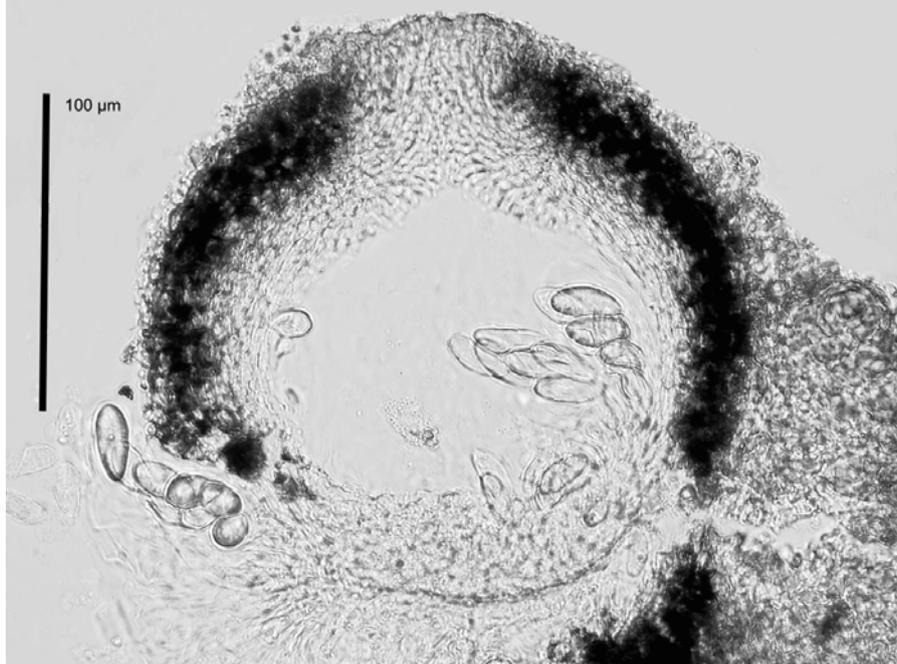
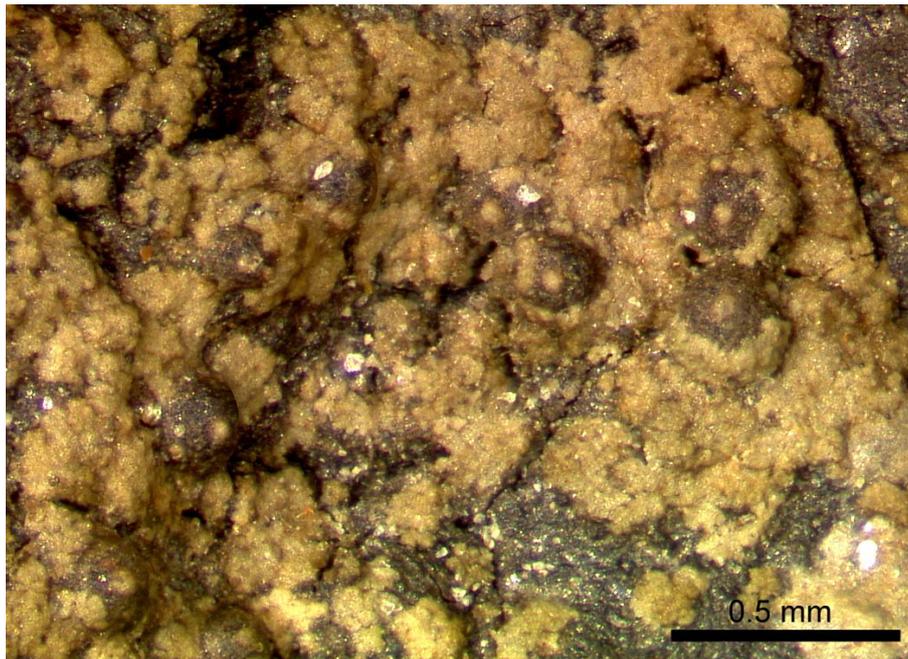
Verrucaria ceuthocarpa, on dolomite, Norway (19243).

Verrucaria consociata Serv. (1951)

Thallus composed of goniocyst-like clusters. Perithecia forming projections 170-240 μm diameter, often prominent, covered by thallus or thalline cover almost absent; ostiole pale or visible as low papilla to 40 μm wide. Involucrellum weakly developed, appressed and scarcely distinguishable from exciple, or possibly sometimes slightly spreading at base; exciple 150, 210 μm diameter. Ascospores simple, colourless, (16.8-)19.5-**21.8**-24.1(-26.7) \times (8.2-)8.9-**10.0**-11.2(-11.9) μm , L/W = (1.9-)2.02 - 2.2 -2.34(-2.6) [32 measured]. (Description of holotype).

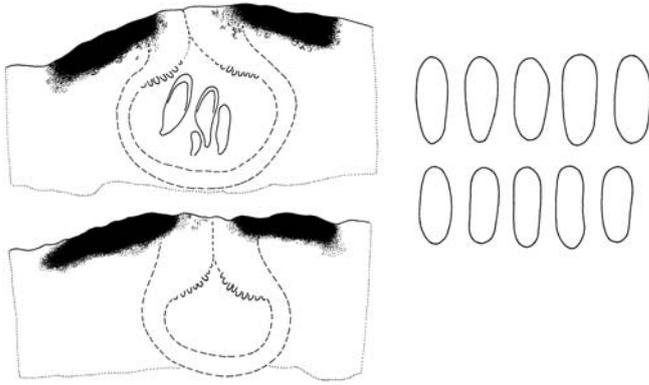
On stones in streams, probably also on damp stones elsewhere. Wales, Sweden, Czech Republic, Germany, Austria.

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.



Verrucaria consociata, holotype.

Verrucaria conturmatula Nyl. (1879)



Non-lichenized; forming infected spots up to 3.3 mm diam. on thallus of host, these darker than healthy host thallus; infected parts becoming thinner then disappearing or falling away. Perithecia immersed in the host thallus, visible as plane or slightly convex black dots up to 170 μm diam., often confluent in small groups, forming black areas up to 400 μm diam. Exciple 85–140 μm diam., colourless or locally brown. Involucrellum disc-shaped,

extending laterally from apex of exciple along the surface of the host, 85–270 μm diam., often confluent with other involucrella. Ascospores oblong to oblong-ellipsoid, sometimes slightly constricted, (11.5–)12.5–**14.1**–15.5(–18) \times (3.5–)5–**5.4**–6(–6.5) μm , length/width ratio (1.8–)2.3–**2.6**–2.9(–3.5) [63/7].

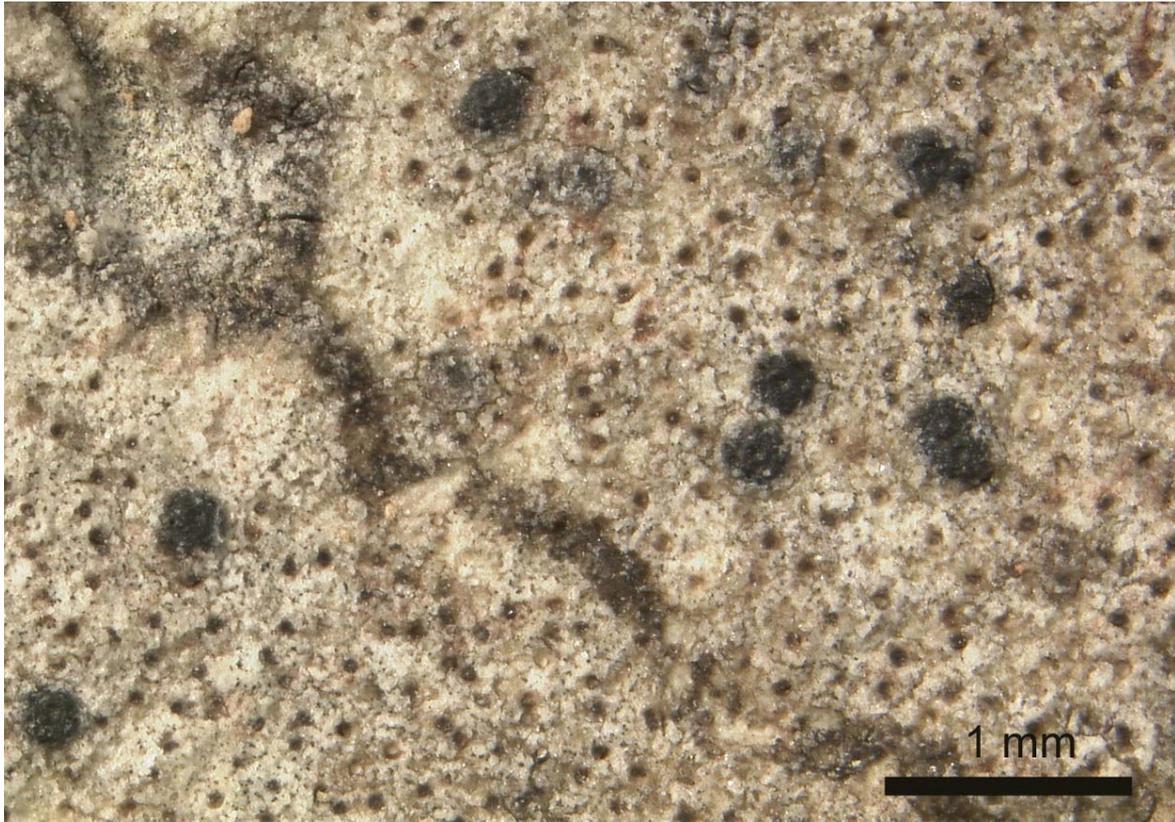
Parasitic on *Ionaspis lacustris*; probably frequent. North and west Britain, Ireland.

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, more or less single or double 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 confined to apex of exciple, or spreading sideways and downwards. Ascospores (13.5–)14–**15.5**–17(–18.5) \times (5.5–)6–**7.0**–8(–9) μm , length/width ratio (1.8–)2.0–**2.2**–2.5(–2.8) [27/4].

On exposed calcareous rocks; rare. N. Wales, S.W. England. Ireland, Norway, Sweden, C. & S. Europe.

Differs from *V. 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 that of its neighbour, so the lines often appear double.



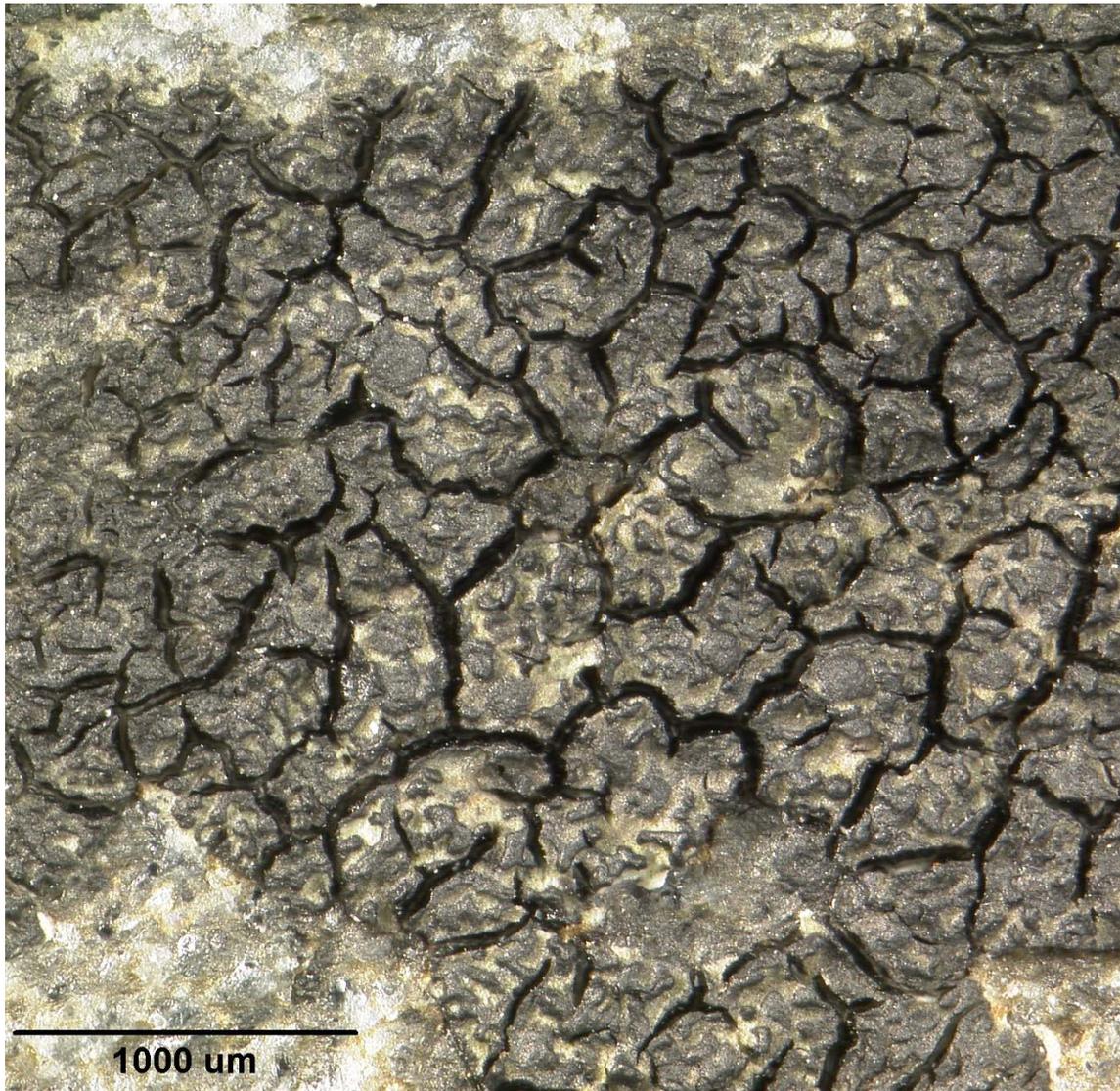
Verrucaria cyanea (V. Giavarini, North Wales).

***Verrucaria degelii* R. Sant. (1939)**

Prothallus white. Thallus superficial, to 1 mm thick, dull blackish green, scabrid, finely and regularly cracked; areoles with thickened, sharply raised, black edges, and with black ridges forming a network on the upper surface. Perithecia immersed, *c.* 100 μm diam. Involucrellum small, plate-like.

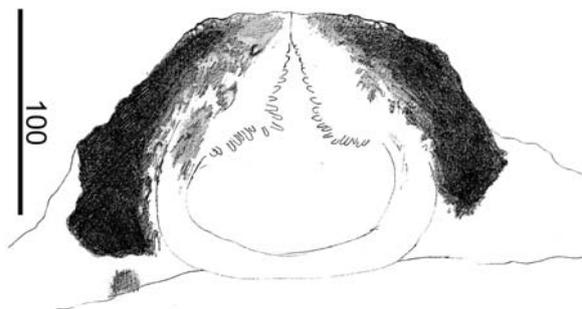
Ascospores 7–10 \times 4–7 μm .

On rocks on sheltered sea shores, amongst other maritime lichens. N. Scotland (Sutherland: Caithness). Iceland, Norway, N. America.



Verrucaria degelii

***Verrucaria ditmarsica* Erichsen (1937)**



Thallus dark greenish brown to blackish brown, thin, cracks usually absent or few; surface smooth, or rough with numerous small dark dots and irregular ridges 10–100 × 10–60 μm. Perithecia forming low to medium conical-hemispherical projections 120–280 μm diam. Involucrellum more or less conical, or contiguous with upper exciple and somewhat spreading. Ascospores (7.5–)8.5–**9.6**–10.5(–12) × (5–)6–**6.6**–7.5(–8) μm, length/width ratio (1.2–)1.3–**1.5**–1.7(–2.4) [44/4].

On intertidal rocks and stones, often abundant on sheltered shores and in estuaries. Widespread in Britain and Ireland. Europe. N. America.

The dark dots in the thallus may be very sparse. Differs from thin morphs of *V. maura* in the smaller perithecia and ascospores. 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. *V. erichsenii* has been generally been regarded as a synonym by British authors, but the distinction needs to be re-examined.



Verrucaria ditmarsica, with *Hydropunctaria maura* (left). (1949).

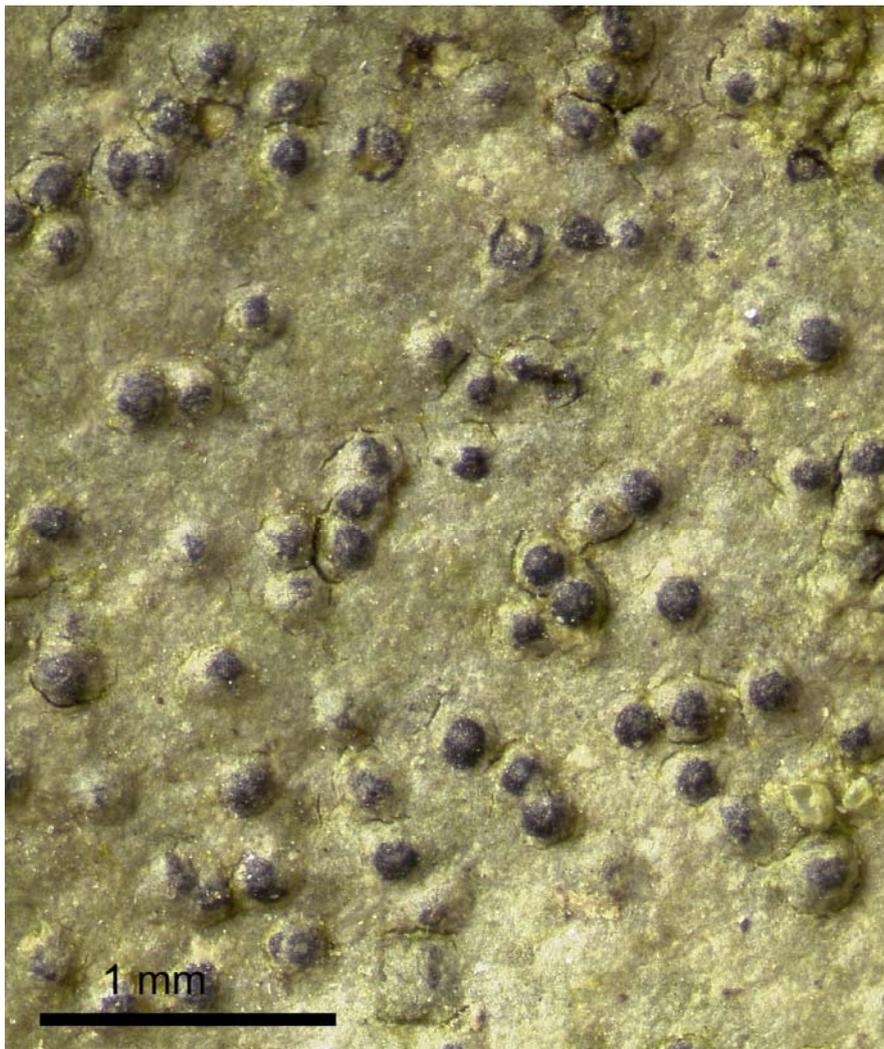
Verrucaria dolosa Hepp (1860)



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–**16.1**–18(–21.5) \times (5–)6–**6.9**–8(–9.0) μm , length/width ratio (1.9–)2.1–**2.4**–2.6(–3.1) [78/10], perispore not detected. Pycnidia not detected.

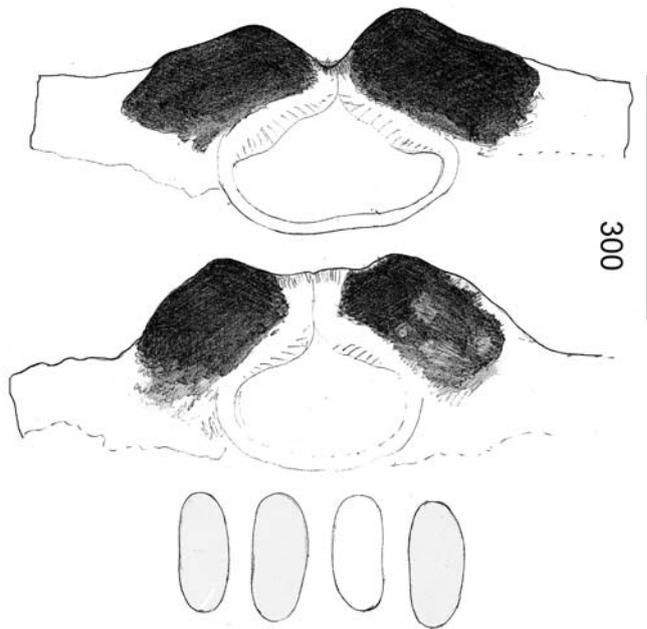
On siliceous and limestone rocks and pebbles, often in ephemeral habitats.

Distinguished by the small perithecia, small ascospores, and more or less conical involucrellum. *V. sublobulata* differs in the thicker thallus and mostly immersed perithecia. *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.



Verrucaria dolosa (18082).

Verrucaria dufourii DC. (1805)



Thallus immersed, usually level with surrounding rock or slightly lower, pale grey to brownish grey, not cracked; sometimes thallus units reaching to surface of rock as minute brownish specks; prothallus not seen, but leading edge of thallus sometimes whitish; junction with neighbouring conspecific thalli marked by a fine crack, a groove, a change in level, a whitish (rarely brownish) line, or a row or double row of brown pycnidia. Perithecia forming distinct projections 280–440 μm wide, black, not covered by thallus, apex flat or usually concave, leaving shallow pits in rock when decayed; ostiole inconspicuous, or appearing as a slightly paler area 30–80 μm wide, or as a paler area up to 140 μm wide and occupying much of concavity. Involucrellum well-

developed, thick, flanking upper half of exciple, pigment dark reddish brown, K + dark brown. Exciple pale below. Ascospores oblong to ellipsoid, (15.5–)16.5–18.1–20(–23.5) \times (6.5–)7–7.8–8.5(–9) μm , length/width ratio (1.9–)2.0–2.4–2.7(–3.4) [25/5], often with a perispore to 1.5 μm thick. Pycnidia frequent, scattered, often numerous and easily seen, appearing as brown pits 60–100 μm wide. Conidia rod-shaped, 3.3–4.5 \times 0.8–1.2 μm .

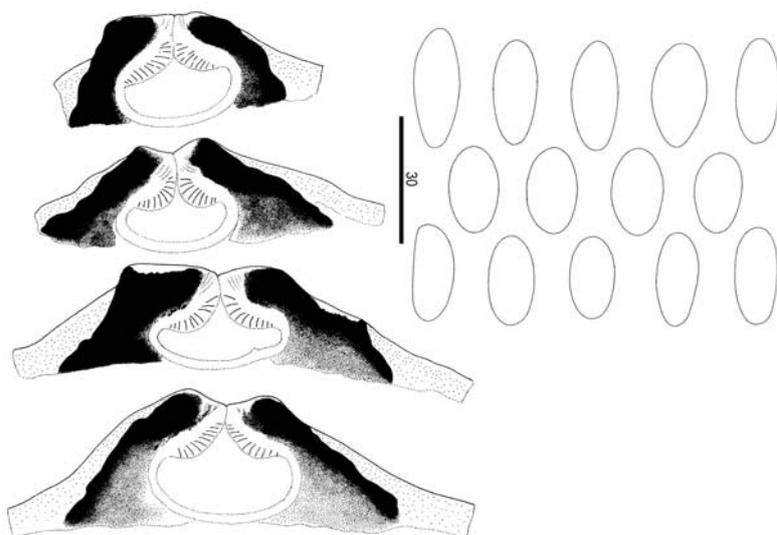
On hard limestones; occasional. Widespread in limestone areas of Britain and Ireland. Italy.

Distinguished by the immersed thallus, often dotted with pycnidia, the perithecia which typically have a concave apex, and the usually somewhat oblong ascospores. Perhaps previously over-recorded for *V. 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. *V. pinguicula* is probably a more northern species than *V. dufourii*.



Verrucaria dufourii (16662)

Verrucaria elaeina Borrer (1830)

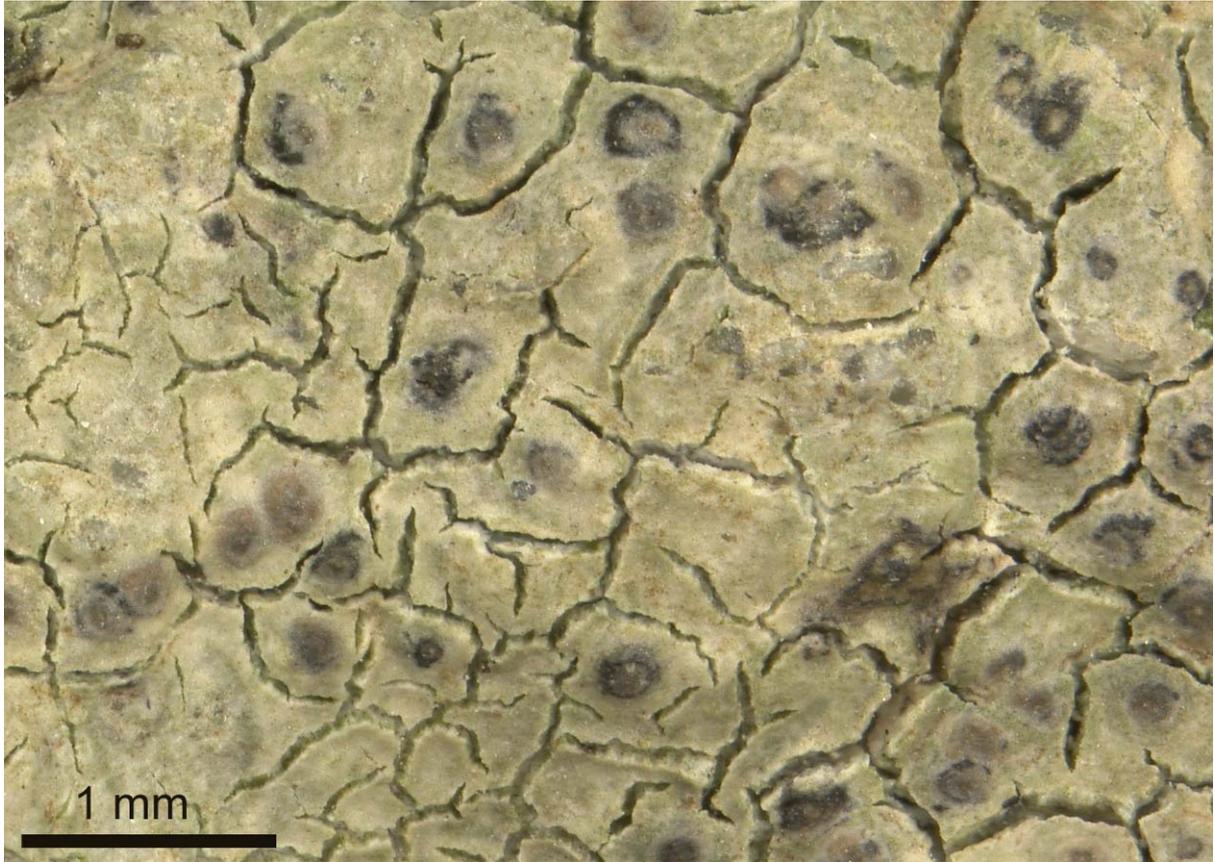


Thallus crustose, epilithic, non-gelatinous, light grey-green to pale brownish green, rarely mid-brown, thin to moderately thick, 25–90(–105) μm thick, rimose; cracks usually numerous, but often few in young or poorly developed areas of thallus; surface smooth; surface of cracks unpigmented. Prothallus white; adjacent thalli of same species often separated by dark lines. Epinecral layer absent; cells of thallus irregularly arranged or in very weak vertical columns; cortex ill-

defined, comprising only 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 apex, or usually upper part naked; apex black, rounded to 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 plane 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 more or less spreading from the exciple below, usually \pm 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 lower part of involucrellum; lower cells often with large oil droplets within. Exciple 160–280 μm diam., usually unpigmented except for ostiolar region with dilute brown or greenish-brown, K + slightly darker pigment; sometimes outer part of exciple pigmented below with a similar pigment to the involucrellum. Ascospores ellipsoid to narrowly ellipsoid or oblong-ellipsoid, (15.0–)16.5–**19.4**–22.5(–24.0) \times (6.0–)7.0–**8.0**–9.0(–9.5) μm , (1.7–)2.0–**2.4**–2.9(–3.5) times as long as wide [476/27]; perispore absent. Conidiomata not detected.

On shaded limestone, concrete, siliceous rock and brick, in woodland or beneath herbaceous vegetation, in natural habitats or on wasteground, in gardens or on damp walls; particularly characteristic of weakly calcareous rock in shade; common and locally abundant. Throughout British Isles. Norway, Belgium, Luxembourg, Germany, Switzerland, Austria, Italy, Slovakia.

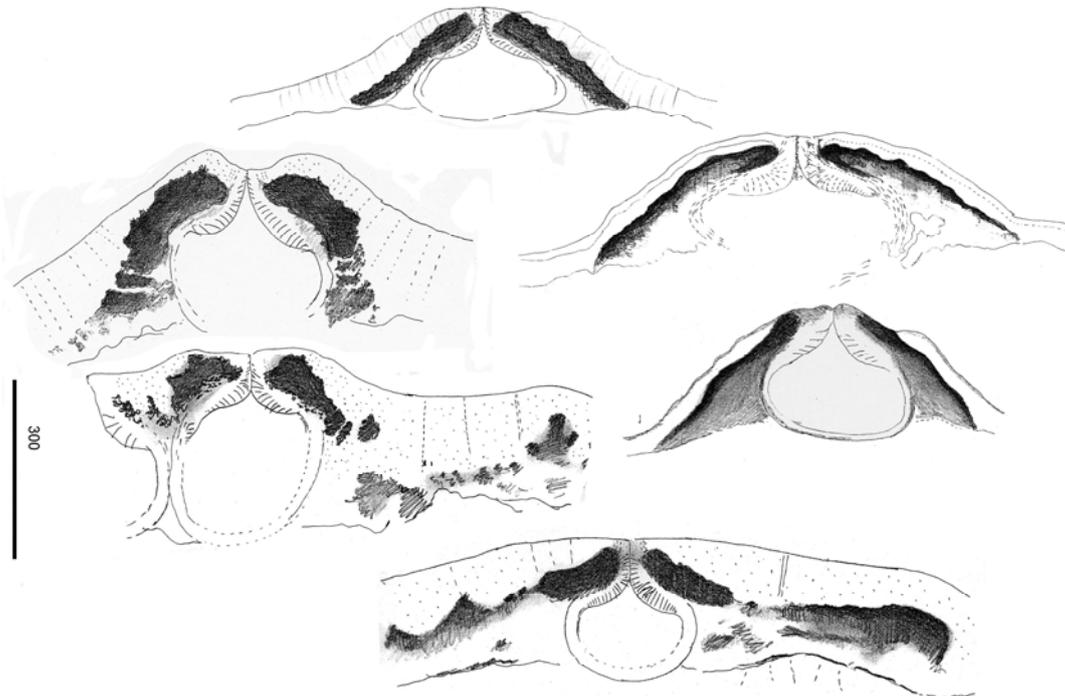
The pale grey-green thallus on shaded rocks is characteristic and often easily recognised with the unaided eye; the apex of the involucrellum is often irregular, showing as a ring of dark dots surrounded by the pale opaque thallus. Some weakly developed morphs have a much less distinctive appearance 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.



Verrucaria elaeina (16628)

Verrucaria elaeomelaena (A. Massal.) Arnold (1868) *sensu lato*

Verrucaria andesiatica auct.

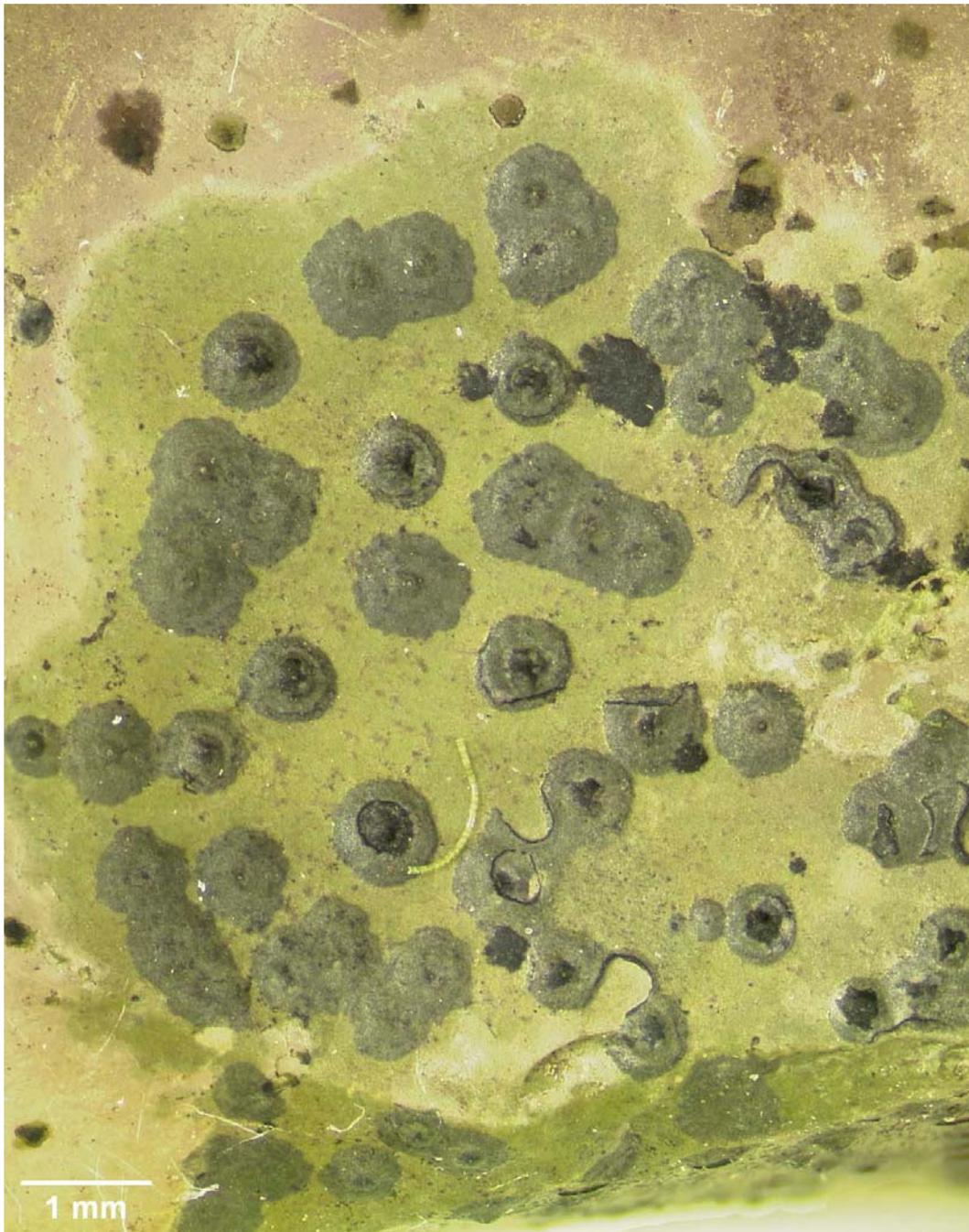


Thallus subgelatinous, light to mid grey-green to mid brown, 20-210 µm thick. Perithecia forming low to moderate projections, covered to near apex by a layer of thallus. Involucrellum typically conical, but very variable in shape in some of the thicker thalli. Ascospores (17-)20-27(-32) × (9.5-)11-13.5(-15.5) µm, (1.2-)1.6-2.3(-2.7) times as long as wide.

On rocks and stones in streams and seepages.

The description above applies to several very similar taxa (Thüs *et al.* in prep.). In Great Britain, the name *V. elaeomelaena* has often been restricted to specimens with broadly ellipsoid ascospores, growing on limestone.

Similar to *V. hydrophila*, but distinct in the larger ascospores, and the larger and less 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'.



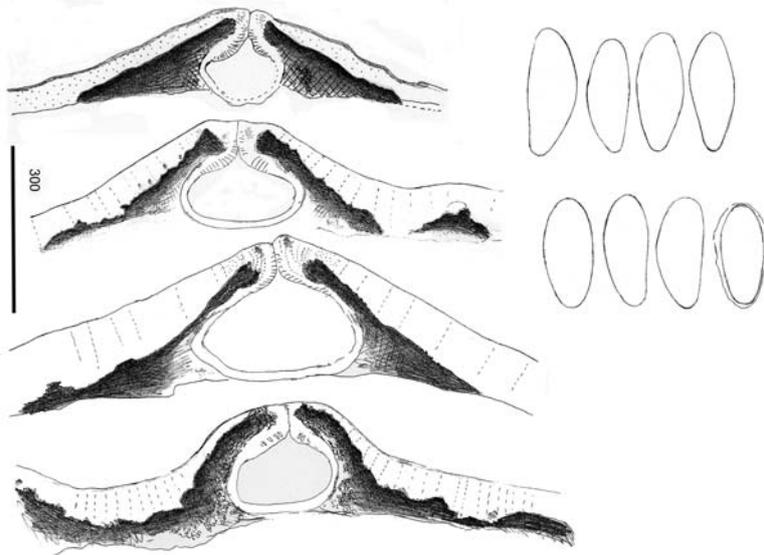
Verrucaria elaeomelaena s.l., a thin morph, growing on glass (19398).



Verrucaria elaeomelaena s.l., a thick morph (Lansdown, River Avon, Wiltshire).

Verrucaria funckii (Spreng.) Zahlbr. (1921)

Thallus light grey-green to grey-brown brown, subgelatinous, well-developed, (20–)80–160(–240) μm , uncracked, rarely with a few cracks, surface smooth. Prothallus whitish, not fimbriate; contiguous conspecific thalli separated by dark lines. 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 thallus, the apex visible at the surface only as a small grey dot, or exposed by abrasion to form a small black disc. Exciple 180–390 μm wide, colourless at sides and base, often dilute brown at ostiole. Involucrellum well-developed,



reaching to base of thallus, distinctly conical with straight or even slightly concave sides, or sometimes sides convex; often wide-spreading at base, and merging into basal layer of thallus when present.

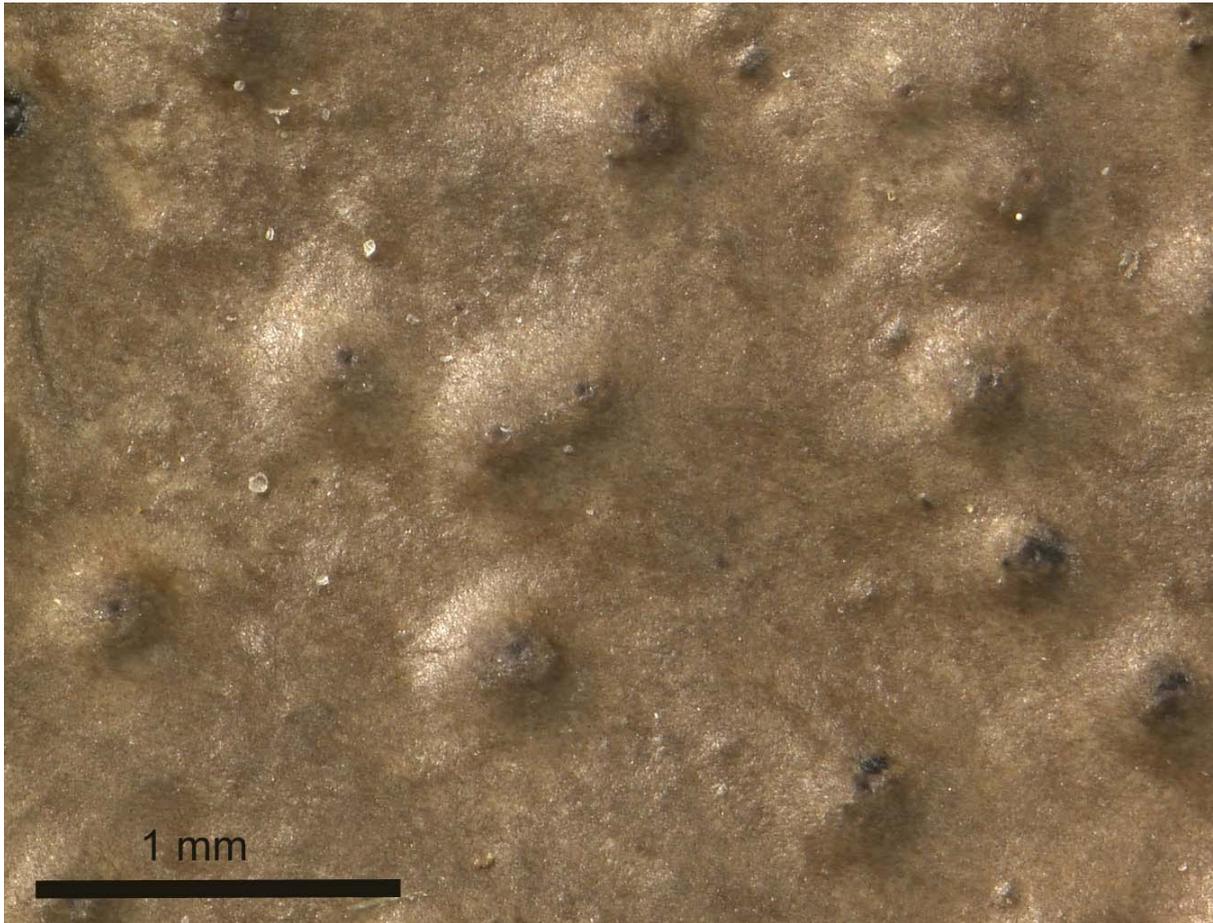
Pigment in involucrellum red-brown, K + grey. The thallus often completely covers the involucrellum, and then an alga-free ostiolar region extends to the thallus surface.

Ascospores ellipsoid to narrowly ellipsoid, (19.5–)22.5–**23.8**–25.5(–28.5) \times (8–)9–**10.1**–11(–13) μm , (1.8–)2.1–**2.4**–2.6(–3.1) times as

long as wide [206/12], a thin perispore 0.5(–2) μm thick present on at least some spores.

On frequently or permanently submerged siliceous rocks in rivers and lakes, in small streams and in springs, frequent in upland areas of Britain and Ireland. Iceland, Norway, Sweden, Germany, N. America.

The very smooth uncracked thallus with very shallow perithecial projections is distinctive. *V. andesiatica* differs in the thinner thallus, higher perithecial projections, absence of a basal layer, and slightly broader ascospores.



Verrucaria funckii, a brown morph from an upland stream (11527).

***Verrucaria fusconigrescens* Nyl. (1872)**

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, plane 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, 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, pigment reddish brown, K + grey-brown. Exciple 200–377 μm diam., wall colourless or locally pigmented like the involucrellum, ostiole often with brown pigment. Ascospores oblong-ellipsoid, (17–)19.5–**21.4**–23.5(–26) \times (6.5–)8–**8.8**–9.5(–11), length/width ratio (2.1–)2.3–**2.4**–2.6(–2.8) [61/7]. Vegetative propagules and conidiomata not seen.

On siliceous rocks on or near the coast, or on slightly calcareous rocks inland; frequent. N. and W. Britain, Ireland. Europe, Asia (Taiwan).

Distinguished by the well-developed (though not thick) brown thallus, absence of thalline layer on perithecia, more or less conical involucrellum, and medium sized spores. *V. nigrescens* differs in the more immersed perithecia, and usually occurs on calcareous rocks.

This is a collective species on which work is progressing.



Verrucaria fusconigrescens agg. (18167).

Verrucaria halizoa Leight. (1871)

Thallus superficial, thin, *c.* 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 conical-hemispherical projections 140–260 μm diam. Involucrellum spreading. Exciple pale at the base. Ascospores oblong-ellipsoid to narrowly oblong-ellipsoid, (7–)8–**9.1**–10.5(–12) × 3.5–**4.1**–4.5(–5.5) μm, length/width ratio (1.3–)1.7–**2.3**–2.8(–3.5) [60/7]. Pycnidia occasional, visible as black dots *c.* 40 μm diam. Conidia straight to slightly curved, 2.9–3.3 × 1 μm.

In crevices and shade on rocks on the sea shore, in the mid-littoral, usually amongst *V. mucosa*, *V. striatula*, and the crustose red alga *Hildenbrandia*. Throughout western British Isles. Europe, N. America, Asia (Taiwan).

Distinguished by the thin thallus without ridges or punctae, but the pycnidia, when present, could be mistaken for punctae. Smooth morphs of *V. striatula* typically have greener thalli and larger, more irregularly shaped, perithecia.



Verrucaria halizoa

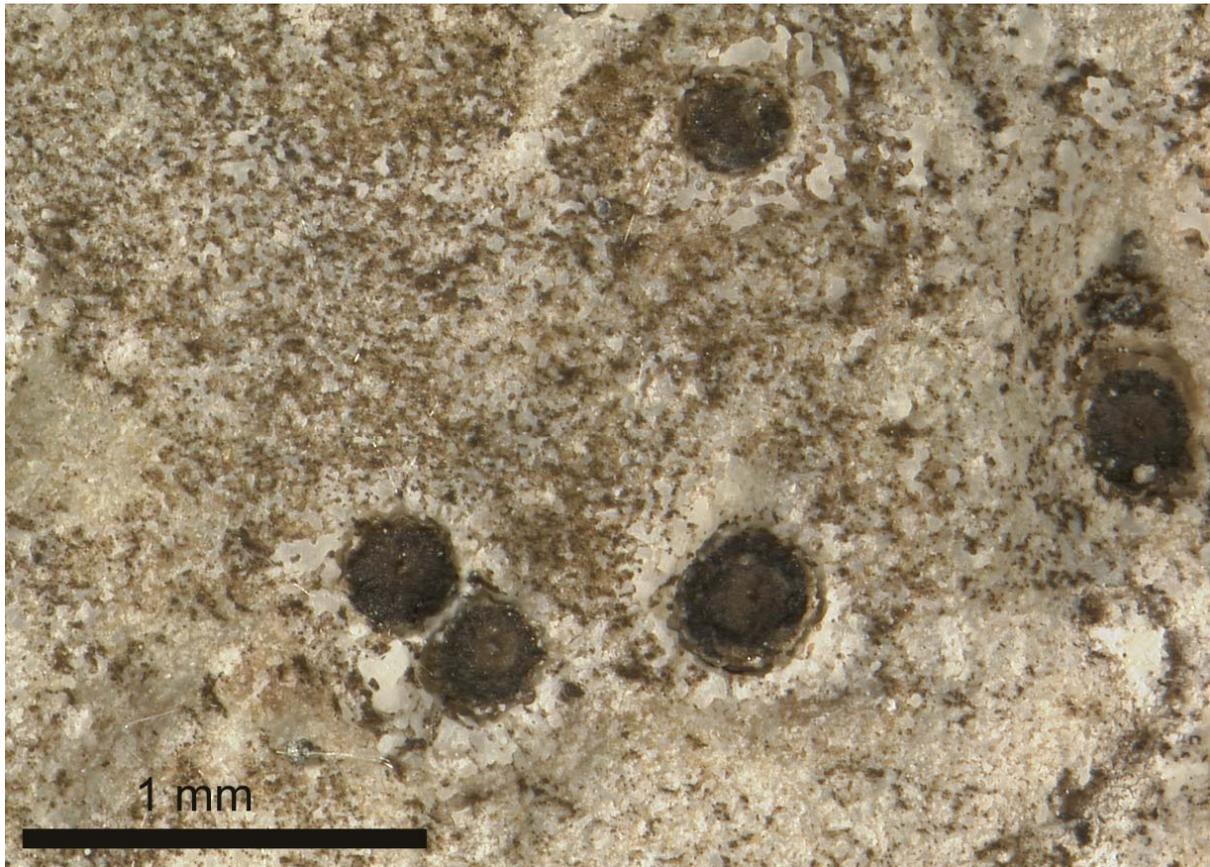
***Verrucaria hochstetteri* Fr. (1831)**



Thallus endolithic, whitish to light grey, without cracks. Perithecia 375–700 μm wide, immersed in well-defined pits in rock. Exciple pigmented throughout, brown, K + darker brown. Involucrellum absent. Ascospores ellipsoid to broadly ellipsoid, (24.5–)29–**31.8**–34.5(–41.5) \times (14–)16–**18.0**–20(–24.5) μm , length/width ratio (1.2–)1.5–**1.8**–2.0(–2.4) [34/6]; 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.

On calcareous rocks; common. Throughout British Isles. Europe, Taiwan.

Identified by the immersed thallus, large perithecia in pits, absence of an involucrellum, and large ascospores. The perispore may be confused with the ascospore wall; the presence of a distinct ornament is unusual in the genus.



Verrucaria hochstetteri (16183).

Verrucaria hydrophila Orange (2013)

Verrucaria hydrela auct., non Ach. (1814)

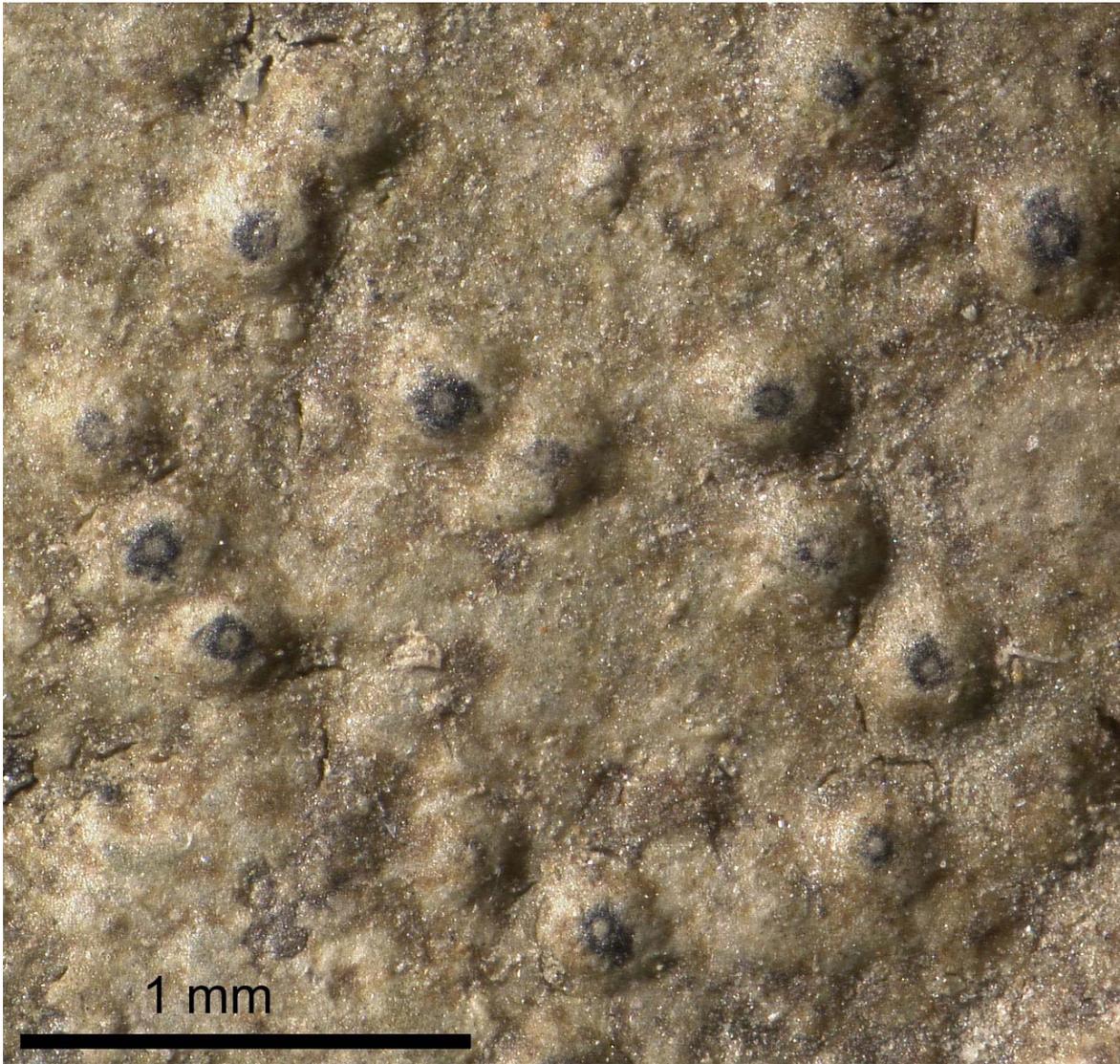
Verrucaria denudata Zsch. (1927) *nom. illeg.*

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 diameter, covered by thallus at first, sometimes eroded later to reveal black apex; ostiolar area inconspicuous, plane or convex, appearing as a pale dot 15–50 μm diam. Involucrellum conical, pigment brown to reddish brown, K + darker brown to dark grey-brown. Exciple 180–310 μm diam., colourless except at apex. Ascospores (16.0–)19.5–**21.3**–23.1(–26.5) \times (6.5–)8–**8.8**–10(–12) μm , (1.7–)2.2–**2.4**–2.7(–3.3) times as long as wide [254/14]. Pycnidia not detected.

On rocks and stones in streams and streamlets, and on wet banks, often in shade; frequent. Throughout British Isles. Widespread in Europe.

Distinguished by the conical involucrellum, covered by a layer of thallus, and rather small ascospores. *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.

Possibly a collective species.



Verrucaria hydrophila, holotype.



Verrucaria hydrophila (top section from holotype).

***Verrucaria internigrescens* (Nyl.) Erichsen (1928)**

Thallus superficial, non-gelatinous, uneven, usually cracked, whitish to brownish white; adjacent conspecific thalli sometimes separated by dark lines. Perithecia forming projections 320–780 μm diam., not covered by thallus. Involucrellum well-developed, reaching to level of base of exciple, more or less clasping exciple and spreading slightly below, to conical. Ascospores oblong-ellipsoid, (15–)19.5–**22.3**–25(–30) \times (7.5–)9–**10.3**–11.5(–13) μm , length/width ratio (1.6–)1.9–**2.2**–2.4(–3.2) [137/9].

On shaded damp siliceous rocks in the supralittoral zone on seashores, common, throughout British Isles. Europe, N. America.

Distinguished by the whitish superficial thallus, medium-sized ascospores, and maritime habitat. *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.

This species needs to be revised.

Verrucaria knowlesiae P.M. McCarthy (1988)

Thallus more or less endolithic and inconspicuous, to thinly epilithic, brownish grey, and cracked. Perithecia semi-immersed to almost superficial, not covered by a thalline layer. Involucrellum hemispherical to conical, 150–250(–300) μm wide, extending to base-level of exciple. Exciple 100–150 μm wide, brown. Ascospores ellipsoid, (7.5–)8.9(–11) \times (5.5–)5.9(–7) μm [25/1].

On shaded limestone; very rare. W. Ireland (Galway). Known from two collections. Differs from *V. bulgarica* in the larger perithecia.

Verrucaria latericola Erichsen (1943)

Thallus parasitic, of scattered or contiguous areoles, or placodioid, growth form largely dependent on form of host thallus; grey-green, grey-brown or brown, epinecral layer (5–)15(–25) μm thick, cortex brown except in shade. Perithecia three-quarters immersed to completely immersed, up to 20 per areole, exciple 100–150(–180) μm wide, usually colourless below, pigmented at apex. Ascospores ellipsoid to narrow-ellipsoid, occasionally with one concave side, (10.5–)14.0(–19) \times (4.5–)5.8(–7.5) μm . Pycnidia frequent, conidia rod-shaped, 4–8 \times 1 μm .

Parasitic on lichens, particularly *Caloplaca flavescens* and *C. citrina* agg., but also on *C. flavovirescens*, *Lecanora albescens* and *Diplotomma alboatrum*; rare. S.W. England, N. Wales, Scotland, Ireland. France, Spain.

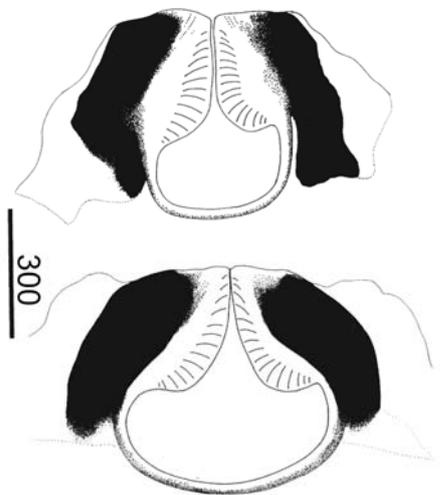
British records under this name probably refer to more than one species and need to be revised.

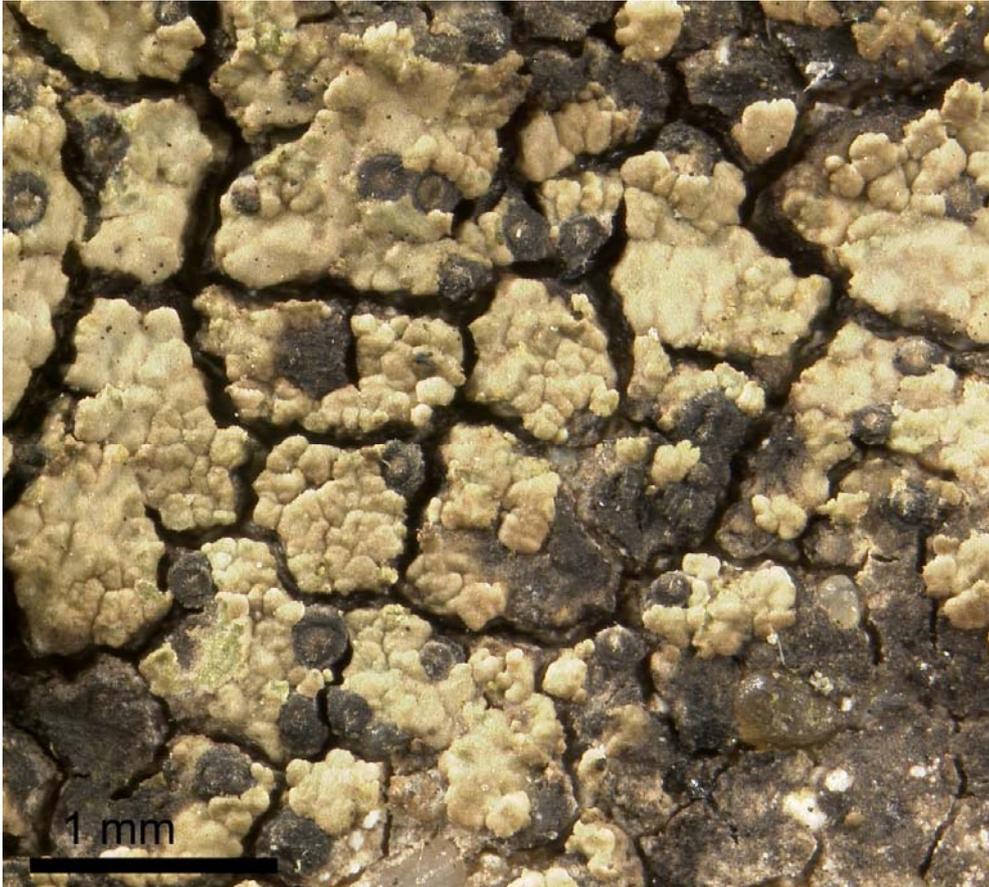
Verrucaria macrostoma Dufour ex DC. (1805)

Thallus superficial, well-developed, pale to dark brown (typically mid brown), at first comprising rounded or lobes areoles up to 400 μm wide, these becoming crowded and often coalescing, and thallus usually soon cracked into large secondary areoles 160–1600 μm wide; blastidia absent to abundant, 40–80 μm wide, formed on the edges of the secondary areoles; dark basal layer absent; epinecral layer often present. Perithecia forming low to moderate conical-hemispherical projections 300–520 μm wide, black, not covered by a thalline layer, not forming pits. Involucrellum well-developed, often more or less reaching base-level of exciple, slightly spreading to more or less conical. Ascospores ellipsoid, (21.5–)25–28.4–31.5(–36) \times (9.5–)11.5–13.0–14.5(–16.5) μm , length/width ratio (1.7–)2.0–2.2–2.4(–2.8) [54/6], perispore not seen. Conidiomata not found.

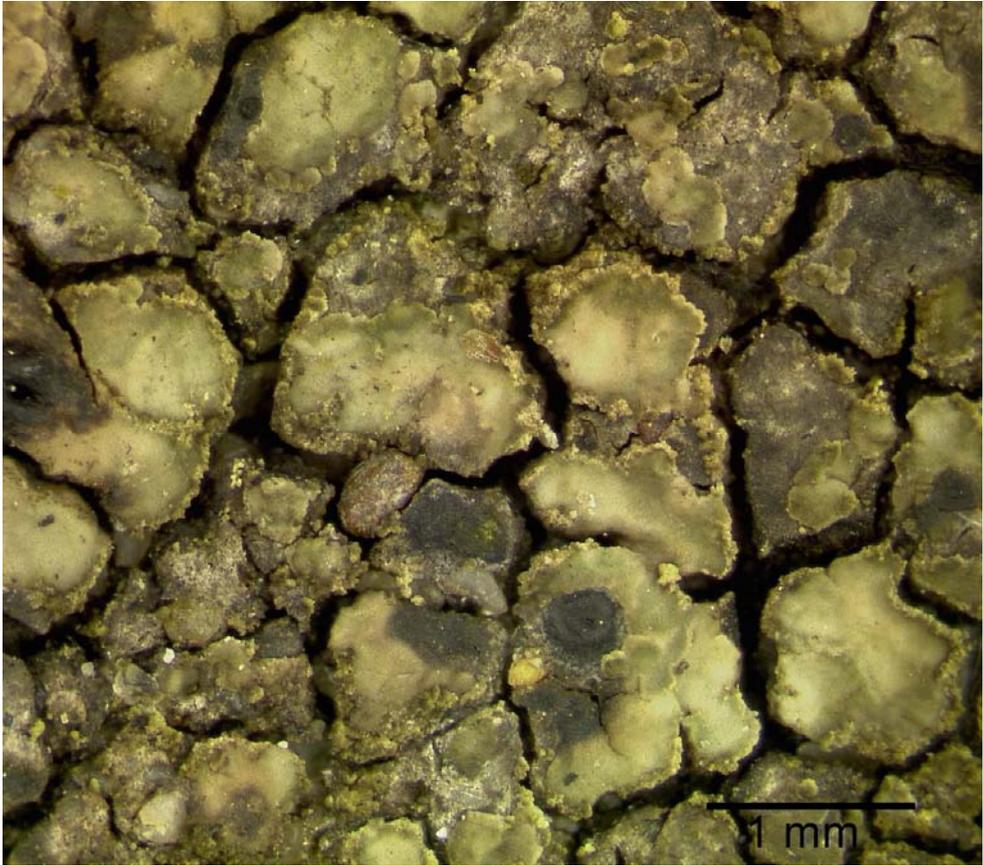
On limestone, mortar and calcareous sandstone, in semi-natural habitats but often on walls, probably favoured by slight nutrient enrichment; frequent. Widespread in England and Wales, local in Scotland and Ireland.

The thallus is typically mid brown but can be dark on exposed rocks, and pale brown in shade. *Verrucaria squamulosa* has more discrete, subsquamulose areoles. *V. viridula* differs in the perithecia immersed in the substratum and having a less well-developed involucrellum. Blastidiate specimens have been referred to f. *furfuracea* de Lesd.



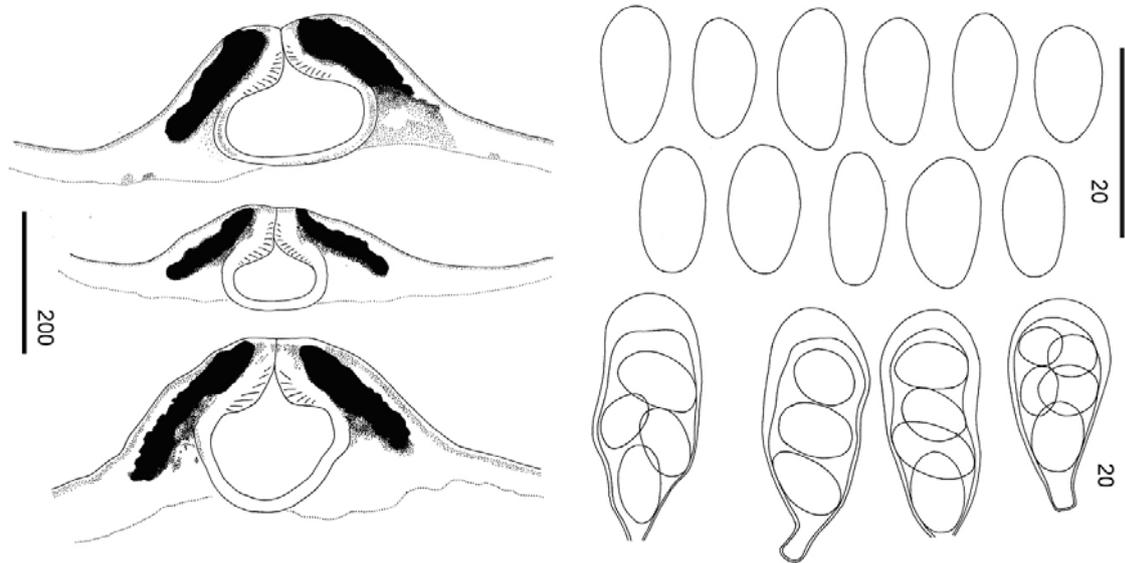


Verrucaria macrostoma, shaded wall (17560).



Verrucaria macrostoma, blastidiate thallus.

Verrucaria madida Orange (2004)



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 thalline layer has been eroded. Exciple 140–290 µm diam., colourless or brown below; ostiole with dull green pigment similar to that in thallus. Involucrellum conical, or somewhat spreading at sides and then curved down slightly. Asci (3–)4(–5)–spored. Ascospores ellipsoid, without perispore, (9–)10.5–**12.1**–13.5(–15) × (5.5–)6–**6.6**–7(–7.5) µm, length/width ratio (1.4–)1.6–**1.8**–2.1(–2.6) [67/3]. Conidiomata not detected.

On frequently immersed siliceous rock in streams and streamlets. South Wales (Brecon Beacons), Scotland (Stirlingshire). Norway (Hordaland), France (Cantal), Poland.

Distinguished by the green, 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, *V. rheitrophila* differs in the immersed perithecia and presence of punctae in the thallus, and *V. scabra* differs in the presence of immersed punctae and a dark basal layer, and in the larger, oblong ascospores.

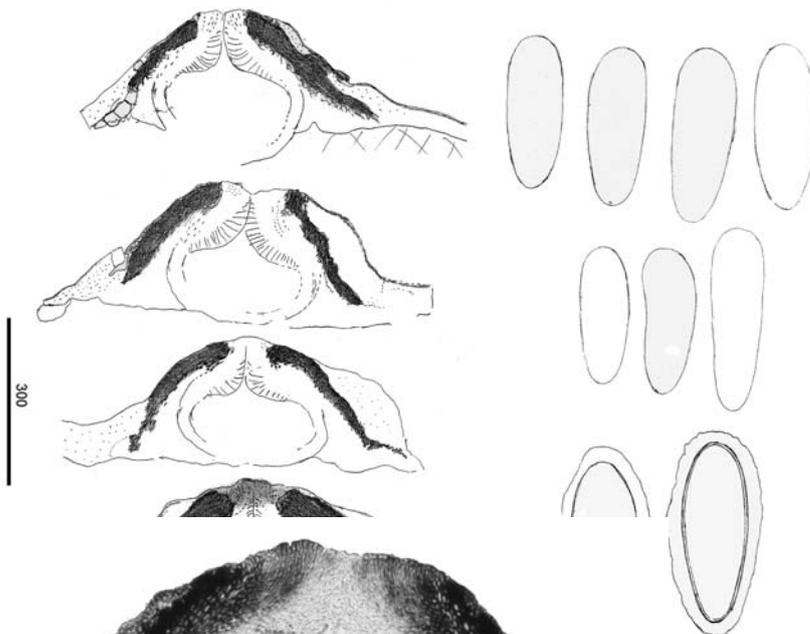


Verrucaria madida

***Verrucaria margacea* (Wahlenb.) Wahlenb. (1812)**

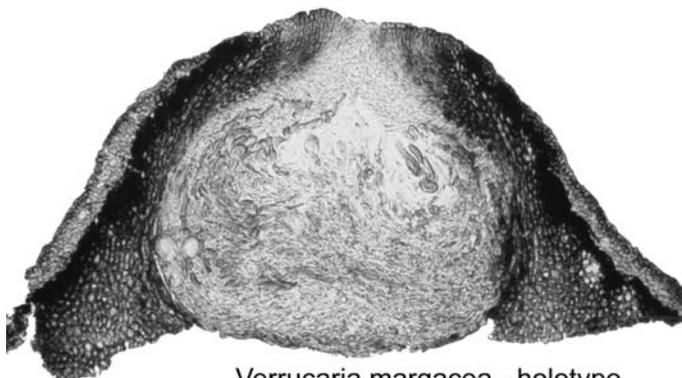
Thallus superficial, non-gelatinous, more or less continuous or with numerous cracks, pale brown to brown, smooth or somewhat uneven, giving a finely mottled appearance. Perithecia forming projections 280–540(–700) μm diam., usually mostly covered by thallus, but often partly exposed later. Involucrellum conical, often reaching to substratum, but sometimes a little weakly developed and irregularly conical; angle between involucrellum and base of exciple colourless or with pigment evenly distributed throughout cell walls. Exciple 180–320 μm diam. Ascospores (20–)26–**29.3**–32.5(–

40.5) \times (9–)11–**12.6**–14(–17.5) μm , length/width ratio (1.6–)2.1–**2.3**–2.6(–3.4) [418/27], a perispore up to 2 μm thick often present. Conidiomata not known.



On siliceous rocks beside streams and lakes; frequent. N. and W. Britain, Ireland. Widespread in Europe; India, Australia, Greenland, mainland N. America.

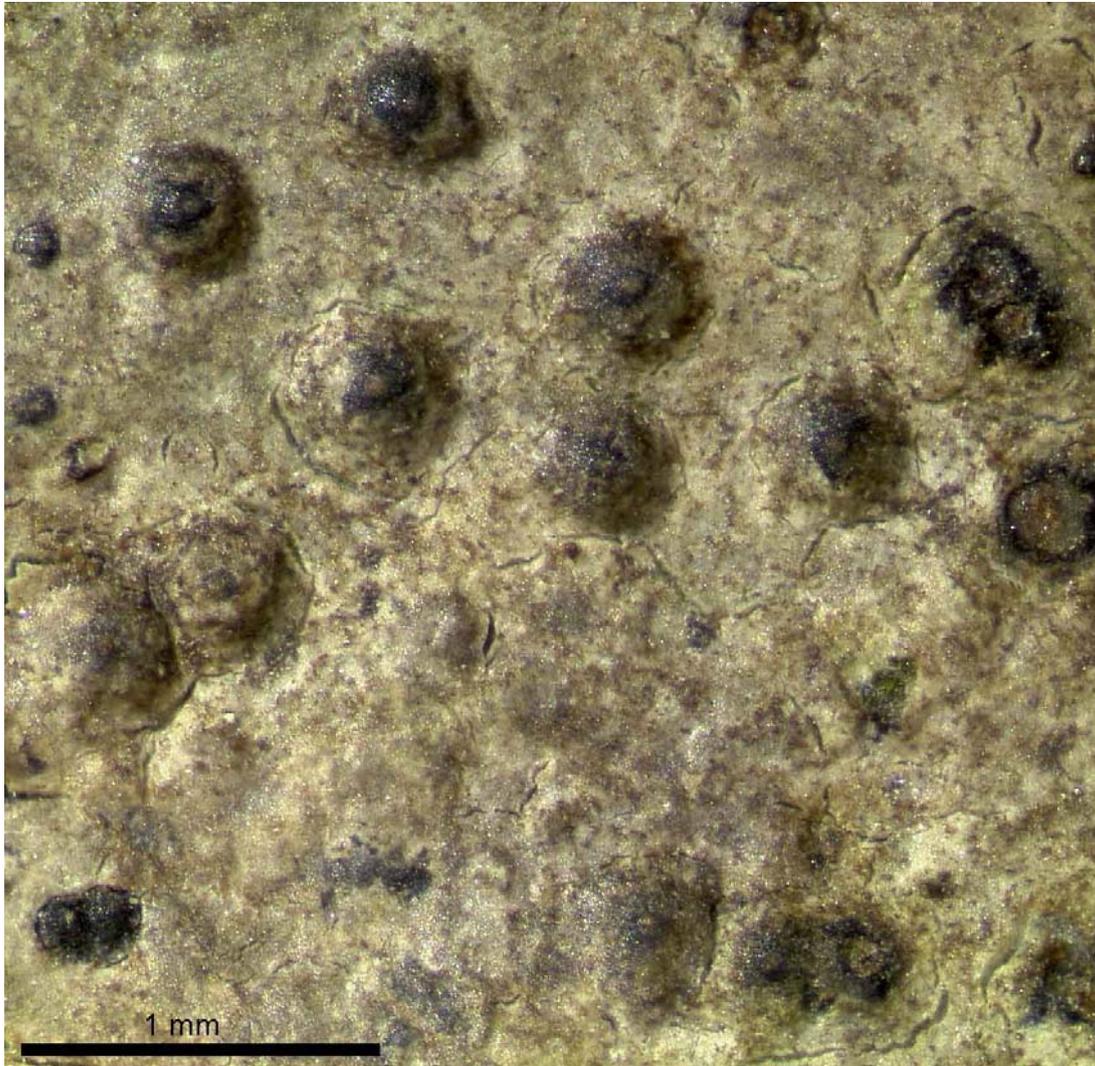
Distinguished by the non-gelatinous thallus, a conical involucrellum which is usually covered by a layer of thallus (often partly lost later) and large ascospores. *V. elaeomelaena*



Verrucaria margacea - holotype

s.l. differs in the smooth, subgelatinous thallus. *V. aethiobola* 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. aethiobola* tends to be smooth between the cracks, but many specimens deviate from this.

This is a collective species; British material differs from the type of *V. margacea*.

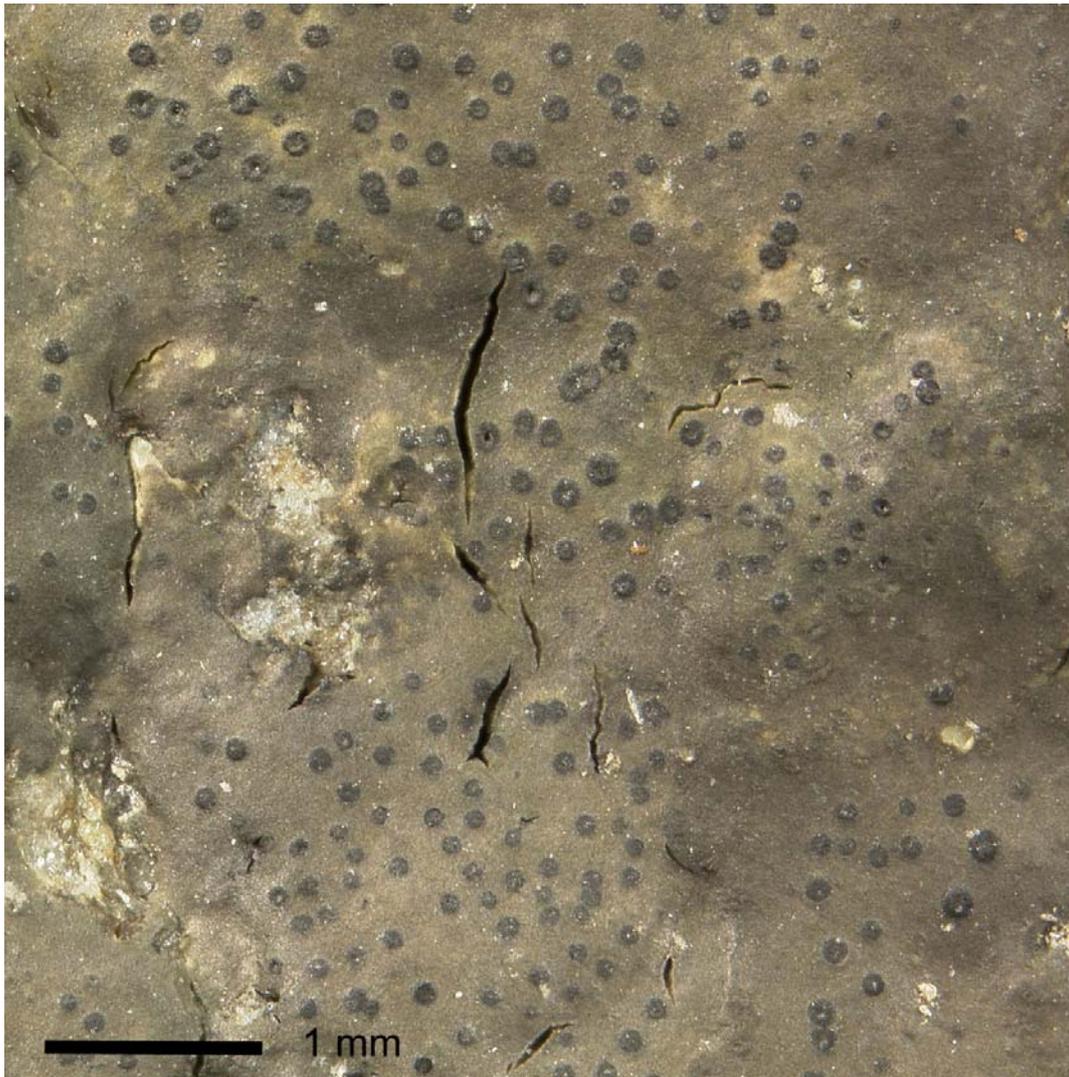


Verrucaria margacea s.l., Wales (16288).

Verrucaria mucosa Wahlenb. (1803)

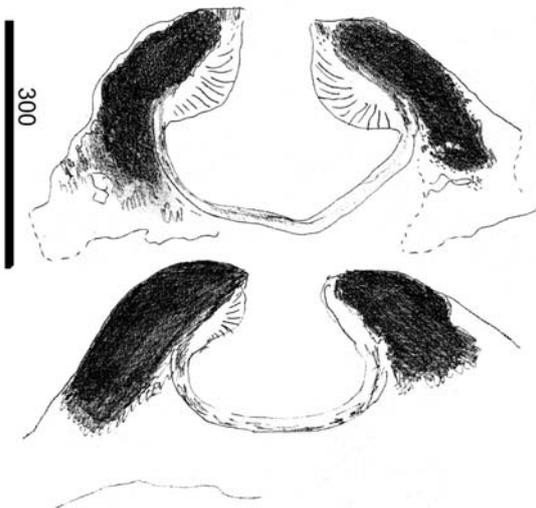
Thallus superficial, to 1 mm thick, subgelatinous, smooth, olive-green to dark green or black, weakly translucent when fresh and wet, prothallus white. Perithecia immersed. Involucrellum small, surrounding apex of exciple; exciple to 150 μm , pale except at apex. Ascospores 7–10 \times 4–7 μm , relatively thick-walled.

On rocky seashores in the mid-littoral zone, in sun or shade, with barnacles and macroalgae, rarer on sheltered shores and intolerant of silt, forming more or less extensive patches; very common. Throughout British Isles except S.E. and E. England. Cosmopolitan.



Verrucaria mucosa, from near type locality in Norway (19124).

***Verrucaria muralis* Ach. (1803)**

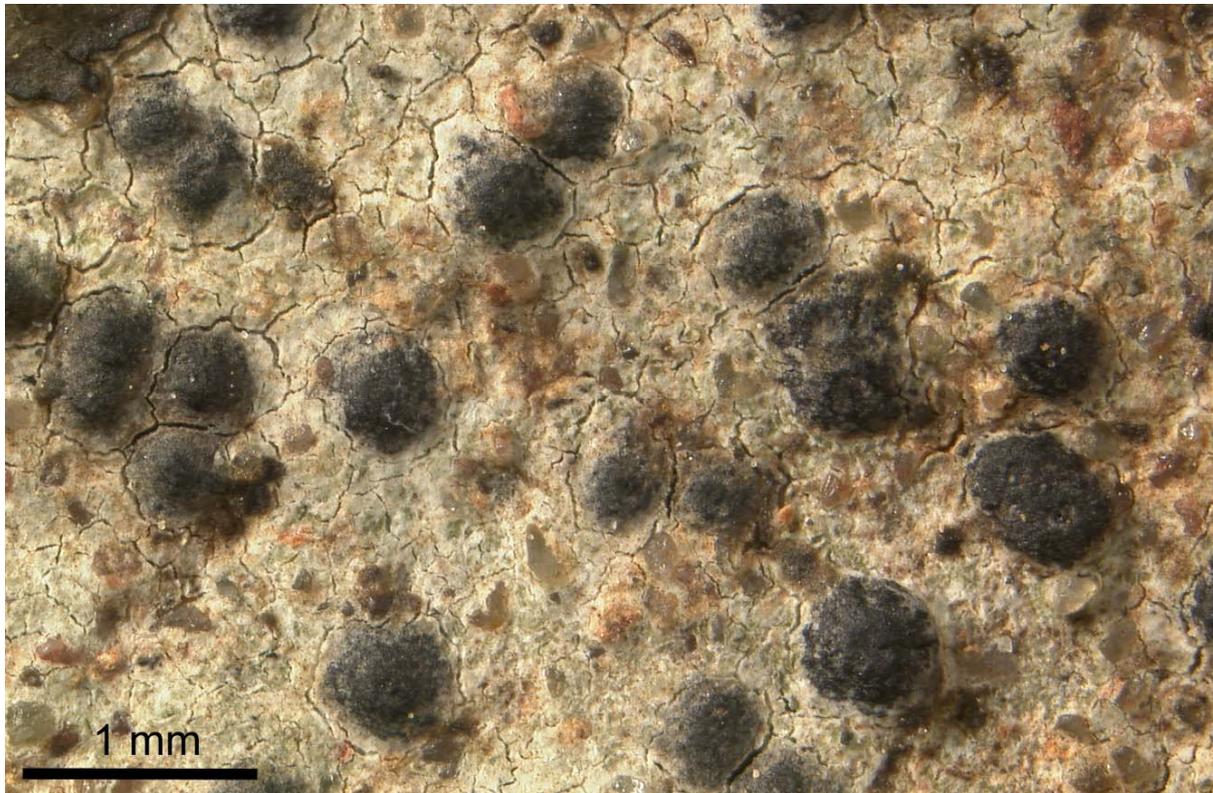


Thallus immersed to thinly superficial, whitish to brown, cracks absent to numerous; cortex usually without pigment, or with dilute brown pigment. Perithecia forming shallowly convex to conical-hemispherical projections 240–500 μm diam., black, or greyish below from particles of substratum, not covered by a layer of thallus, apex rounded to slightly flattened, sometimes shallowly depressed; perithecia not in pits, or forming rather shallow pits in rock. Exciple 200–380 μm wide, colourless to pigmented at base. Involucrellum present around upper half of exciple, or reaching to base-level of exciple, more or less hemispherical or sometimes spreading. Ascospores (17–)20–22.0–24(–27) \times

(7.5–)10–**11.2**–12.5(–14.5) μm , length/width ratio (1.4–)1.7–**2.0**–2.3(–3.1) [196/22].

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; common. Widespread and frequent in Britain and Ireland. Widespread in Europe; N. Africa, Japan, N. America, Taiwan, Australia, New Zealand.

This species needs further study, especially in relation to *V. rupestris*.



Verrucaria muralis (18003).

***Verrucaria murina* auct.**

Thallus immersed or usually superficial, thin, greenish to dark brown, often in small flecks and patches, often comprising distinct goniocysts. Perithecia moderately projecting to prominent, 120–280 μm diam., not covered by thallus; occasionally collapsed when dry (in shaded specimens with a thin involucrellum). Involucrellum appressed to exciple and scarcely distinguishable from it, or appressed above and spreading slightly below. Ascospores (13.5–)18.5–**21.1**–24(–28.5) \times (6–)8.0–**9.6**–11.5(–14.5) μm , length/width ratio (1.6–)2.0–**2.2**–2.5(–3.3) [523/38].

On siliceous rock, limestone, chalk, and brick; usually on small stones in woodland, by streams and on waste ground; frequent. Throughout Britain and Ireland. Norway, France, Austria, Lithuania.

Distinguished by the thin thallus, prominent perithecia and medium-sized ascospores. *V. dolosa* is often found in similar microhabitats, but differs in the somewhat smaller ascospores and the usually more conical involucrellum. *V. rosula* differs in the well-developed thallus, often forming minutely lobed rosettes with an abrupt margin.

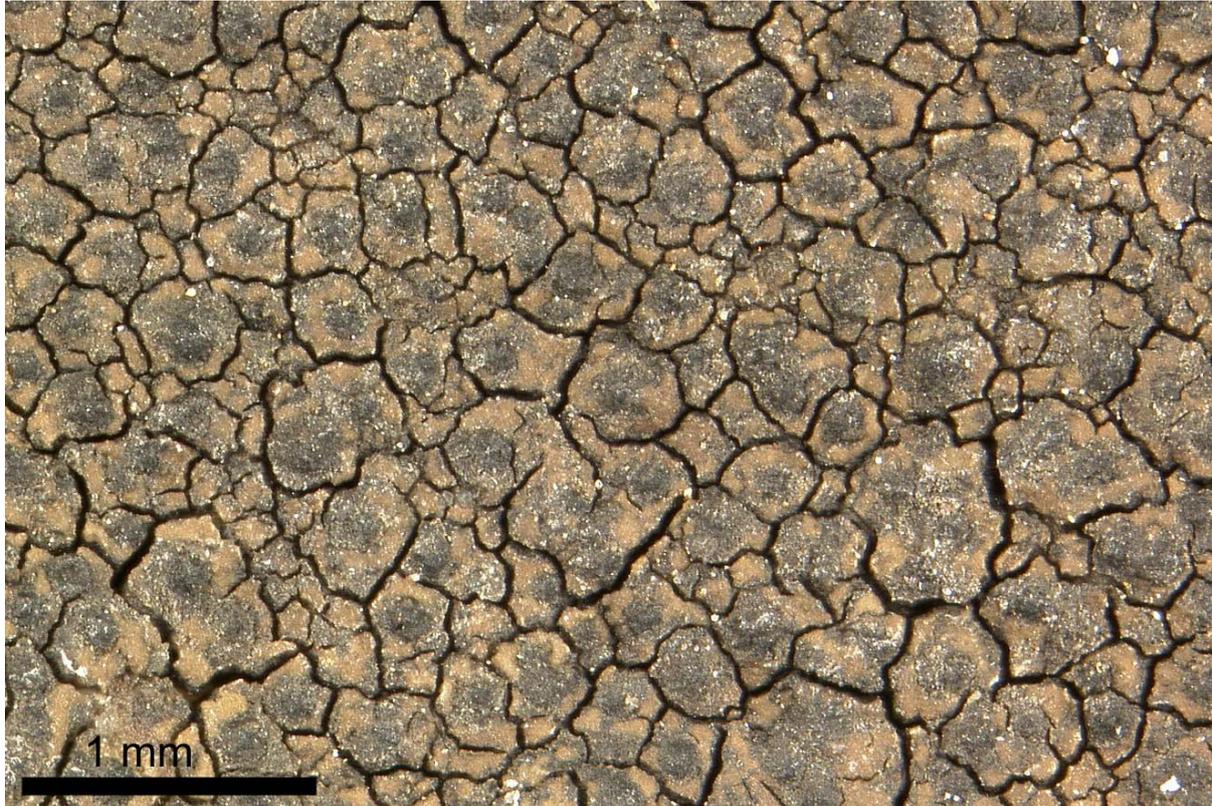
This name is a dustbin taxon for a number of unrelated species which are currently being studied.

Verrucaria nigrescens Pers. (1795)

Thallus superficial, dark brown, regularly cracked into areoles 200–800 µm wide, these usually smooth, flat to slightly convex, occasionally with sorediate margins; sides of areoles brown. Perithecia 0.5–0.75-immersed in thallus. Involucrellum 200–400 µm diam., hemispherical or extending to base-level of exciple. Exciple 150–250 µm wide, brown. Ascospores (17–)19–27(–30) × 8–14 µm.

On well-lit limestone and mortar, rarely on siliceous rocks; very common. Throughout British Isles. Scandinavia, C. and S. Europe, N. Africa, Australia, N. America.

Several similar but as yet unidentified species occur in Great Britain.



Verrucaria nigrescens (18034).

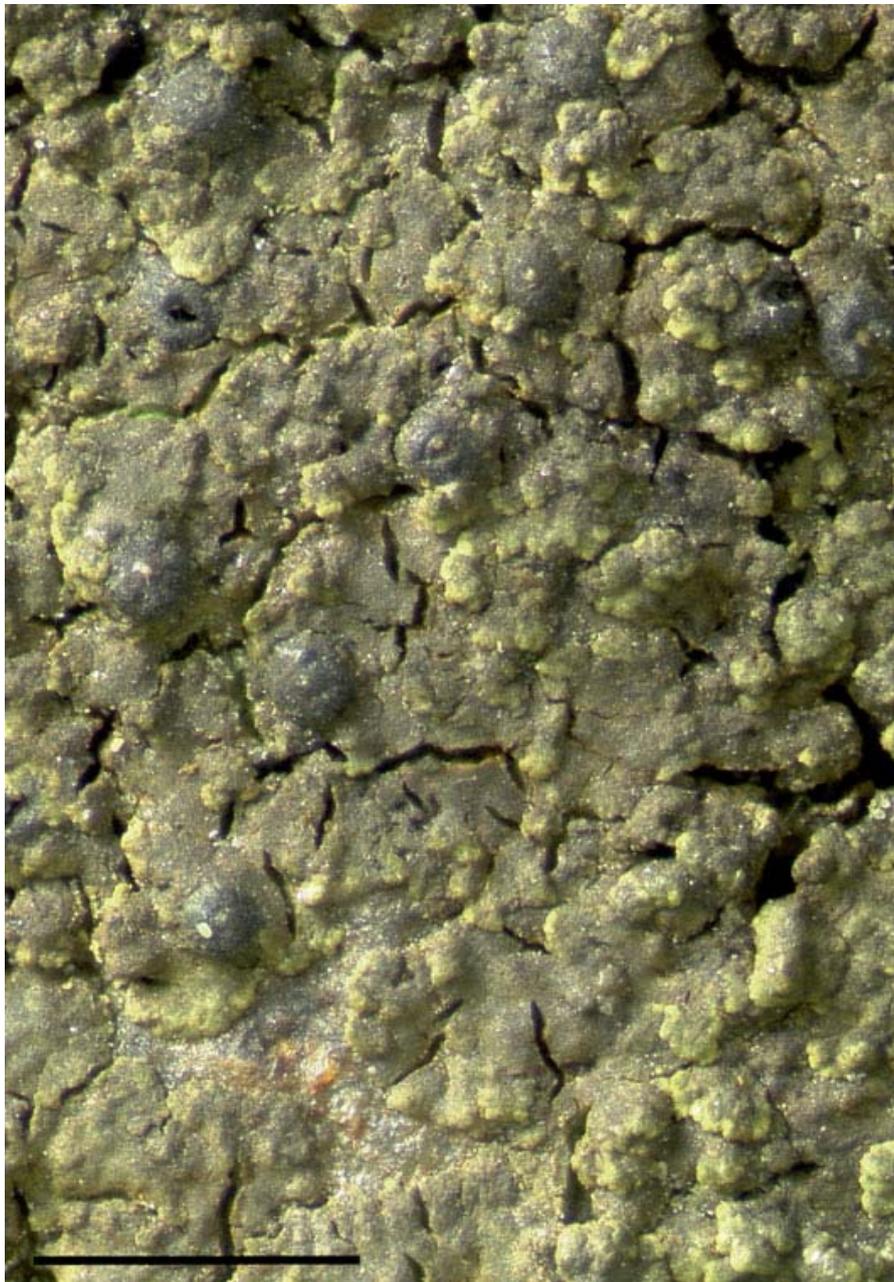
Verrucaria nodosa Orange (2013)

Prothallus not detected. *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, paraplectenchymatous; cells isodiametric to shortly oblong, *c.* 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. *Photobiont* cells 5.5–9 × 4–6.5 µm. *Perithecia* forming low to moderately convex conical-hemispherical projections 220–460 µm diameter, sometimes only the lower 0.2–0.3 of perithecium height is immersed in thallus, the projecting part naked or with an irregular thalline cover below, or sometimes perithecium partly or almost completely overtopped by thallus units. Ostiole inconspicuous or appearing as a pale dot 20–40 µm wide, plane or slightly projecting. *Involucrellum* appressed to exciple above, usually becoming broader below, rather steeply conical-hemispherical in outline, densely pigmented throughout, or with a pale area adjacent to base of exciple; pigment dark brown to dark reddish brown, ostiolar area often with dark green pigment. *Exciple* 190–310 µm

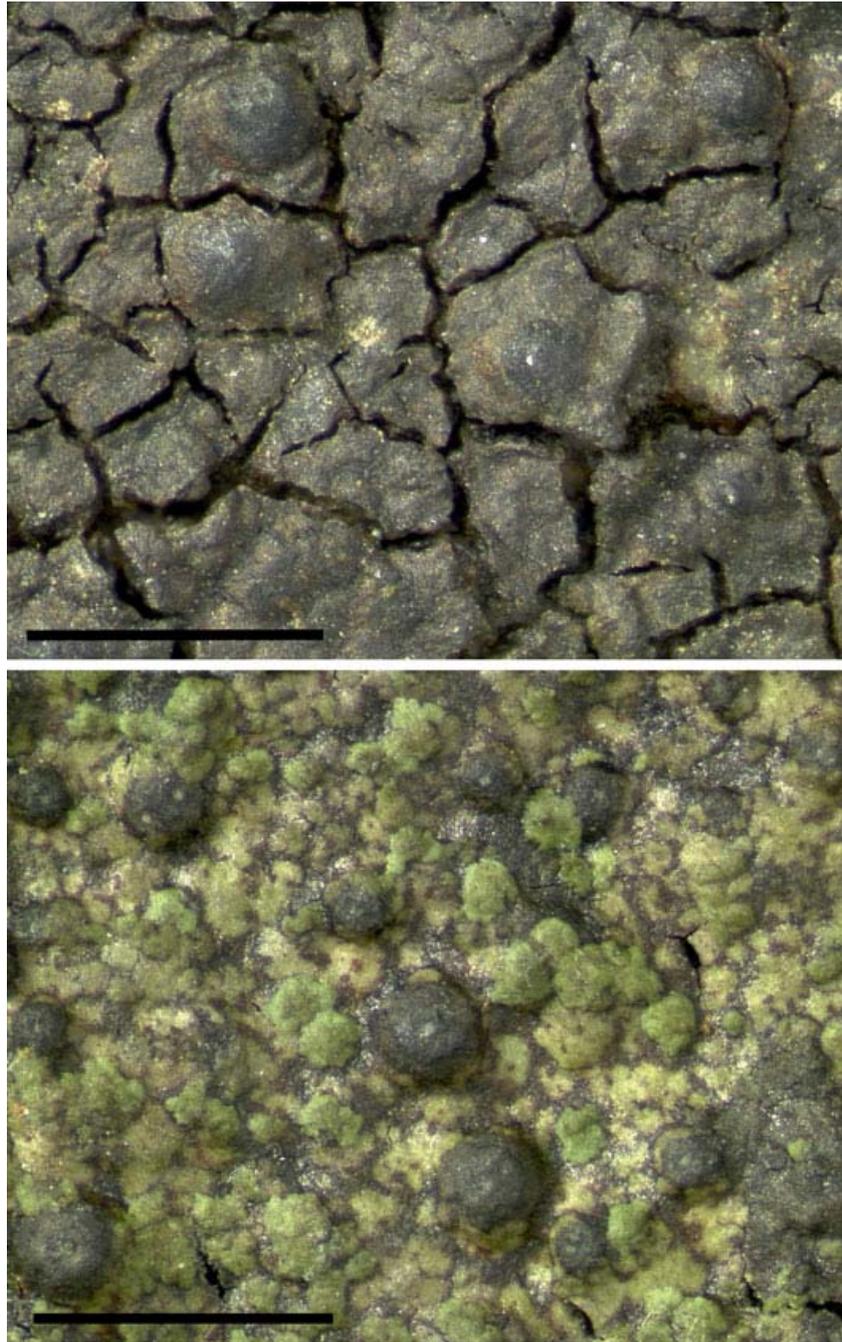
diameter, colourless or the outer layer pigmented throughout. Periphyses c. 25–40 μm long (measured *in situ*). *Ascospores* colourless, ellipsoid, simple, (17–)20.5–22.2–24(–28) \times (8–)9–9.7–10.5(–11.5) μm , (2–)2.1–2.3–2.5(–3) times as long as wide [75/4]. *Pycnidia* not detected.

On rocks beside streams, unshaded or lightly shaded, in open woodland or unimproved grassland. North Wales.

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.



Verrucaria nodosa, holotype.



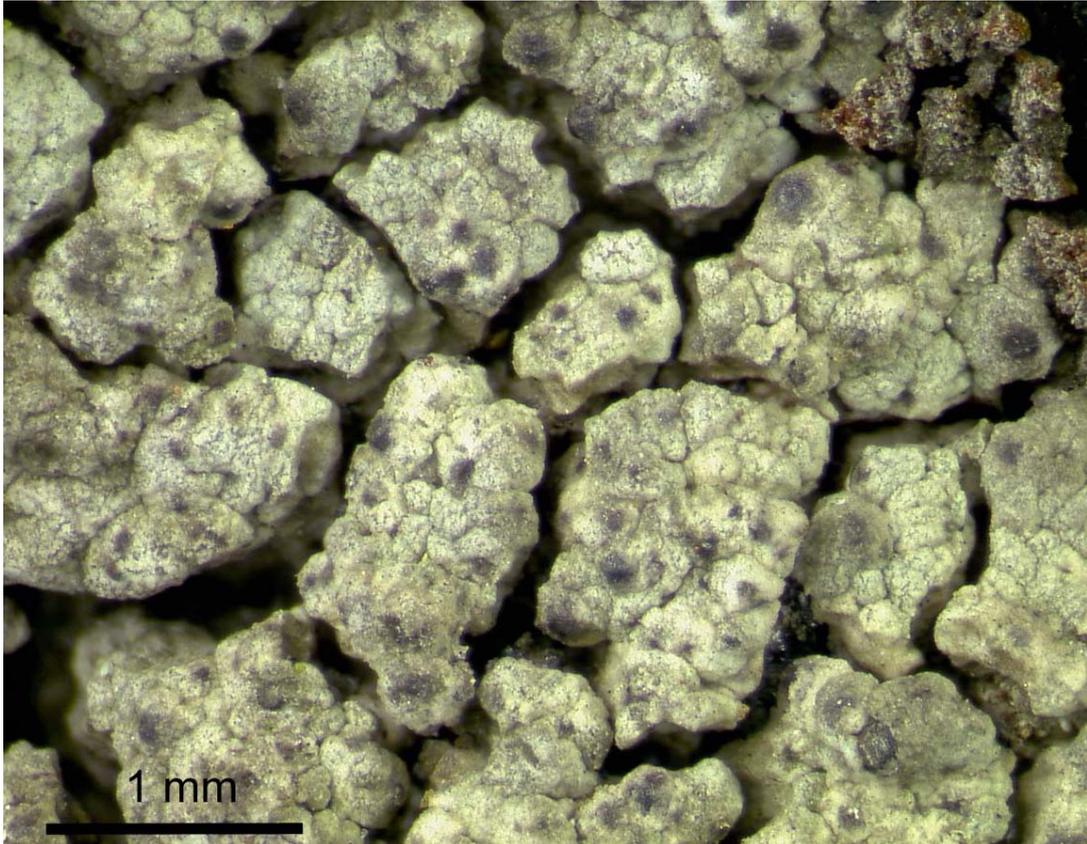
Verrucaria nodosa. Scales = 1 mm.

Verrucaria ochrostoma (Borrer ex Leight.) Trevis. (1860)

Thallus superficial, pale grey to grey-brown, of more or less convex and mostly crowded areoles, forming a crust which becomes secondarily cracked; a distinct epinecral layer present. Perithecia completely immersed, possibly the base immersed in the substratum, only the plane brown apex visible. Involucrellum absent, exciple pigmented throughout. Ascospores (15.5–)18.5–**20.9**–23.5(–27) × (8.5–)10–**11.5**–13(–14) μm, length/width ratio (1.5–)1.6–**1.8**–2.1(–2.4) [20/2].

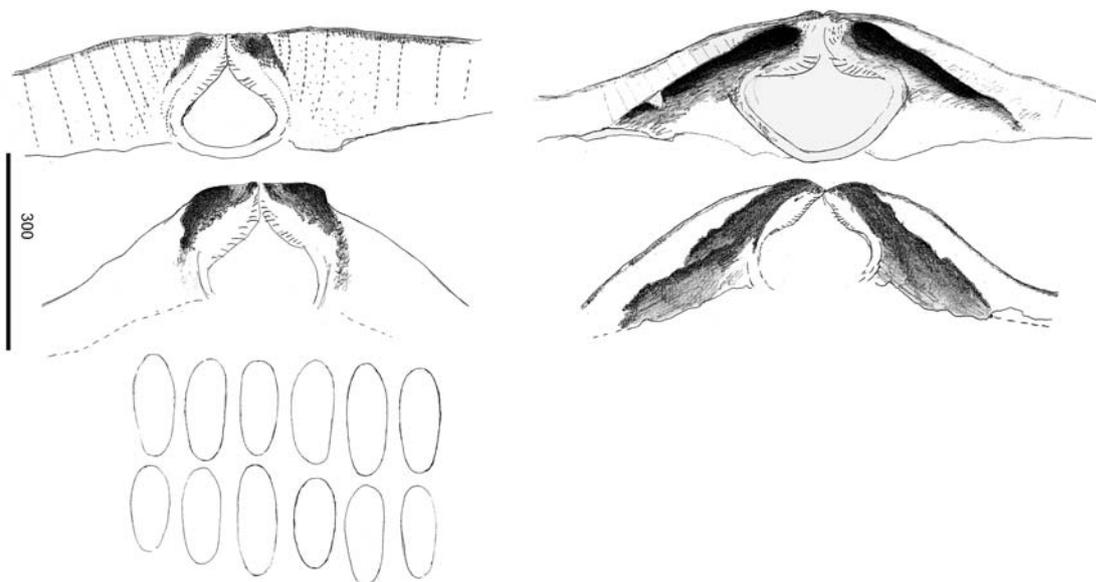
On limestone, mortar and plaster; rare. S.E. England. Italy, Asia (Taiwan)

Characterized by the superficial thallus and immersed perithecia without an involucrellum. The epinecral layer can give a somewhat cartilaginous appearance to the thallus.



Verrucaria ochrostoma (20530).

***Verrucaria pachyderma* (Arnold) Arnold (1880)**

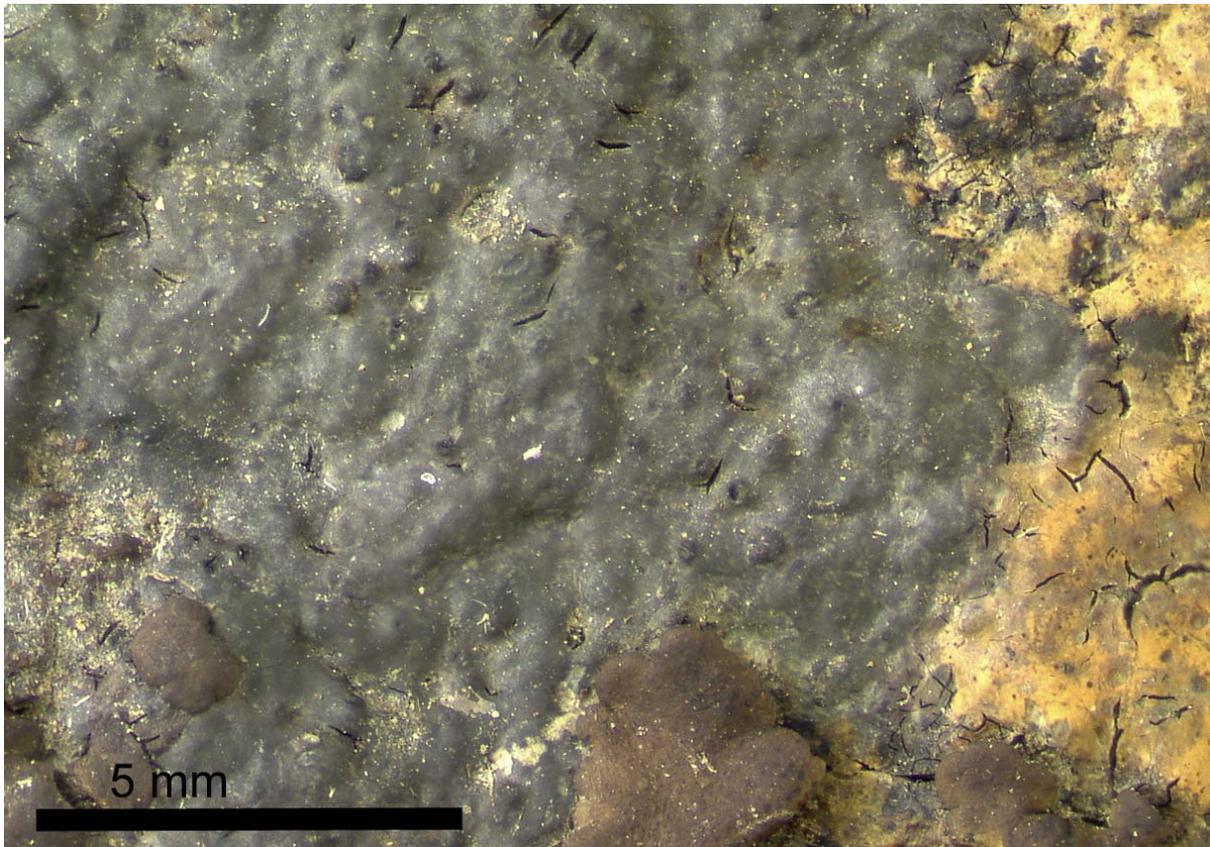


Thallus dull to dark grey-green, sometimes with a brownish tinge, subgelatinous, uncracked or with a few splits developing after collection, 40–180 μm thick, surface smooth; cells in columns, cortex weakly defined, with dull green to dull brown pigment; medulla absent or weakly defined as a zone

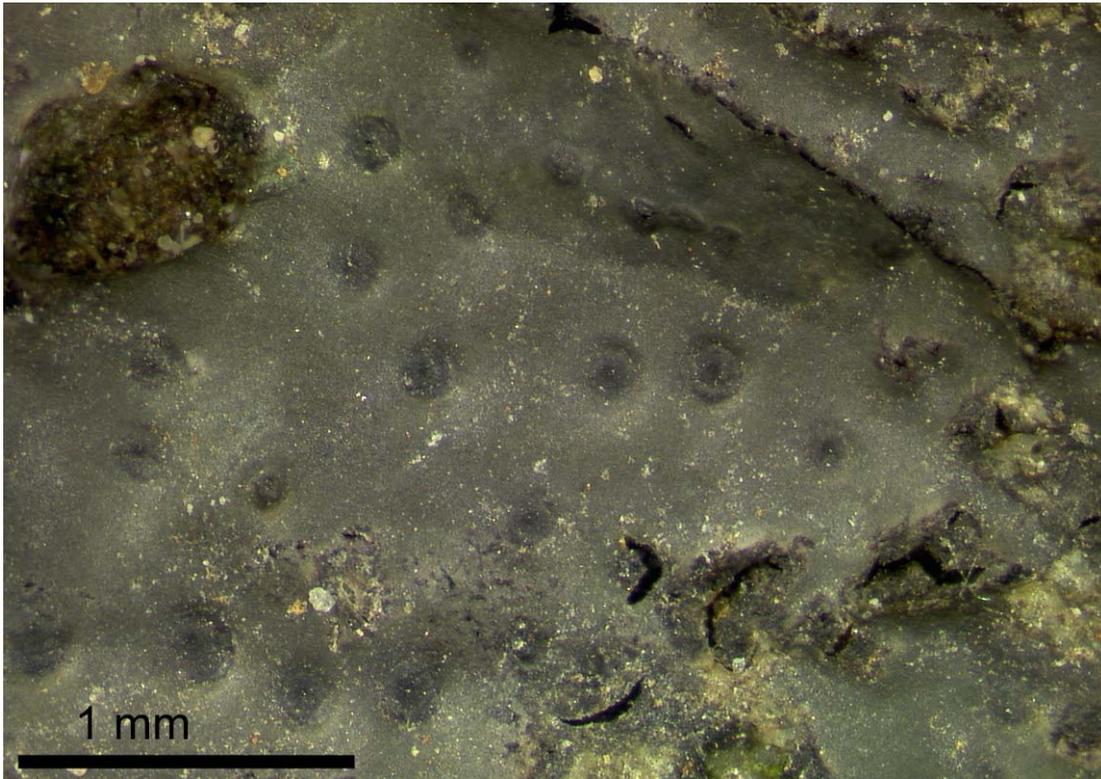
with few living algae, the cells with oil drops, and sometimes with dilute brown pigment, but a dark basal layer not developed. Perithecia immersed in thallus, not projecting, or forming low to moderate projections up to 400 μm diam. when measurable, apex visible as a grey dot, or a black disc, rarely a black apex more widely exposed in eroded perithecia. Exciple 160–350 μm wide, colourless at sides and base. Involucrellum present, varying from thin and appressed to apex of exciple, to conical and narrowly or widely spreading, sometimes reaching to base of thallus; pigment reddish brown, K + grey, but sometimes obscured by additional greenish pigment. Ascospores ellipsoid to oblong-ellipsoid or narrowly so, (15–)16–**19.1**–22(–23.5) \times (6–)6.5–**7.7**–9 μm , length/width ratio (1.9–)2.1–**2.5**–3.0(–3.2) [160/10], perispore absent, or perhaps thinly present (*c.* 0.5 μm) in some. Pycnidia not detected.

On frequently submerged siliceous rocks in rivers; local. N. and W. Britain. Norway, Sweden, Austria, Switzerland, Italy.

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. Possibly a mixture of green and brown pigment is found in the thallus of some specimens.



Verrucaria pachyderma



Verrucaria pachyderma (16642).

***Verrucaria parmigerella* Zahlbr. (1919)**

Thallus immersed, grey, dark grey-green or blue-green, often glossy, uncracked; upper thallus containing blue-green pigment. Perithecia almost completely immersed in pits in rock, numerous but often sterile. Involucrellum disc-like, flat to slightly convex, 150–220 μm , spreading sideways but scarcely downwards; in surface view usually with 3–6 fine cracks radiating from ostiole; exciple 200–300 μm diam., colourless to pale brown below. Ascospores 14–21 \times 6–8 μm .

On hard, exposed limestone; locally abundant. S.W. England, W. Ireland. Europe, widespread.

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

***Verrucaria phaeosperma* Arnold (1874)**

Apparently non-lichenized; vegetative hyphae I + blue? (one specimen). Perithecia in pits (formed by host?) in rock or half- to two-thirds immersed in the thallus of the host, 160–240 μm , exciple pigmented throughout but sometimes paler at base, pigment reddish brown or purplish brown, K + darker or dark grey-brown. Involucrellum absent. Ascospores (16–)17–**19.3**–21.5(–24) \times (8–)8.5–**9.0**–9.5(–10) μm , length/width ratio (1.7–)1.9–**2.2**–2.4(–2.8) [39/4]; wall dilute to dark brown, sometimes with a purplish tinge; perispore present, thin, rough.

Parasitic on lichens on limestone, including *Hymenelia prevostii*, *Thelidium decipiens*, ?*Verrucaria* spp.; rare, but probably under-recorded. Wales, W. Scotland, W. Ireland.

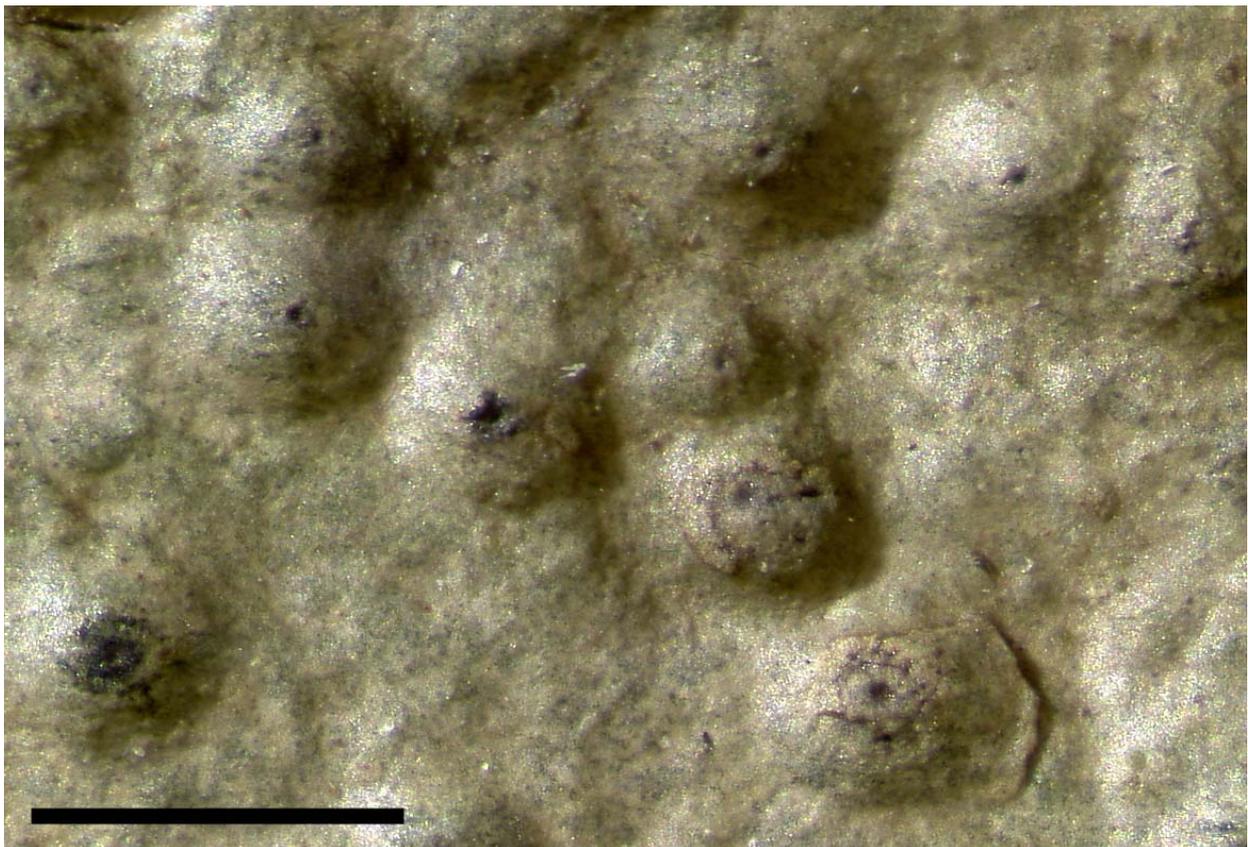
Sometimes clearly parasitic, but in some specimens there is little trace of a host. Differs from other British species of *Verrucaria* in the distinctly pigmented ascospore wall.

Verrucaria placida Orange (2013)

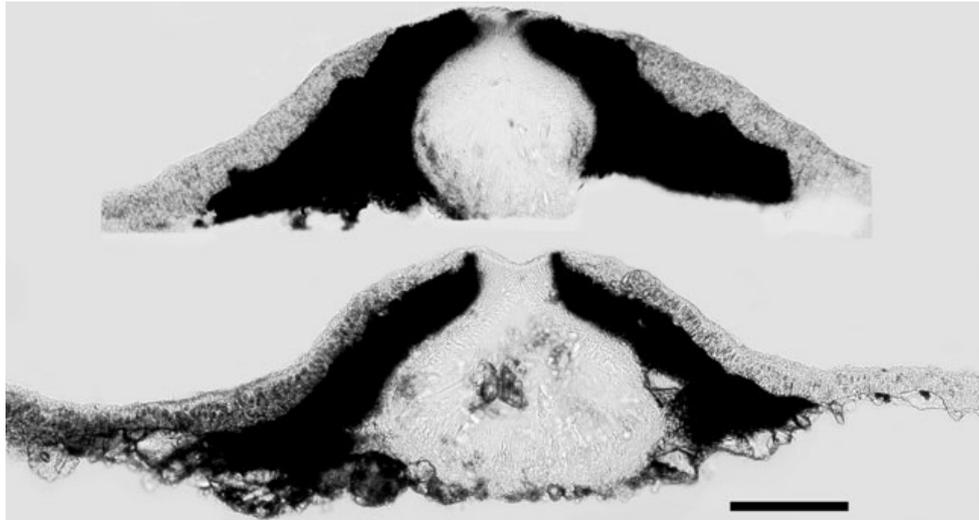
Thallus thin, 26–65 µm thick, subgelatinous, translucent when fresh and wet; smooth, more or less matt or slightly glossy, continuous, grey-green to mid brown; contiguous conspecific thalli not separated by dark lines; cells irregularly arranged or in weakly defined columns, coherent, without air-spaces 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 wide, at first covered by thallus up to apex, later sometimes eroded to expose black apex, 13–21–27 in an area of 25 mm² (18 areas measured, on 6 specimens). *Exciple* 250–310 µm wide. *Involucrellum* conical, reaching to substratum, pigment dark brown, K + dark grey. *Periphyses* 20–45 µm long. *Asci* 8-spored. *Ascospores* simple, hyaline, ellipsoid, (19.0–)21.5–**24.0**–26.5(–30.5) × (8.0–)9–**9.9**–10.5(–12.0) µm, length/width ratio (2.0–)2.2–**2.4**–2.7(–3.0) [133/8], perispore apparently absent in mature spores. *Pycnidia* not detected.

On shaded siliceous rocks and stones in small streams in woodland. Wales, Norway, Germany.

This species is related to *Verrucaria hydrophila*, but the ITS sequence shows considerable differences. *Verrucaria hydrophila* differs in 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 wider ascospores, and the perithecia are usually a little less densely spaced, 12–**16**–26 in an area of 25 mm².



Verrucaria placida.



Verrucaria placida

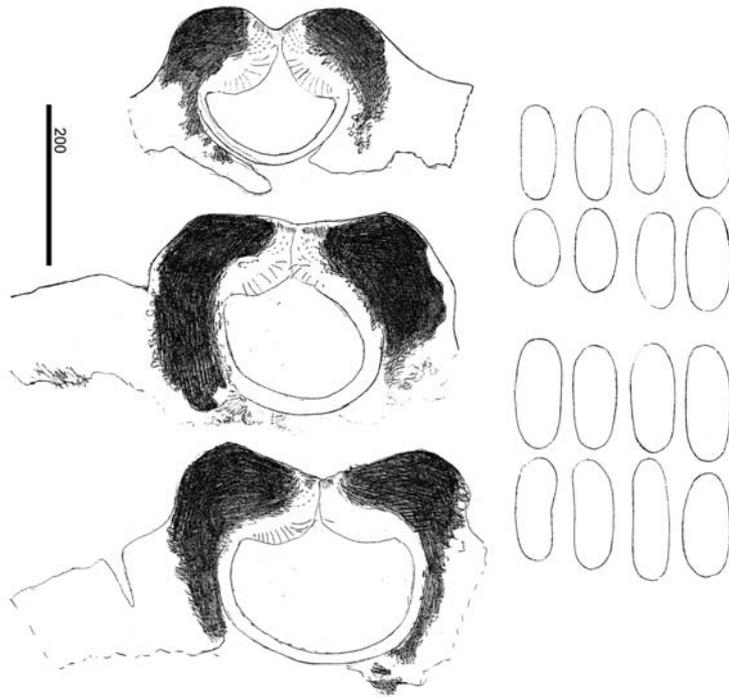
Morphological differences between *Verrucaria elaeomelaena* s.l. p.p., *V. placida* and *V. hydrophila*.

	<i>V. hydrophila</i>	<i>V. placida</i>	<i>V. elaeomelaena</i> s.l. p.p.
density of perithecia*	29–42–64	13–21–27	12–16–26
perithecial projections, diameter (µm)	240–400	400–600	280–680
centrum diameter (µm)	145–225	250–310	(100–)235–330
spore length	(15.0–)19.5– 21.1 –23(–26)	(19.0–)21.5– 24.0 –26.5(–30.5)	(19–)23– 25.2 –27(–32)
spore width	(6.5–)8– 8.9 –9.5(–11)	(8.0–)9– 9.9 –10.5(–12.0)	(9.5–)11.5– 12.4 –13.5(–16.5)

*number of perithecia in an area 25 mm².

Verrucaria pinguicula A. Massal. (1856)

Thallus superficial, rarely almost immersed, often raised above surrounding rock, continuous to extensively cracked, whitish to light brown; prothallus not seen; 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 wide, black, not covered by thallus, apex flattened or occasionally concave, sometimes leaving shallow pits in rock when decayed (or only in thallus?); ostiole inconspicuous, or visible as a slightly paler dot or shallow pit 20–60(–140) µm wide. Involucrellum well-developed, thickest beside upper half of exciple, but often more or less clasping exciple below and reaching to its base; pigment dark reddish brown, K + dark brown or dark grey-brown. Exciple 190–280 µm wide, pale below. Ascospores oblong to ellipsoid, (12–)13.5–**15.8**–18(–21) × (5–)5.5–**6.9**–8.5(–11) µm, (1.5–)2–**2.3**–2.7(–3.4) times as long as wide [132/12], perispore usually not visible, rarely apparently present and up to 0.8 µm thick.

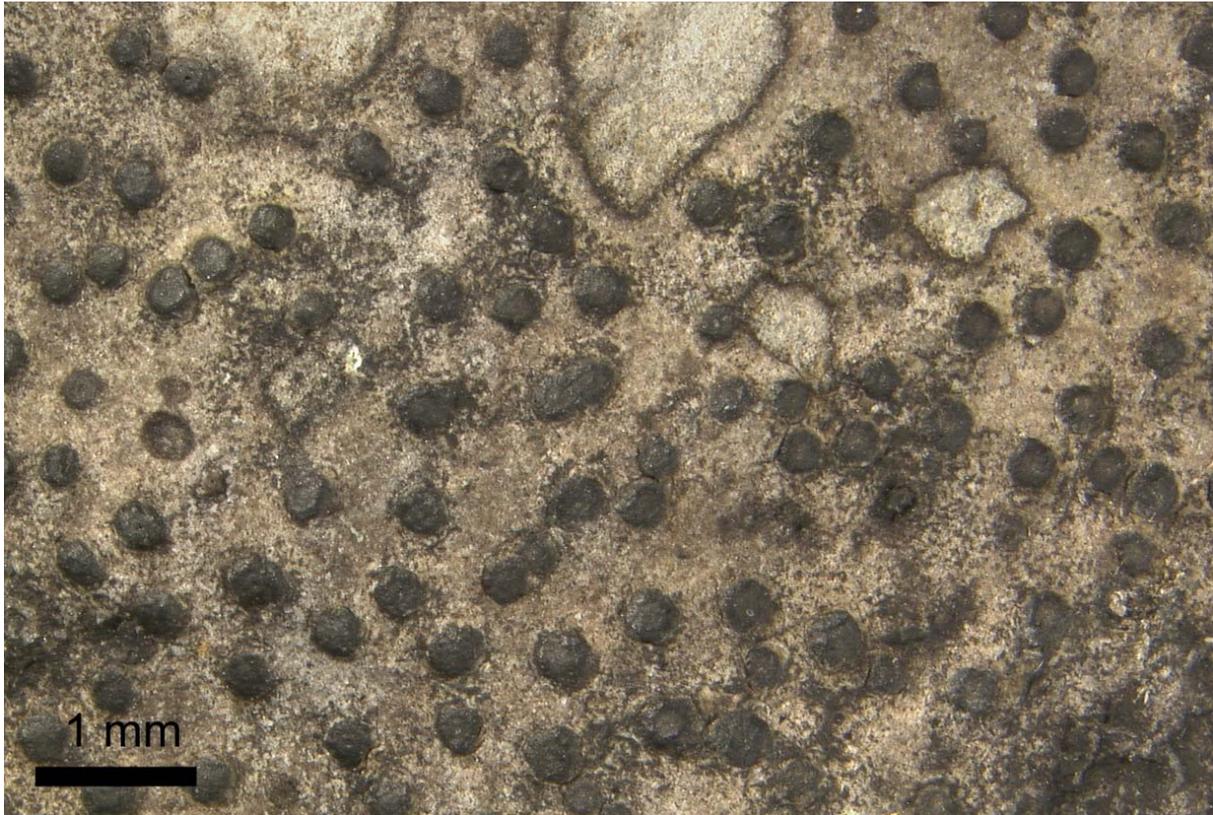


On hard limestones; locally frequent but under-recorded. Throughout British Isles. Sweden. Asia (Taiwan).

The thallus is at least thinly superficial, but pale uncracked thalli may superficially resemble immersed thalli. Close to *V. 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.

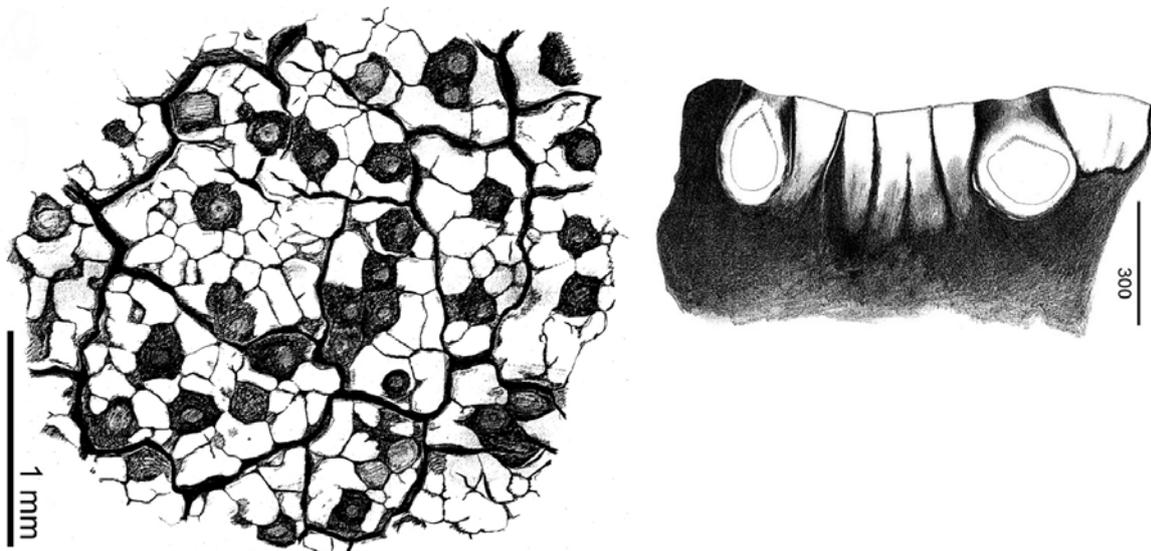


Verrucaria pinguicula (14772).



Verrucaria pinguicula (18136).

***Verrucaria polysticta* Borrer (1834)**



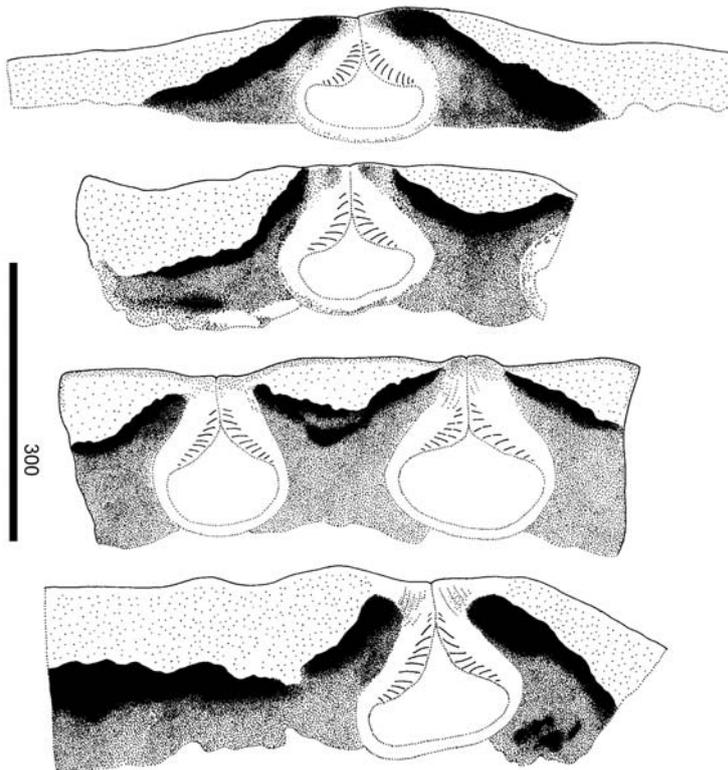
Prothallus present, usually blackish, non-fimbriate, rarely appearing as a very thin grey to brown film. Thallus epilithic, well developed, 280–1000 µm thick. Margin thin, primary areoles arising on prothallus, these round or oblong, up to 400 × 280 µm, soon becoming crowded and sometimes indistinguishable from each other, forming a crust which then becomes cracked into the mature areoles. Mature areoles 300–1100 µm diam., angular in outline, plane or slightly concave; upper surface grey to light 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 thallus thickness;

pigment dark reddish brown, K + darker dull brown, sometimes retaining a reddish tinge. 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; apex appearing at thallus surface as a greyish to usually black, slightly concave to slightly convex disc 100–260 μm wide. Exciple 180–290 μm wide, lightly to strongly pigmented below, strongly pigmented above, pigment brown or dull greenish brown, K + slightly darker. Involucrellum absent, but the exciple usually flanked by dark tissue belonging to the edges of the upper thallus units, and which has a pigment-type like the medulla. Ascospores oblong-ellipsoid or ellipsoid, (10.5–)12.5–14.1–15.5(–16.5) \times 5.5–6.2–7(–8) μm , (1.8–)2.1–2.3–2.5(–3.1) times as long as wide [47/6], perispore absent. Conidiomata not seen.

On calcareous rock, including limestone and calcareous mudstone; on natural outcrops or on walls; once on *Verrucaria cernaensis*; local. S.W. England, Wales, Scotland, Ireland. Norway, Sweden, France, Germany, Turkey.

Differs from *Placopyrenium canellum* and *P. fuscillum* 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.

Verrucaria praetermissa (Trevis.) Anzi (1864)



Thallus superficial, diffuse, non-gelatinous, pale greenish grey to dark brown or grey-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 margin, but usually up to 100–240 μm thick when mature. Prothallus whitish; adjacent thalli often separated by dark lines. Epinecral layer absent; cortex weak, without pigment or with brown pigment; cells of thallus irregularly arranged or in weakly defined vertical columns; thallus with distinct, extensive, black basal layer, which is often absent or discontinuous in young areas.

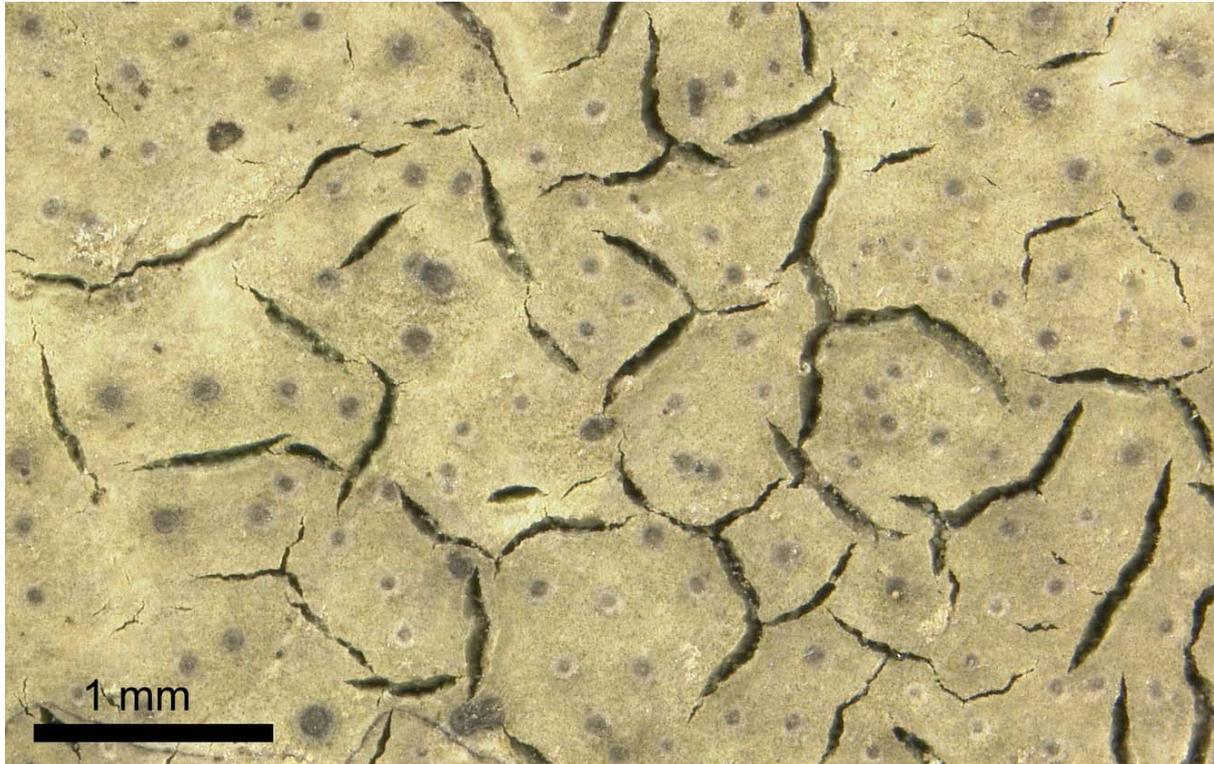
Perithecia immersed in thallus,

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 plane black disc or ring of black dots 60–200 μm diam.; ostiolar region more or less plane, appearing as a small dot or papilla 20–60 μm diam., or as a pale area up to 120 μm diam.. Involucrellum present, \pm conical, extending laterally below, and typically contiguous with adjacent involucrella, forming the dark 'basal layer' of the thallus; involucrellum densely pigmented at surface, but remainder often with cell outlines clearly visible in thin section; pigment dark reddish-brown, K + dark greyish brown. Exciple 140–270 μm diam., thin, c. 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 (16.0–)18.0–21.0–25.0(–28.0) \times (6.5–)7.0–

8.7–10.0(–10.5) μm , length/width ratio (1.7–)2.0–**2.4–2.9(–3.3)** [355/23], often with thin perispore *c.* 0.5 μm thick. Conidiomata not detected.

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. Widespread in N. and W. Britain; Ireland. Reported from much of Europe, from N. America, N. Asia, New Guinea, Hong Kong and E. Australasia.

This species as currently understood in Great Britain includes two taxa which are under investigation.



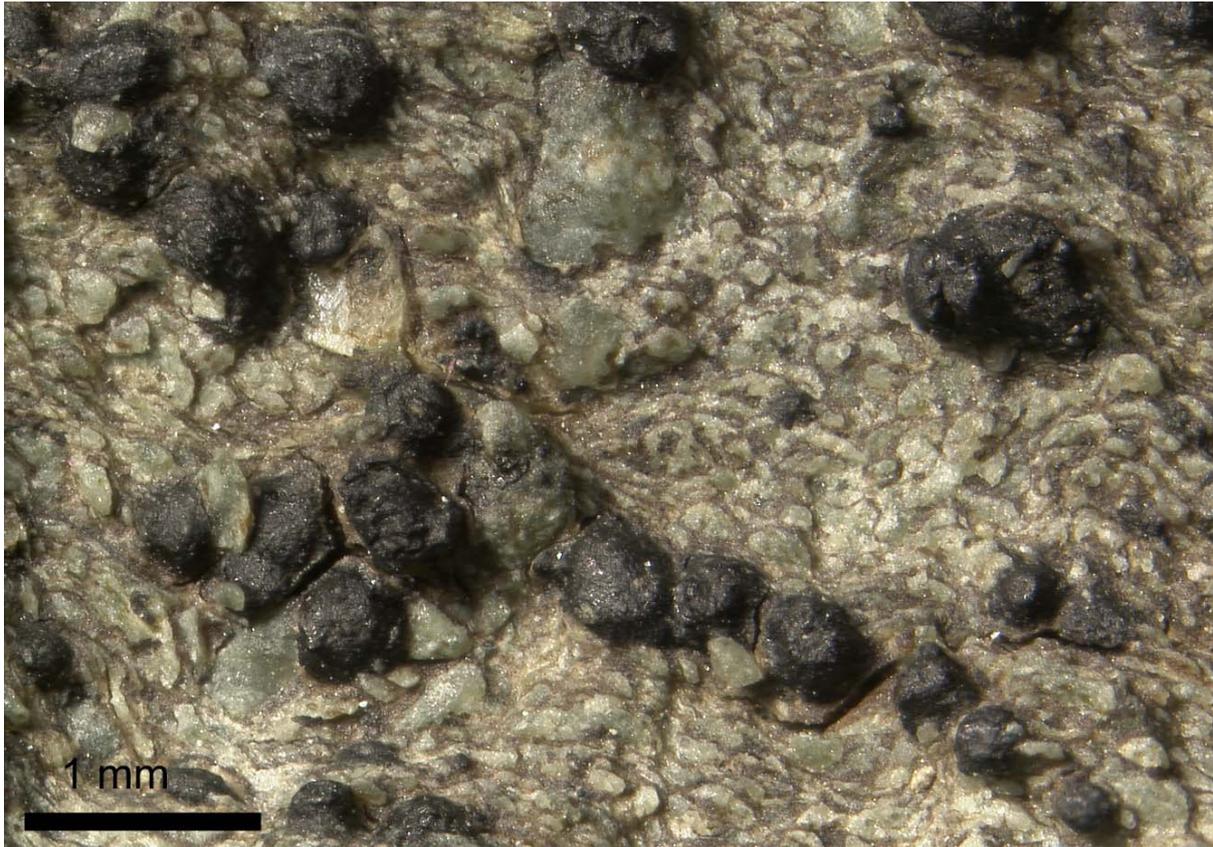
Verrucaria praetermissa (18815).

***Verrucaria prominula* Nyl. (1861)**

Thallus superficial, often very thin, up to 140 μm thick in small depressions in the substratum, whitish, grey or pale brownish, with a slightly waxy appearance when well-developed. Perithecia moderately projecting to usually prominent, 320–520(–800) μm diam, rounded or flattened at apex, not covered by thallus. Involucrellum thick, appressed to exciple, somewhat broadened below. Ascospores oblong with rounded apices, occasionally a few slightly constricted, (10.5–)11.5–**12.9–14(–16)** \times (4.5–)6.5–**7.4–8(–9)** μm , length/width ratio (1.4–)1.5–**1.8–2.0(–2.3)** [65/6].

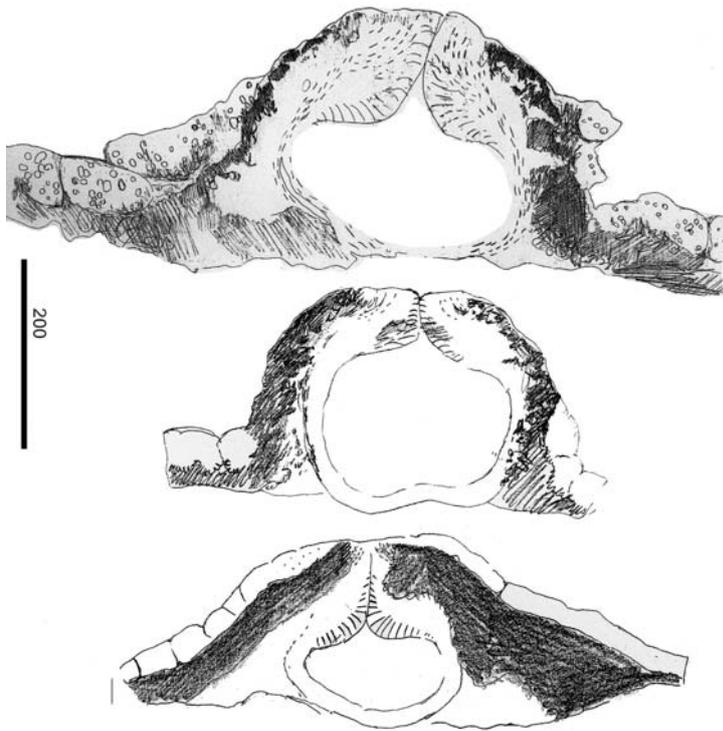
On vertical, shaded faces or in dry crevices on soft siliceous rocks on seashores, most frequently in the mesic to xeric-supralittoral zones; occasional. W. British Isles, rare elsewhere. Europe, N. America, Asia (Taiwan).

Distinguished by the large perithecia, thin thallus, and small, distinctly oblong ascospores.



Verrucaria prominula (17821).

***Verrucaria rosula* Orange (2013)**

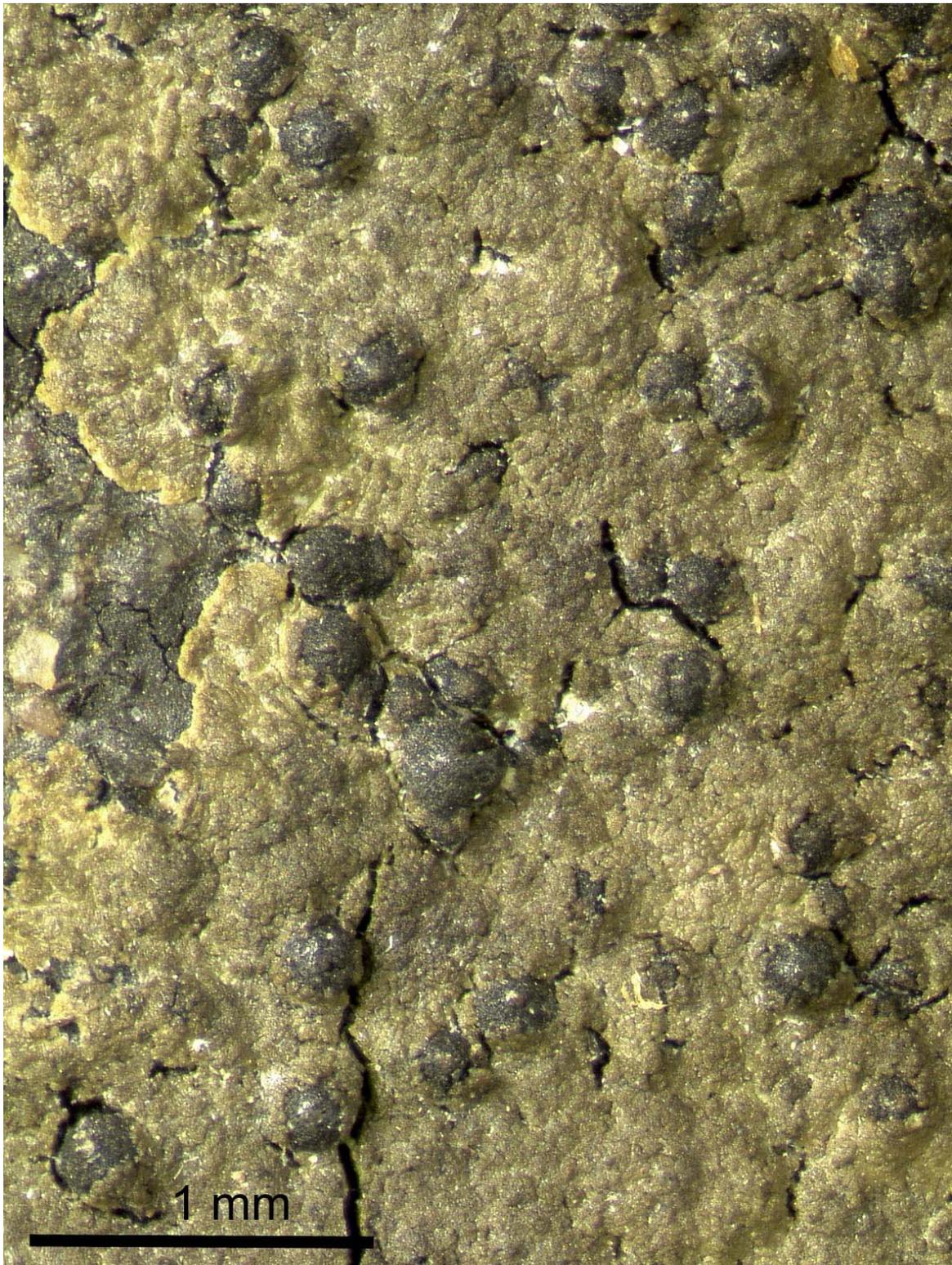


c. $5 \times 1.2 \mu\text{m}$.

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, ostiole rather frequently projecting as a pale papilla, but often plane. Involucrellum hemispherical and more or less appressed to exciple except near base, to more or less conical. Ascospores (20.5–)22.5–**24.6**–26.5(–28.5) \times (7.5–)9–**9.8**–10.5(–12.5) μm , length/width ratio (2.0–)2.3–**2.5**–2.7(–3.1) [136/8]. Pycnidia rare (seen once), conidia

On damp and shaded siliceous rocks and stones in woodland and in or near streams; frequent. England and Wales. France.

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.



Verrucaria rosula, holotype.

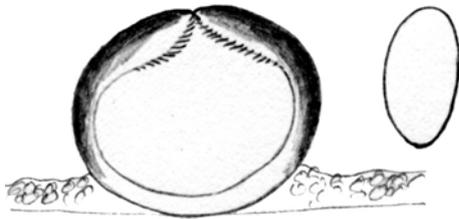
Verrucaria sandstedei de Lesd. (1911)

Thallus superficial, very thin, subgelatinous, dark brown to blackish, without ridges or punctae. Perithecia forming hemispherical projections up to 150 µm diam., often flattened above. Involucrellum rough. Exciple colourless at base. Ascospores narrowly oblong-ellipsoid, 12–16 × 2–3.5 µm.

On sheltered siliceous rocks on the sea shore, amongst barnacles; rare. S. and E. England, S. Wales, E. Ireland.

Distinguished from *V. halizoa* by the very narrow ascospores.

Verrucaria simplex P.M. McCarthy (1988)



Thallus very thin, brown. Perithecia forming prominent black projections 80–130 µm diam., not covered by thallus. Involucrellum absent. Ascospores ellipsoid or occasionally constricted below, (6–)7–**8.2**–9.5(–10.5) × (3.5–)4–**4.4**–5(–5.5) µm, length/width ratio (1.7–)1.8–**1.9**–2.0(–2.1) [20/3].

On siliceous or calcareous pebbles and on bone, in woodland or light shade; local but doubtless overlooked. England, Wales. Iceland.

A minute and easily overlooked species. *V. bulgarica* differs in the presence of an involucrellum. Perithecia with constricted ascospores may occur together with those with ellipsoid ascospores, but need further study.

Verrucaria sphaerospora Anzi (1860)

Thallus well-developed, knobby. Perithecia small, completely- to half-immersed; exciple dark, without a distinguishable involucrellum. Ascospores subglobose to broadly ellipsoid, 9–12 × 7.5–10 µm.

The only British record so far is by Mark Powell from a roof in Somerset, 2012.



Verrucaria sphaerospora (coll. Mark Powell).

***Verrucaria squamulosa* Brand & van den Boom (2003)**

Thallus areolate, areoles initially dispersed, subsquamulose, 100-300(-500) μm diameter, greenish grey to pale brown. Perithecia mostly half-immersed, half- to completely covered by areoles. Involucrellum well-developed. Spores (23-)24-27(-28) × (8-)9-13(-15) μm. Pycnidia inconspicuous; conidia 3.8-4.4 × 0.9-1.1 μm.

On moist, slightly calcareous rock or brick beside rivers or on waste ground. Wales, Belgium, Netherlands. Probably overlooked. *V. macrostoma* has less discrete areoles which are more crenulate and often form a regularly cracked crust. The two species are genetically distinct.



Verrucaria squamulosa (21251).

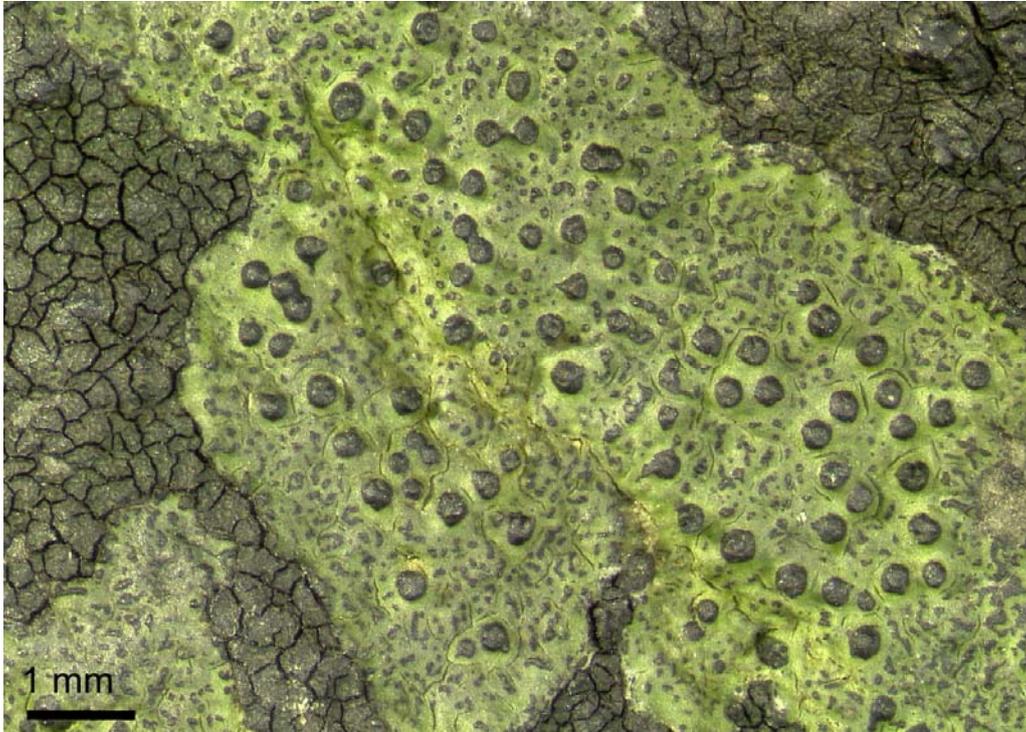
***Verrucaria striatula* Wahlenb. (1803)**

Thallus superficial, green to dark dull green, subgelatinous, very thin or up to *c.* 60 μm ; not cracked, but cracks often develop in the herbarium; with black spots and simple or branched ridges 40–600 \times 40–120 μm , these sparse or absent in shade, but often abundant and very conspicuous in sun; cortical pigment dull green (always?) when present. Perithecia forming moderate to prominent projections 180–360 μm diam., these often irregular in shape, often more or less angular in surface view, the apex rounded or often flattened, slightly depressed, or lobed; not covered by thallus. Involucrellum thick, appressed to exciple and broadened at base. Ascospores ellipsoid, 8–9.1–10(–12) \times (5–)5.5–5.6–6 μm , length/width ratio (1.3–)1.4–1.6–1.8(–2.1) [47/6]. Pycnidia occasional, often abundant when present, visible as black dots up to 70 μm diam. with a paler centre. Conidia straight or slightly curved, 2.9–4.1 \times 1.2–1.6 μm .

On siliceous or calcareous rocks, in mid-littoral zone on rocky seashores, between zones of *V. amphibia* and *V. mucosa*, often amongst the red alga *Hildenbrandia*; very common. Throughout

British Isles except S.E. and E. England. Europe from Iceland to Portugal, N. America, Australia, New Zealand.

Thallus very variable. *V. amphibia* differs in the longer ascospores, perithecium shape and thinner black ridges; shade morphs of *V. halizoa* differ in perithecial shape and less green thallus. *V. ditmarsica* differs in the smaller ridges.



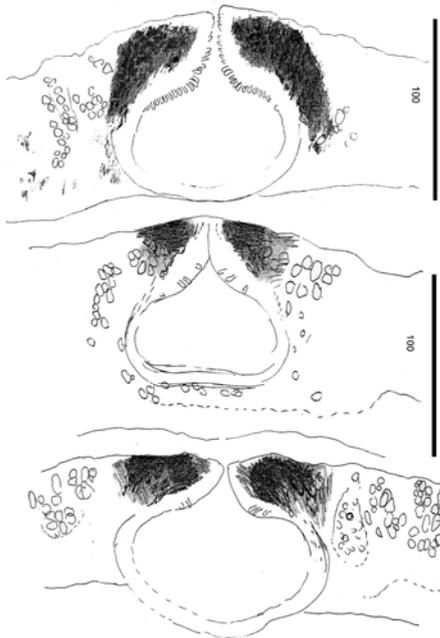
Verrucaria striatula, with short ridges; growing with *Hydropunctaria maura*.



Verrucaria striatula, dark green morph with no ridges (confirmed by ITS sequence (21036)).

Verrucaria sublobulata Eitner ex Serv. (1950)

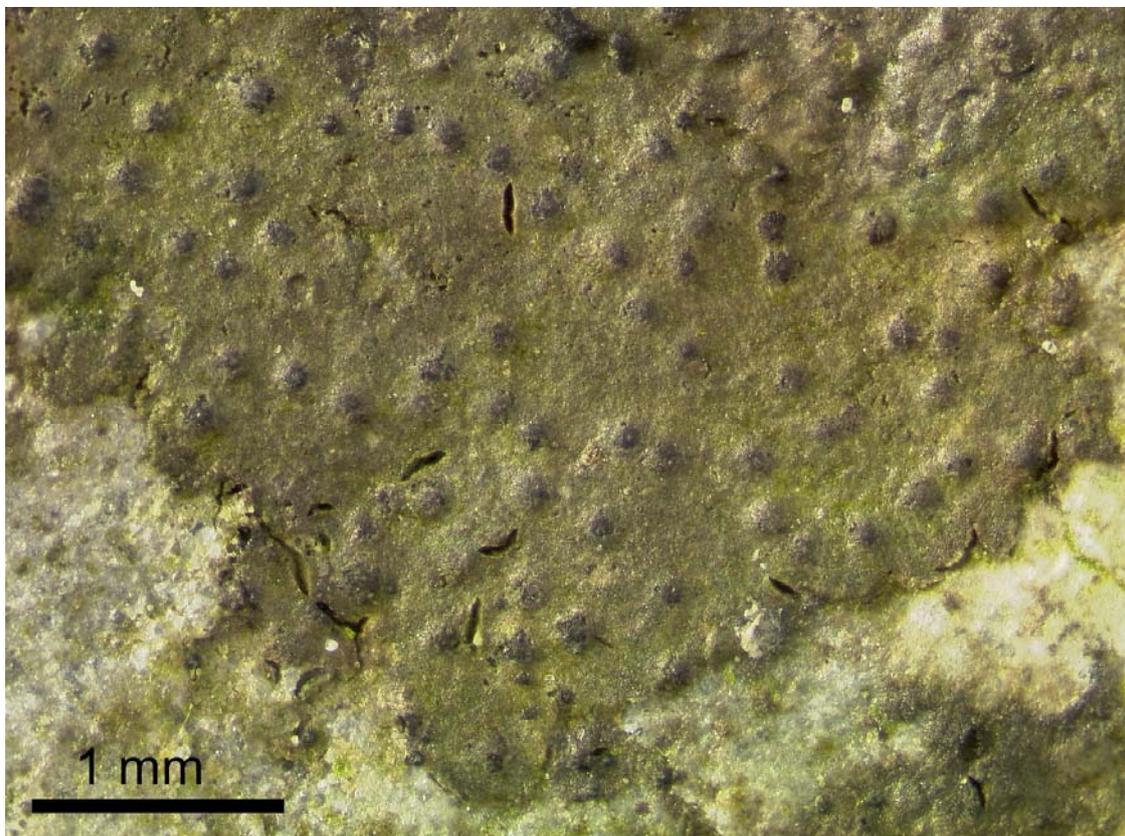
Thallus superficial, thin, in delimited patches or continuous, non-gelatinous, typically uncracked,



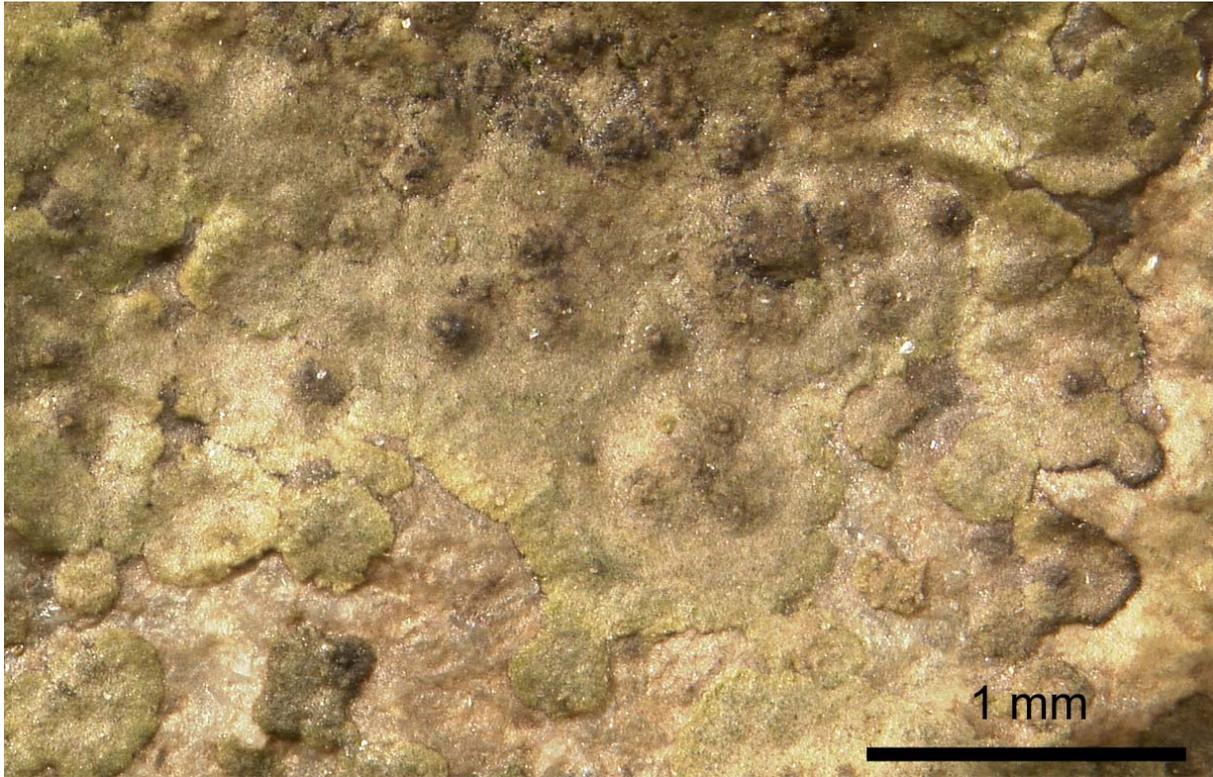
margin typically thinning abruptly, giving a well-defined appearance to the thallus; prothallus absent or very narrow and inconspicuous. Perithecia immersed or forming only low projections. Exciple 105–175 μm diam. Involucrellum often confined to the apex of the exciple, occasionally (in slightly prominent perithecia) extending down the sides of the exciple. Ascospores (13.5–)15–**16.4**–18(–21.5) \times (6.0–)7–**7.6**–8.5(–9.0) μm , length/width ratio (1.8–)2.0–**2.2**–2.4(–2.7) [67/9]. .

On siliceous rocks and stones in streams and rivers, in shaded and unshaded sites, probably frequent in north and west Britain; Ireland. Norway, Spain, Germany, Czech Republic, Poland.

The small, rather densely arranged, largely immersed perithecia and the often sharply delimited thallus margin are distinctive.



Verrucaria sublobulata (17492).



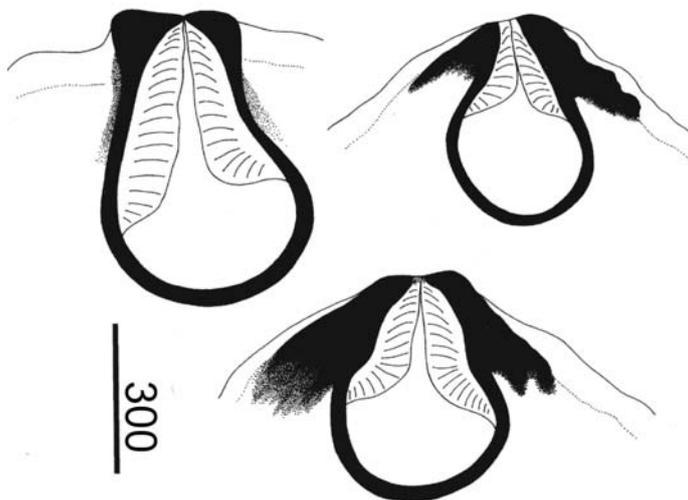
Verrucaria sublobulata (19379).

Verrucaria viridula (Schrad.) Ach. (1803)

Verrucaria papillosa Ach. (1810)?

Thallus more or less immersed, visible as brownish flecks at surface of substrate; or superficial: whitish, pale grey, greenish grey, or pale brown, areolate, divided by cracks; vegetative propagules absent. Perithecia to half- to almost completely immersed in thallus, appearing as convex to conical-hemispherical projections 150–500 μm wide, the base immersed in the substrate. Exciple 350–600 μm wide, apex somewhat produced into a short beak; pigmented, pigment brown, K + darker brown. Involucrellum weakly developed and spreading from apex of exciple, to more or less appressed to upper half of exciple or slightly spreading, pigment like exciple. Ascospores ellipsoid to broadly ellipsoid, (27–)28.5–**31.1**–34(–41) \times (12–)14.5–**17.1**–20(–23.5), length/width ratio (1.3–)1.5–**1.9**–2.2(–2.6) [72/10], perispore sometimes apparent, to 0.5 μm thick. Pycnidia appearing as dark dots to

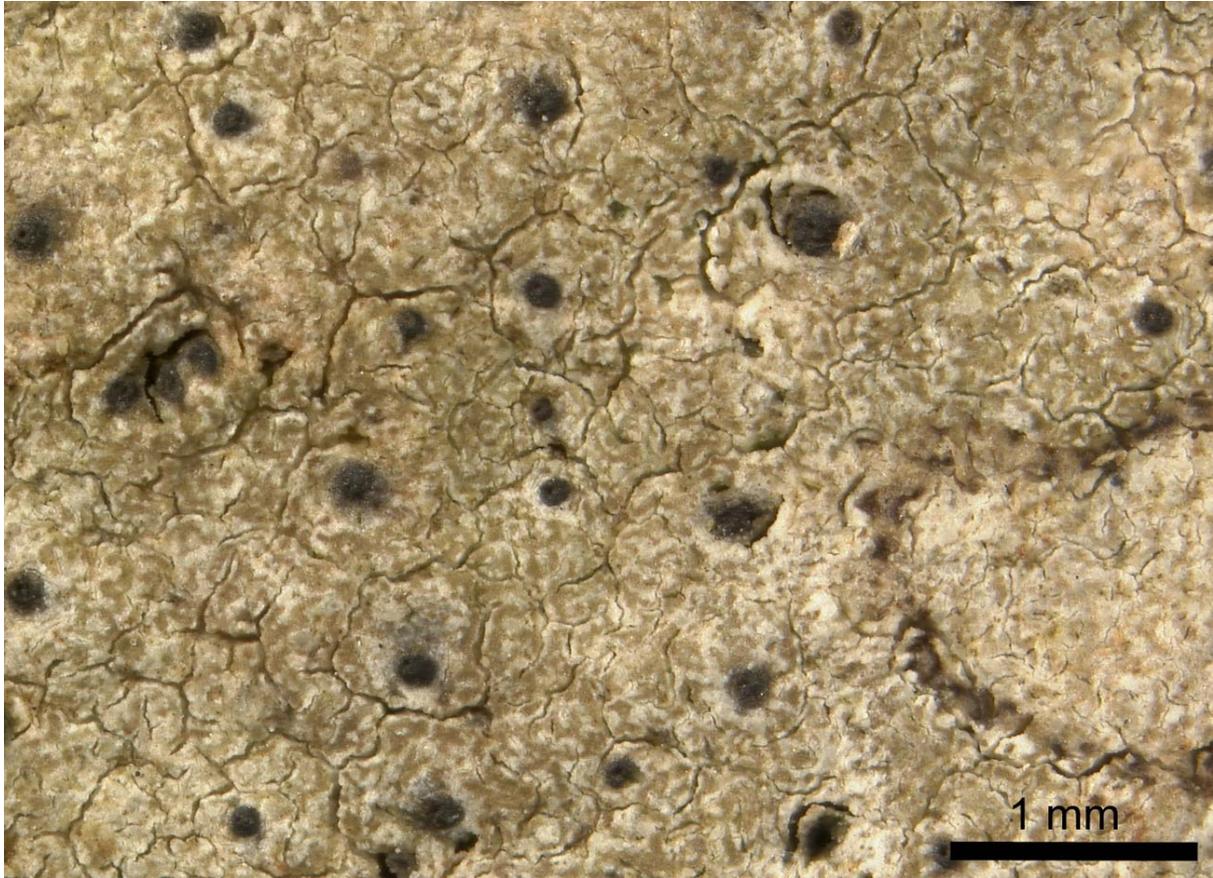
60 μm wide or more, conidia straight to slightly curved, 7–10 \times c. 1 μm .



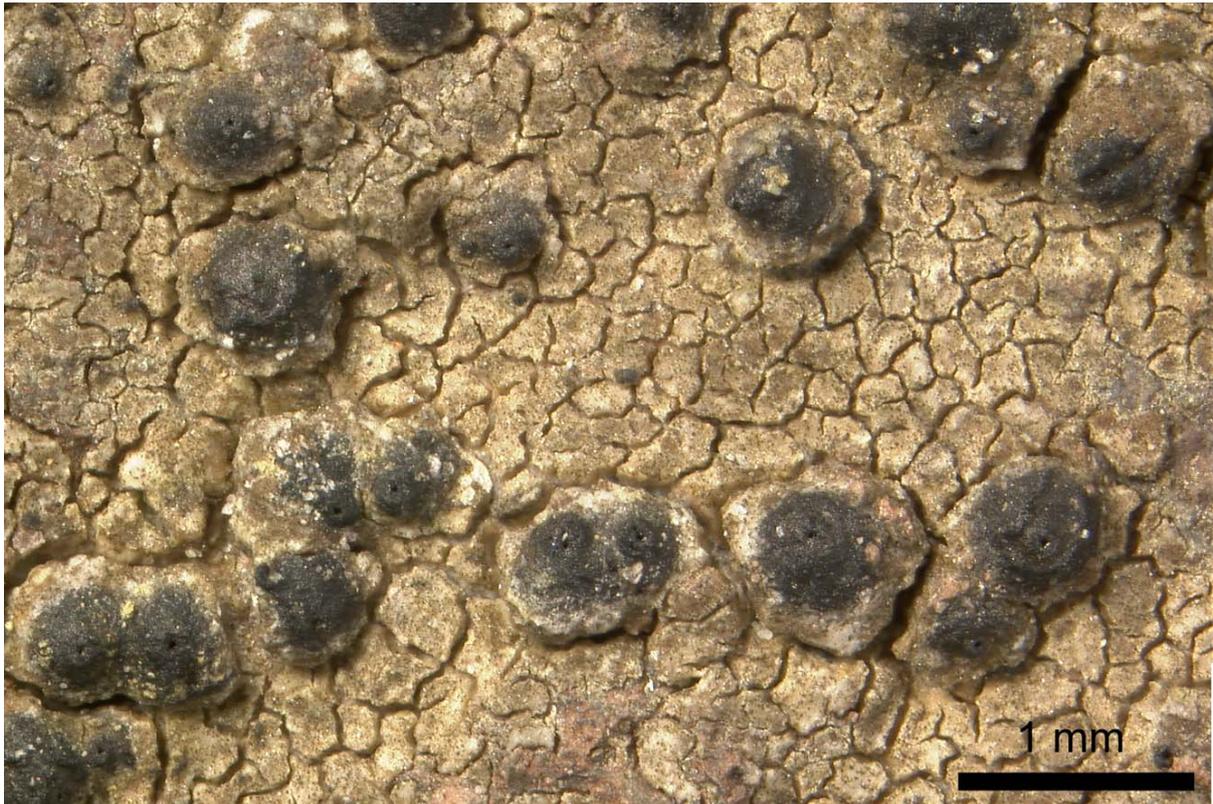
Calcareous rock, including limestone, mortar, mudstone, brick; occasionally on soil; in semi-natural habitats or on walls; common. Throughout British Isles.

Variable, but distinguished by the large perithecia and large ascospores; the apex of the perithecium is often produced into a 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 apparent. *V. hochstetteri* differs in the always endolithic thallus, the absence of an involucrellum, and in some specimens the presence of an ornamented perispore.

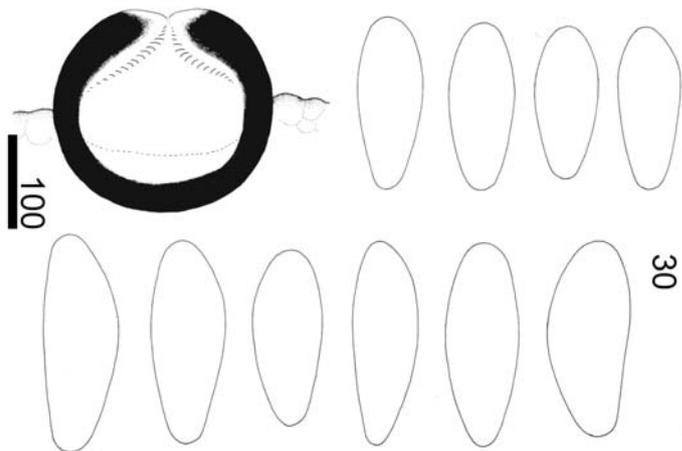


Verrucaria viridula, on shaded limestone (15821).



Verrucaria viridula, on brick (10340).

***Verrucaria xyloxena* Norman (1867)**



Thallus superficial, granular-verrucose, brown to blackish brown, composed of goniocysts 15–35 μm , with brown pigment on exposed side. Perithecia (0.3–)0.5(–0.75)-immersed, brownish black to black, 140–260 μm diam.; exciple pigmented throughout, pigment dark brown, K + dark green-brown to dark grey-green; involucrellum absent. Ascospores ellipsoid, simple, rarely 1-septate when overmature, (13.5–)16.5–**18.8**–21(–27) \times (5.5–)6.5–**7.3**–8(–10) μm , length/width ratio (1.9–)2.3–**2.6**–

3.0(–3.8) [226/22], without perispore or appendages.

On calcareous soil, very rare (England, West Suffolk). Norway, Sweden, Russia (Karelia).

The spore size includes measurements from many non-British specimens.

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***Verrucaria*, *Heteropladidium*, *Hydropunctaria* and *Placopyrenium* species, arranged in descending order of mean ascospore length**

Measurements given as: *minimum*, mean – standard deviation, **mean**, mean + standard deviation, *maximum*.

Major habitat/habit: F = freshwater, M = maritime, T = terrestrial, L = lichenicolous

species	length					width					habitat			
	<i>min</i>		mean		<i>max</i>	<i>min</i>		mean		<i>max</i>	F	M	T	L
<i>V. hochstetteri</i>	24.6	29.1	31.8	34.4	41.4	13.1	15.2	17.6	20.0	24.6			T	
<i>V. viridula</i>	24.2	27.4	30.3	33.2	41.0	12.0	14.8	17.1	19.4	23.4			T	
<i>V. margacea</i>	20.1	26.2	29.3	32.3	40.5	9.0	11.2	12.6	14.0	17.5	F			
<i>V. macrostoma</i>	21.3	25.2	28.5	31.8	36.1	9.4	11.6	13.2	14.9	17.2			T	
<i>V. anziana</i>	23.0	25.5	28.4	31.2	36.5	10.3	11.4	12.2	13.1	14.5	F			
<i>V. aethiobola</i>	19.0	23.9	26.6	29.3	36.5	8.5	10.5	11.6	12.6	14.5	F			
<i>V. elaeomelaena</i> s.l. p.p.	19.0	23.2	25.2	27.1	32.0	9.5	11.3	12.4	13.4	16.4	F			
<i>V. rosula</i>	20.5	22.8	24.8	26.8	32.0	7.5	9.0	10.0	10.9	13.9	F			
<i>V. calciseda</i>	20.9	22.7	24.7	26.7	29.1	8.6	10.0	11.3	12.7	14.8			T	
<i>V. funckii</i>	19.3	22.3	24.0	25.8	30.0	8.0	9.2	10.1	11.0	13.0	F			
<i>V. placida</i>	19.0	21.4	24.0	26.5	30.3	8.2	9.2	9.9	10.7	12.0	F			
<i>P. canellum</i>	18.5	21.3	23.9	26.5	30.3	6.6	7.7	8.5	9.4	10.3			T	L
<i>V. internigrescens</i>	15.0	19.6	22.3	24.9	30.0	7.5	9.1	10.3	11.6	13.1		M		
<i>V. elaeomelaena</i> s.l. p.p.	17.0	20.2	22.3	24.3	27.5	11.0	11.9	12.8	13.7	15.6	F			
<i>V. nodosa</i>	17.2	20.5	22.2	23.9	27.9	7.8	9.0	9.7	10.4	11.5	F			
<i>V. muralis</i>	16.8	19.9	22.0	24.0	27.1	7.4	9.9	11.2	12.5	14.4			T	
<i>V. bryoctona</i>	15.0	19.3	22.0	24.7	29.0	5.0	5.8	6.4	7.0	8.0			T	
<i>V. fusconigrescens</i>	17.2	19.4	21.4	23.4	25.8	6.6	7.9	8.8	9.6	11.1		M	T	
<i>V. murina</i>	13.5	18.4	21.1	23.8	28.7	6.0	8.0	9.6	11.3	14.4			T	
<i>V. hydrophila</i>	14.8	19.3	21.1	22.9	25.8	6.5	8.1	8.9	9.7	11.5	F			
<i>V. praetermissa</i>	16.0	19.2	21.0	22.9	28.0	6.5	7.9	8.7	9.5	10.5	F			
<i>V. ochrostoma</i>	15.6	18.4	20.9	23.5	27.1	8.6	10.2	11.5	12.9	13.9			T	
<i>V. nigrescens</i>	15.2	15.6	20.6	25.5	24.6	7.8	7.3	9.5	11.7	12.3			T	

P. formosum	14.0	17.8	20.3	22.8	27.9	7.0	8.2	9.0	9.8	11.1	F		L
V. cernaensis	15.0	18.0	19.9	21.9	27.0	7.5	9.5	10.6	11.7	14.0	F		
V. elaeina	15.0	17.7	19.4	21.0	24.0	6.0	7.4	8.0	8.7	10.0		T	
V. phaeosperma	16.0	17.1	19.3	21.5	24.2	8.2	8.5	9.0	9.5	9.8		T	L
V. sandstedei	16.0	?	?	?	21.0	3.0	?	?	?	5.0		M	
V. pachyderma	15.0	16.1	19.1	22.0	23.5	6.0	6.5	7.7	8.8	9.4	F		
V. xyloxena	13.5	16.6	18.8	21.0	27.0	5.5	6.3	7.3	8.2	10.0		T	
P. cinereoatratum	12.7	16.2	18.5	20.8	25.4	5.3	6.5	7.2	8.0	9.4	F		L
V. dufourii	15.6	16.4	18.1	19.8	23.4	6.6	7.1	7.8	8.4	9.0		T	
V. baldensis	14.0	?	?	?	21.0	6.0	?	?	?	10.0		T	
V. parmigerella	14.0	?	?	?	21.0	6.0	?	?	?	8.0		T	
V. sublobulata	13.5	15.3	16.9	18.4	21.5	5.5	6.8	7.6	8.4	9.8	F		
V. pinguicula	11.9	13.9	16.7	19.5	24.6	4.9	5.7	7.0	8.4	11.0		T	
H. amphibia	13.1	15.0	16.6	18.1	19.7	4.9	5.6	6.2	6.8	7.4		M	
V. dolosa	14.4	14.9	15.9	17.0	18.0	5.7	6.4	7.0	7.5	7.8		T	
H. maura s.l.	12.3	14.2	15.8	17.3	19.7	5.7	6.9	7.6	8.3	10.3		M	
H. scabra	11.0	13.9	15.7	17.5	21.3	7.0	7.6	8.3	9.0	10.5	F		
V. cyanea	13.5	14.1	15.5	16.9	18.5	5.7	6.1	7.0	7.8	9.0		T	
P. fuscillum	11.5	13.2	15.1	17.0	20.5	4.5	5.2	5.7	6.2	7.4		T	L
V. caerulea	11.9	12.8	15.0	17.3	23.5	5.0	5.3	6.2	7.0	9.5		T	
V. polysticta	10.3	12.6	14.1	15.7	16.4	5.3	5.6	6.2	6.9	7.8		T	
V. conturmatula	11.5	12.6	14.1	15.6	18.0	3.3	4.9	5.4	6.0	6.5	F		L
V. latericola	10.6	?	14.0	?	18.9	4.5	?	5.8	?	7.5		T	L
V. prominula	10.3	11.7	12.9	14.2	16.0	4.5	6.7	7.4	8.2	9.0		M	
H. rheitrophila	8.5	11.2	12.8	14.4	16.0	6.0	6.6	7.4	8.2	9.5	F		
V. madida	9.0	10.6	12.1	13.6	14.8	5.3	6.1	6.6	7.1	7.4	F		
V. sphaerospora	9.0	?	?	?	12.0	7.5	?	?	?	10.0		T	
Het. fuscillum	7.0	10.0	?	13.0	15.0	6.0	?	?	?	10.0			
V. aranensis	6.9	?	9.8	?	11.1	5.6	?	6.3	?	7.2		T	

V. ditmarsica	7.4	8.6	9.6	10.6	12.0	5.0	5.9	6.6	7.3	8.0	M	
V. striatula	7.8	8.2	9.1	10.1	11.9	4.9	5.3	5.6	5.9	6.2	M	
V. halizoa	7.0	7.8	9.1	10.5	11.9	3.3	3.6	4.1	4.7	5.3	M	
V. knowlesiae	7.5	?	8.9	?	11.0	5.6	?	5.9	?	7.0		T
V. ceuthocarpa	8.5	?	?	?	10.5	6.0	?	?	?	7.5	M	
V. mucosa	7.0	?	?	?	10.0	4.0	?	?	?	7.0	M	
V. degelii	7.0	?	?	?	10.0	4.0	?	?	?	7.0	M	
V. bulgarica	7.0	7.9	8.6	9.4	10.0	4.5	4.4	4.8	5.1	5.5		T
V. simplex	6.0	7.0	8.2	9.4	9.5	3.5	3.8	4.4	4.9	5.0		T
V. aquatilis	6.5	7.4	8.2	8.9	10.0	4.5	5.6	6.1	6.7	8.0	F	