Revisions of British and Irish Lichens

British Lichen Society

Volume 49 **March 2025**

Lecanorales: Stereocaulaceae

Cover image: *Stereocaulon vesuvianum* on dolerite rocks, Clee Hill, nr Ludlow, Shropshire.

Revisions of British and Irish Lichens is a free-to-access serial publication under the auspices of the British Lichen Society, that charts changes in our understanding of the lichens and lichenicolous fungi of Great Britain and Ireland. Each volume will be devoted to a particular family (or group of families), and will include descriptions, keys, habitat and distribution data for all the species included. The maps are based on information from the BLS Lichen Database, that also includes data from the historical Mapping Scheme and the *Lichen Ireland* database. However, these are not comprehensive and there are many further records that have not yet been digitized. The choice of subject for each volume will depend on the extent of changes in classification for the families concerned, and the number of newly recognized species since previous treatments.

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to compile new printed editions of the entire lichen biota of Britain and Ireland is extensive, and many parts are out-of-date even as they are published.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

Editorial Board

Dr P.F. Cannon (Royal Botanic Gardens, Kew, Surrey TW9 3AB, UK).
Dr A. Aptroot (Laboratório de Botânica/Liquenologia, Instituto de Biociências, Universidade Federal de Mato Grosso do Sul, Avenida Costa e Silva s/n, Bairro Universitário, CEP 79070-900, Campo Grande, MS, Brazil)
Dr B.J. Coppins (Royal Botanic Garden, Inverleith Row, Edinburgh EH3 5LR, UK)
Dr A.M. Fryday (Department of Plant Biology, Michigan State University, 612 Wilson Rd., East Lansing, MI 48824, USA)
Mr N.A. Sanderson (3 Green Close, Woodlands, Southampton, Hampshire SO40 7HU, UK)
Dr J.M. Simkin (School of Natural and Environmental Science, Newcastle University, Newcastle upon Tyne NE1 7RU, UK)
Dr R. Yahr (Royal Botanic Garden, Inverleith Row, Edinburgh EH3 5LR, UK)

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

Made available under Creative Commons Licence CC BY-SA

ISSN 2634-7768 © British Lichen Society, 25 March 2025

Revisions of British and Irish Lichens **vol. 49**

Lecanorales: Stereocaulaceae

including *Hertelidea*, *Lepraria*, *Squamarina* and *Stereocaulon*

by

Rebecca Yahr
Royal Botanic Garden Edinburgh, 20A Inverleith Row, Edinburgh EH3 5LR, UK

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

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

Alica Košuthová
Department of Botany, Swedish Museum of Natural History, P.O. Box 50007, SE-104 05, Stockholm, Sweden

Bruce McCune
Oregon State University, Dept. Botany & Plant Pathology, 2701 SW Campus Way, Corvallis, Oregon 97331, U.S.A.

André Aptroot
Laboratório de Botânica/Liquenologia, Instituto de Biociências, Universidade Federal de Mato Grosso do Sul, Avenida Costa e Silva s/n, Bairro Universitário, CEP 79070-900, Campo Grande, MS, Brazil

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

This publication can be cited as:
Yahr, R., Cannon, P., Coppins, B., Košuthová, A., McCune, B., Aptroot, A. & Simkin, J. (2025). Lecanorales: Stereocaulaceae, including *Hertelidea*, *Lepraria*, *Squamarina* and *Stereocaulon*. *Revisions of British and Irish Lichens* **49**: 1–24.

STEREOCAULACEAE Chevall. (1826)

Thallus very varied; leprose, squamulose or crustose, corticate or not, in *Stereocaulon* composed of a crustose to squamulose primary thallus, often degenerating at an early stage, mostly with pseudopodetia consisting of a solid erect fruticose secondary thallus. **Photobiont** chlorococcoid, sometimes with **cephalodia** containing cyanobacteria. **Ascomata** apothecial, flat or domed, usually brown, mostly without well-developed marginal tissues; absent in *Lepraria*. **Hamathecium** of sparingly branched, paraphyses with hardly to strongly swollen apices, sometimes with brown caps. **Asci** with a strongly J+ apical cap with a central dark tubular structure, without an outer J+ gelatinized layer. **Ascospores** colourless, often elongate, transversely septate, sometimes muriform. **Anamorph** coelomycetous, pycnidial; in one genus with sporodochia.

The Stereocaulaceae currently contains five genera (Lücking *et al.* 2017), of which four occur in Britain and Ireland. The family appears to be related to the Cladoniaceae, which also has complex thalli with podetia in many species (Lendemer & Hodkinson 2013, Miadlikowska *et al*. 2014).

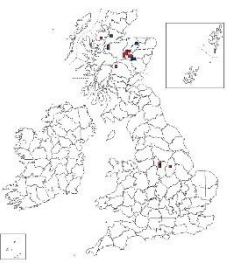
HERTELIDEA Printzen & Kantvilas (2004)

Thallus crustose, smooth, granular or subsquamulose, with or without soredia. **Photobiont** chlorococcoid. **Ascomata** apothecia, lecideine, sessile, basally constricted, typically forming irregular clusters of individual apothecia proliferating from the hymenium and margins of older apothecia. **Disc** dark brown to black, occasionally pruinose. **Margin** persistent, cup-shaped in section, composed of densely entangled hyphae with ± rounded cell lumina, often inspersed with granules. **Hymenium** ± colourless, with a granular epihymenial layer. **Paraphyses** weakly to moderately branched and anastomosing, typically with brown tips. **Asci** 8-spored, lacking a well-developed ocular chamber, *Micarea*-type, with a K/I+ blue tholus pierced by an inconspicuous, darker blue tubular structure. **Ascospores** colourless, aseptate or rarely 1-septate, without a gelatinous perispore. **Conidiomata** pycnidia; conidia filiform. **Chemistry**: typically depsides; one species with fatty acids. **Ecology**: on burnt or decaying wood, soil or bryophytes.

Characterized by the lecideine apothecia that often grow in clusters, the persistent, cup-shaped margin, the *Micarea*-type asci and non-septate ascospores.

Literature:
Kantvilas (2009), Kantvilas & Elix (2006), Printzen & Kantvilas (2004).

Hertelidea botryosa (Fr.) Printzen & Kantvilas (2004) **NT**



Thallus rather thick, pale to dark grey, greenish or brownish, composed of scattered incised subsquamulose warts 0.1–0.4 mm diam. that soon coalesce, become sorediate and at length form a thick contiguous leprose-sorediate crust; photobiont cells 5–12 µm diam. Apothecia 0.15–0.35 (–0.6) mm diam., typically forming dense, ± substipitate botryose clusters; disc dark brown to brown-black, sometimes greyish pruinose, flat or weakly convex, sometimes slightly concave; margin thin, typically pale to dark brown and paler than the disc, ± pruinose when young, in section patchily dark brown with a greenish or reddish hue and with a dark brown outer edge; hymenium colourless to pale brownish, 35–55 µm thick with a brown to red-brown, granular epithecial layer that dissolves and becomes colourless in KOH; hypothecium dark brown, inverted cone-shaped; paraphyses 0.7–1.5 µm thick, with a brown apical cell 1–2 µm diam. Asci 28–33 × 6–10 µm. Ascospores

ellipsoidal, aseptate or very rarely 1-septate, 7–11.3 (–16) × 3–3.9 (–5) µm. Conidia 13–14 × *ca* 1 µm. Thallus K–, KC–, C–, Pd–, UV+ white (perlatolic acid). **BLS 0703**.

On wood and exposed old bark of *Pinus* and *Quercus* in old growth native pinewoods in Scotland and an ancient deer park and a former royal forest in E. England; rare. England (Chatsworth Park, Peak District and Sherwood Forest, Nottingham) and N. Scotland (C. & E. Highlands).

LEPRARIA Ach. (1803)

Thallus crustose, leprose, not corticate, diffuse or with a more or less well-defined margin, mostly comprising a layer of ecorticate soredia-like granules, sometimes with a weakly defined medulla below, but granules absent in the young parts of some species with well-defined lobes; colour whitish, grey, blue-grey, green or yellowish. **Prothallus** absent. **Hypothallus** developed in some species, comprising white to dark brown hyphae; in many species subthalline hyphae are sparse, or locally abundant in cracks in the substratum. **Photobiont** a green alga. **Ascomata** unknown. **Conidiomata** unknown. **Chemistry**: fatty acids, benzyl esters, depsides, depsidones, dibenzofuranes, anthraquinones, xanthones and triterpenoids. **Ecology**: on bark, rock and soil, frequently on surfaces sheltered from direct rain, and then often in shaded and humid habitats.

Characterized by the powdery or granular, completely ecorticate thallus, and absence of ascomata and conidiomata. A useful review on a global basis was contributed by Saag *et al.* (2009). The genus was found to be related to *Stereocaulon* in the early days of lichen phylogenetic research by Ekman & Tønsberg (1992), and more recent studies confirm that the genus is largely monophyletic in its current circumscription.

Species may be confused with other sterile sorediate crustose lichens, which differ in features such as local presence of a cortex, presence of a prothallus, chemistry, or photobiont. *Botryolepraria* differs in the byssoid thallus in which the photobiont cells are arranged in clusters at the ends of hyphal branches, and in the occurrence of a triterpenoid as the only major substance. It is provisionally placed in the Verrucariales. *Dendrographa latebrarum* (Roccellaceae, Arthoniales) differs in the trentepohlioid photobiont. *Lepraria ecorticata* has been transferred to the genus *Lithocalla* (uncertain position within Lecanorales); see Orange (2020) for more information. *Andreiomyces obtusaticus*, recently identified from our region and formerly placed in *Lepraria* (Tønsberg 1992), is now placed within its own family based on sequence data, as part of the Arthoniales (Hodkinson & Lendemer 2013). It is distinguished chemically from *Lepraria* by the presence of obtusatic acid as a major compound. Species of *Leprocaulon* superficially resemble *Lepraria*, but are phylogenetically distinct, contain usnic acid and have distinctive haustoria (Lendemer & Hodkinson 2013, Orange *et al*. 2017).

The species are morphologically simple, and chemistry is very important for identification. With experience, it is possible to recognize many species in the field, using the colour and texture of the thallus, the nature of the substratum, and (occasionally) spot tests, but it is essential to check much material using thin-layer chromatography. Although most species are presently under-recorded, there is a danger that the more familiar species will be over-recorded unless material is confirmed by TLC.

The main key requires data from thin-layer chromatography; a supplementary key is provided for tentative identification of species when access to TLC is not available. Descriptions below refer to the colour of the fresh, dry thallus; specimens gradually fade in dried collections. Spot tests are best carried out on acetone extracts on filter paper. Descriptions refer to granules away from the thallus margin, as marginal granules are often larger with projecting hyphae. *Lepraria incana* is the most common species in eastern England, and *L. finkii* (*syn. L. lobificans*) is the most common in the west.

Literature:
Ekman & Tønsberg (2002), Kukwa (2006), Laundon (1992), Lendemer (2013), Lendemer & Hodkinson (2013), Nelsen & Gargas (2008), Orange (2020), Orange & Laundon (2009), Orange *et al.* (2017), Saag *et al.* (2009), Tonsberg (1992, 2002).

1 Containing a terpenoid only (lesdainin); thallus green, spongy; hyphae thin walled, with numerous septa ..... ***Botryolepraria lesdainii***
Containing major compounds other than, or in addition to, terpenoids; hyphae thick walled, with distant septa 2

2(1) Containing only fatty acids and atranorin as major compounds 3
Containing other major compounds instead of, or in addition to, these compounds 9

3(2) Thallus containing jackinic/rangiformic acids as the only major fatty acid 4
Thallus containing other fatty acids as major compounds (jackinic acid may also be present) 7

4(3) Thallus usually on rain-exposed surfaces, composed of rather firmly attached granules 0.06–0.26 (–0.32) mm diam., with a compact, pruinose, and often cracked surface ..... ***borealis***
Thallus on surfaces sheltered from rain, granules less firmly attached, 0.04–0.1 (–0.16) mm diam., typically forming a powdery crust 5

5(4) Thallus with a delimited margin, medulla present, lower surface of thallus usually covered by weft of orange-brown to brown hyphae coated with anthraquinones (K+ purple-red) ..... ***bergensis***
Thallus with a diffuse margin, medulla absent; anthraquinones, when present, restricted to locally occurring subthalline hyphae growing in cracks in the substratum 6

6(5) Anthraquinones present on subthalline hyphae (local and often inconspicuous); growing on rock ..... ***humida***
Anthraquinones absent; mostly on bark ..... ***jackii***

7(3) Thallus granules with projecting hyphae to at least 60 μm long; containing nephrosteranic acid ..... ***rigidula***
Thallus granules without projecting hyphae, or these no more than 20 μm long (sometimes longer on marginal granules); nephrosteranic acid absent 8

8(7) Containing jackinic acid as a major fatty acid; subthalline hyphae (when present) lacking anthraquinones; mainly on bark of conifers ..... ***jackii***
Containing toensbergianic and roccellic acids as major compounds; subthalline hyphae (when present) coated with anthraquinones; mainly on bark of broad-leaved trees ..... ***sylvicola***

9(2) Usnic acid present (sometimes with atranorin) ..... ***Lithocalla ecorticata***
Usnic acid absent 10

10(9) Dibenzofuranes present (either pannaric acid or related compounds, appearing grey on TLC plate, or porphyrilic acid, colourless on TLC plate) 11
Dibenzofuranes absent, depsides or benzyl esters present 15

11(10) Porphyrilic acid present, pannaric acid or related compounds absent 12
Porphyrilic acid absent, pannaric acid or related compounds present 13

12(11) Thallus not powdery, of rather firmly attached granules 0.06–0.26 (–0.4) mm diam., on rain-exposed surfaces ..... ***alpina***
Thallus powdery, granules 0.04–0.1 (–0.16) mm diam., on surfaces sheltered from rain ..... ***atlantica***

13(11) Thallus with more or less well-defined marginal lobes with a raised rim; brown hyphae abundant on the underside; pannaric acid, roccellic acid and atranorin present ..... ***membranacea***
Thallus diffuse or margin slightly delimited, but without lobes; brown hyphae absent or sparse; pannaric acid absent or in trace amounts 14

14(13) 4-Oxypannaric acid 2-methylester present as a major compound, sometimes with unidentified compounds ..... ***diffusa***
Pannaric acid 6-methylester present as a major compound ..... ***vouauxii***

15(10) Containing alectorialic acid (a benzyl ester), with or without additional depsides 16
Containing depsides, without alectorialic acid 17

16(15) Thallus not powdery, of rather firmly attached granules, on rain-exposed surfaces; with alectorialic acid only ..... ***neglecta***
Thallus powdery, on surfaces sheltered from rain; often with protocetraric acid or psoromic acid in addition to alectorialic acid ..... ***eburnea***

17(15) Containing stictic acid, atranorin, and usually zeorin 18
Containing depsides other than stictic acid 19

18(17) Thallus soft, spongy, with a medulla ..... ***finkii***
Thallus firm in appearance, medulla absent ..... ***elobata***

19(17) Containing divaricatic acid, thallus UV+ bluish white 20
Containing other depsides 21

20(19) Nordivaricatic acid present as a major compound; thallus granules with a loose surface, giving the thallus a soft appearance, C+ red ..... ***crassissima***
Nordivaricatic acid absent or in trace amounts; thallus granules with a more compact surface, giving the thallus a firmer appearance, C– ..... ***incana***

21(19) Thamnolic acid present 22
Thamnolic acid absent 23

22(21) Containing roccellic acid and atranorin, thallus whitish to pale blue-grey, margin sometimes delimited ..... ***nylanderiana***
Containing thamnolic acid only; thallus greenish to bluish green, diffuse ..... ***umbricola***

23(21) Obtusatic acid present ..... ***Andreiomyces obtusaticus***
Obtusatic acid absent 24

24(23) Thallus not powdery, of rather firmly attached granules, on rain-exposed surfaces; containing fumarprotocetraric acid or psoromic acid ..... ***caesioalba***
Thallus powdery, on surfaces sheltered from rain, containing protocetraric acid ..... ***nivalis***

Supplementary key:
The following key is a guide to the possible identity of specimens when TLC is not available. It should be used with caution. The morphological differences between the species are often subtle, and spot tests are rarely diagnostic for one species. The spongy or powdery thallus of some species makes the results of spot tests difficult to see. The best method is to extract a piece of thallus in acetone, and to apply the extract to a very small area of filter paper, using a capillary tube. The paper can be cut into several tiny pieces and tested under a dissecting microscope.

Some spot tests can be observed in the field with care, using a minimal amount of reagent. A positive C or KC reaction can be seen by first applying a very small drop of K; on a dry thallus the drop will often remain intact and not be absorbed by the thallus. Then, after a few moments, a small drop of C is added to the drop of K. If a

thamnolic acid-containing species such as *L. umbricola* is suspected, the K reaction is best seen in the field by brushing the surface of the thallus with a pipette wet with K, so that the thallus surface is scarcely wetted. Under a hand lens, the K+ bright yellow reaction of thamnolic acid can be distinguished from the weaker yellow reaction of atranorin (but note that there are other, K+ yellow to orange reactions in the genus).

1 Thallus green, spongy, byssoid, without distinct granules, C–, K–, KC–, Pd–, UV–; hyphae thin walled, with numerous septa; on calcareous rock ..... ***Botryolepraria lesdainii***
Thallus powdery or granular, at least some spot tests positive; hyphae thick walled, with numerous septa 2

2(1) Thallus usually on rain-exposed surfaces, composed of rather firmly attached granules 0.06–0.26 (–0.40) mm diam., granules with a compact, pruinose, and often cracked surface 3
Thallus on surfaces sheltered from rain, granules less firmly attached, typically forming a powdery or rarely membranous crust 5

3(2) Thallus KC+ orange-pink; stains collection packets red-brown after several years; montane species ..... ***neglecta***
Thallus KC– 4

4(3) Thallus Pd+ bright yellow or orange-red; widespread species ..... ***caesioalba***
Thallus Pd± (rather weak) yellow ..... ***alpina*** (rare, montane) and ***borealis*** (widespread)

5(2) Thallus KC+ orange-pink or red 6
Thallus KC–, or KC+ yellow or orange 7

6(5) Thallus Pd+ yellow or orange, UV–; on slightly calcareous rock, rarely bark ..... ***eburnea***
Thallus Pd–, UV+ bluish white; on acidic or slightly calcareous rock ..... ***crassissima***

7(5) Thallus or subthalline hyphae (hyphae in small cavities between thallus and substratum, or in cracks in substratum) with dull orange, orange-brown or pale orange-brown areas which are K+ purple-red 8
Thallus and subthalline hyphae K± yellow to orange, or subthalline hyphae too sparse to observe 10

8(7) K+ purple-red tissues not confined to lower parts of thallus, usually visible on upper surface; medulla absent ..... ***incana***
K+ purple-red tissues confined to lower side of thallus, or to subthalline hyphae 9

9(8) Thallus margin delimited at least when young, margin irregularly raised and forming lobes; medulla ± present; lower surface of thallus typically covered by pale orange-brown to dark brown hyphae, forming a ± distinct hypothallus; on siliceous rock and soil ..... ***bergensis***
Thallus margin diffuse, never with lobes; medulla and hypothallus absent, K+ purple-red tissues confined to subthalline hyphae ..... three morphologically very similar species: ***atlantica*** and ***humida*** (acidic rocks in woodland and on upland cliffs and block scree) and ***sylvicola*** (most frequent on mature *Quercus*, rarely on acid rocks).

10(7) Thallus patchily UV+ dull pink..... ***Andreiomyces obtusaticus***
Thallus UV+ bluish white or UV– 11

11(10) Thallus UV+ bluish white, K–, Pd–; thallus finely granular, medulla absent; frequent on acidic rock and bark ..... ***incana***
Thallus UV– 12

12(11) Thallus diffuse, never with marginal lobes; medulla and hypothallus absent; C–, K± yellow (often weakly yellow, never deep or bright yellow), Pd– or yellowish 13
Thallus various; C± yellow, K+ yellow or orange, Pd+ yellow, bright yellow, or orange, dirty orange or orange 16

13(12) Thallus granules relatively large, 0.1–0.2 mm diam., with projecting hyphae at least 60 µm long (easily seen with a ×10 handlens); thallus shades of grey (not blue-grey); frequent on acidic bark and rock ..... ***rigidula***
Thallus granules relatively small, 0.04–0.16 mm diam., projecting hyphae absent or very short; thallus colour various, but often either bluish grey or yellow 14

14(13) Thallus pale yellowish green (locally bluish grey in deep shade), K–, KC+ yellow; on acid rock in very sheltered but humid overhangs ..... ***Lithocalla ecorticata***
Thallus bluish white to pale blue-grey, K+ yellow (often weak), KC– (meaning no increase in intensity of yellow following C) 15

15(14) Subthalline hyphae (hyphae in small cavities between thallus and substratum, or in cracks in substratum) white, K–; most often on acid bark of conifers, *Alnus* and *Betula*, also on plant remains and acid rock ..... ***jackii***
Subthalline hyphae pale orange-brown, K+ purple-red..... ***atlantica***, ***humida*** or ***sylvicola*** (see couplet 9)
[if subthalline hyphae cannot be found, or are very sparse, the four species in this couplet cannot be distinguished.]

16(12) Thallus margin distinctly delimited at least in some parts, sometimes lobed, sometimes with a narrow raised rim 17
Thallus margin diffuse, without lobes or a raised rim 20

17(16) Lower surface of thallus with dark grey or brown hyphae forming a weakly developed or distinct hypothallus (thallus C+ yellow or dirty yellow, Pd+ orange-yellow or orange) 18
Lower surface of thallus without a layer of dark grey or brown hyphae (thallus C–, Pd+ bright yellow or red) 19

18(17) Thallus margin usually with distinct lobes, often with a narrow raised rim; hypothallus well-developed ..... ***membranacea***
Thallus margin at most weakly delimited, not lobed, without a narrow raised rim; hypothallus not or weakly developed ..... ***vouauxii***

19(17) Thallus often well-delimited, Pd+ red ..... ***nivalis***
Thallus often weakly delimited, Pd+ bright yellow ..... ***nylanderiana***

20(16) Thallus soft and spongy in texture, granules often ill-defined, comprising aggregations of smaller granules, all within a spongy network of abundant free hyphae; thallus bluish white to blue-grey or green (but not cream or yellow); C–, K+ yellow, Pd+ orange; a common species on bark, rock and soil ..... ***finkii***
Thallus various, granules fine and powdery, or soft in texture, but not bound by a network of abundant free hyphae; thallus colour various, sometimes with cream or yellow tints 21

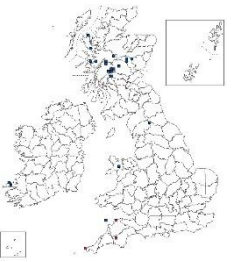
21(20) Thallus K+ bright yellow, Pd+ bright yellow 22
Thallus K–, or K+ yellow or orange, Pd+ yellow or orange 23

22(21) Thallus grey-green to dull blue-green, granules small, 0.06–0.1 mm diam., firm in appearance; on acidic bark, rock and soil, widespread ..... ***umbricola***
Thallus whitish to pale blue-grey, granules larger, 0.1–0.3 mm diam., soft in appearance and often poorly defined; on slightly calcareous rock, rare ..... ***nylanderiana***

23(21) Thallus pale blue-grey to dull blue-grey; granules small, 0.03–0.12 mm diam., firm in appearance; C–, K+ yellow, Pd+ orange; acid bark, on rock and soil ..... ***elobata***
Thallus various, pale blue-grey to grey, cream or yellow; granules sometimes coarser, 0.08–0.28 mm diam., sometimes soft in appearance; C± dirty yellow to orange, K– or K+ yellow, dirty yellow, dirty orange or orange, Pd+ yellow to orange or dirty orange; on acid or calcareous substrata 24

24(23) Medulla absent; on somewhat calcareous rock, rarely on bark ..... ***diffusa***
Medulla weakly developed; substrata various .....***vouauxii***
[these two species are difficult to distinguish with certainty without TLC]

Lepraria alpina (B. de Lesd.) Tretiach & Baruffo (2006) **NE**

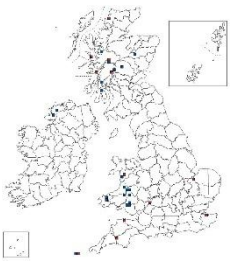


Thallus similar to *L. borealis*. Thallus C–, K+ yellowish, Pd–, UV– (porphyrilic, angardianic and/or roccellic acids [rarely replaced by rangiformic acid] and atranorin). **BLS 1600**.

On unshaded, rain-exposed rocks, mostly montane. S.W. and N. England (Cross Fell, at 850 m), Wales (Caernarvonshire), Scotland (central and western Highlands, Skye), S.W. Ireland.

Morphologically similar to the other species of the *L. neglecta* group (see under *L. borealis*), and needing TLC for identification. *L. atlantica* has a similar chemistry, but has a powdery thallus and grows on surfaces sheltered from rain; non-montane records of *L. alpina* may need to be reassigned there.

Lepraria atlantica Orange (2001) **NE**



Thallus diffuse, pale bluish grey, sometimes whitish or very pale greyish cream, composed of fine powdery granules 0.04–0.10 (–0.16) mm diam., mostly with projecting hyphae absent or very short; medulla absent; hyphae below thallus usually sparse, pale orange-brown. Thallus C–, K+ yellowish, Pd–, UV– (porphyrilic, rangiformic acids [rarely replaced by roccellic acid], atranorin), hyphae below thallus K+ purple-red (anthraquinones). **BLS 2330**.

On acidic rocks, often over bryophytes, on surfaces more or less sheltered from rain, in woodland or in unshaded sites, lowland to montane. Western Britain and N. Ireland, locally frequent, a few records in E. England needing confirmation.

Distinguished from all species of *Lepraria* in the region except *L. alpina* by the presence of porphyrilic acid. *L. alpina* differs in the more coarsely granular, non-powdery thallus on rain-exposed montane rocks. *L. atlantica* can be suspected in the field by the finely powdery, pale thallus, often growing in small patches below very small overhangs, but TLC is necessary to separate it from other species, especially the morphologically similar *L. humida*.

Lepraria bergensis Tønsberg (2002) **NE**

Thallus with delimited margin when young, pale grey to pale bluish grey; margin irregularly raised, forming lobes; thallus granules 0.08–0.16 mm diam., the surface with a soft appearance, without distinctly projecting hyphae, or with very shortly projecting hyphae to 20 μm long; marginal granules sometimes with long hyphae to 60 μm long; medulla more or less developed; lower surface of thallus often with numerous pale orange-brown to dark brown hyphae, forming a more or less distinct hypothallus. Thallus upper surface C–, K+ yellow, Pd± yellowish, UV– (cf. rangiformic acid, atranorin); medulla and hypothallus K+ purple-red (anthraquinones). **BLS 2431**.

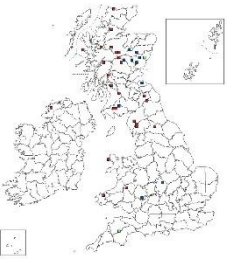
On siliceous rock and associated soil on rain-sheltered surfaces, probably overlooked; Wales (Cardigan), N. England (Cumbria).

Distinguished by the combination of cf. rangiformic acid and atranorin as major substances, presence of lobes, the rather coarse thallus granules, and the presence of a hypothallus. *L. borealis* differs in the lack of medulla and hypothallus and the rain-exposed habitat, *L. humida* differs in the fine granules and lack of lobes and medulla. The K+ purple-red reaction of the lower surface is striking, but K+ hyphae also occur in *L. humida* and other species. The lobes may be inconspicuous.

Lepraria borealis Lohtander & Tønsberg (1994) **NE**

Thallus diffuse or often with a delimited margin, whitish or pale grey, granules 0.06–0.26 (–0.32) mm diam., rather firmly attached to the thallus (but easily broken or dislodged with forceps); granule surface ± compact in

appearance, pruinose, often cracked, without or rarely with short projecting hyphae; medulla absent. Thallus C–, K+ yellow, Pd± yellowish, UV– (rangiformic acid, norrangiformic acid [trace], atranorin). **BLS 1927**.

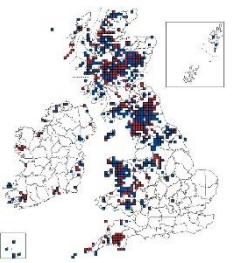


On acidic, rain-exposed rocks in sun or light shade, directly on rock or frequently on mosses such as *Andreaea rothii* and *Racomitrium* spp., rarely on acid soil between rocks; occasionally spreading onto steep and slightly sheltered rock faces. N. & W. Britain and N.W. Ireland, probably frequent, but distribution incompletely known.

Morphologically similar to *L. alpina, L. caesioalba* and *L. neglecta*. In this group of four species the rather firmly attached granules with a compact surface, lack of a medulla and scarcity of free hyphae give a characteristic appearance, which differs from the more powdery appearance of most *Lepraria* species; also the thalli occur on rain-exposed surfaces. Rarely, colonies extend onto steep and sometimes lightly shaded faces, and the appearance of the thallus is then less distinctive, and TLC may be necessary to confirm their identity. Species within the group are best distinguished by TLC, although spot tests can be helpful.

Lepraria caesioalba (B. de Lesd.) J.R. Laundon (1992) **NE**

Thallus similar to *L. borealis*, granules 0.08–0.2 (–0.4) mm. Thallus C–, K± yellow, Pd+ yellow to orange-red, UV– ; chemically variable, with the following chemotypes (atranorin usually present in the first three, perhaps always present in the others): I fumarprotocetraric and angardianic acids, II fumarprotocetraric, psoromic and angardianic acids, III psoromic and angardianic acids, IV psoromic, rangiformic and angardianic acids, V psoromic and rangiformic acids; cf. gyrophoric acid often occurs in trace amounts in most of the chemotypes. Chemotypes I and III are frequent, II and IV are rare, V is occasional. **BLS 0823**.



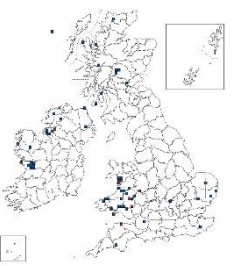
On acidic, rain-exposed rocks in sun or light shade, directly on rock or frequently on mosses such as *Andreaea rothii* and *Racomitrium* spp., rarely on acid soil between rocks. N. & W. Britain, locally frequent, very rare in C. England, mainly near the coasts in Ireland.

Morphologically similar to the other species of the *L. neglecta* group (see under *L. borealis*). The commonest of the four species (or at least the most frequently recorded).

Host to the lichenicolous fungus *Rhymbocarpus neglectus* (Vain.) Diederich & Etayo (2000).

Lepraria crassissima (Hue) Lettau (1958) **NE**

Thallus diffuse, bluish white or pale blue-grey, soft in appearance, composed of granules 0.06–0.12 mm diam., surface of granules loose but mostly without distinctly projecting hyphae except on some marginal granules. Medulla absent. Thallus C+ red, K–, KC+ red, Pd–, UV+ bluish white (divaricatic and nordivaricatic acids, zeorin). **BLS 0819**.



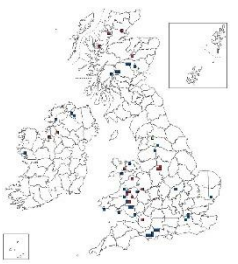
On acidic or slightly calcareous rock below overhangs in woodland. Occasional in Wales, rare in Scotland and S.W. England, but probably under-recorded.

Distinguished by the C+ red reaction (nordivaricatic acid). *L. incana* is similar, but is C– (nordivaricatic acid in trace amounts only), the thallus is darker in colour, and the granules tend to have a firmer surface, giving the thallus a less soft appearance. *L. eburnea* is KC+ pink, C+ faint yellow or pink (but not C+ red), and Pd+ yellow to orange.

Lepraria diffusa (J.R. Laundon) Kukwa (2002) **NE**

Lepraria diffusa var. *chrysodetoides* (J.R. Laundon) Kukwa (2002)

Thallus diffuse, the margin sometimes more or less delimited, but without lobes or a raised edge, pale greyish to cream, rarely pale blue-grey; powdery; granules 0.08–0.28 mm diam., with a loose surface but without projecting hyphae or these very short; medulla absent, tufts of brown hyphae sometimes present below the thallus, but not forming a hypothallus. Thallus C± dirty orange or orange, K± dirty orange, Pd+ yellow to dirty orange (4-oxypannaric acid 2-methylester, often with unknown accessory compound). **BLS 1601**.



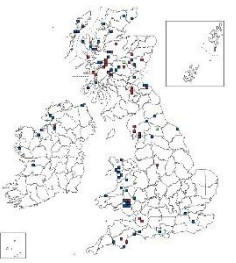
On calcareous or slightly calcareous substrata sheltered from rain, including limestone and siliceous rocks, in shaded or unshaded situations, on natural outcrops or

on walls and tombstones, rarely on bark; scattered records from many parts of Britain and Ireland, but under-recorded.

In the field the often cream-coloured thallus (usually lacking the blue-grey tinges seen in many species) is characteristic, but is similar to *L. eburnea*, which also prefers basic substrata.

L. diffusa var. *chrysodetoides* was considered to be similar to var. *diffusa*, but the thallus is deep cream to dull yellow due to a yellow, acetone-insoluble pigment. Kukwa (2006) placed the variety into synonymy with *L. diffusa* var. *diffusa*.

Lepraria eburnea J.R. Laundon (1992) **NE**

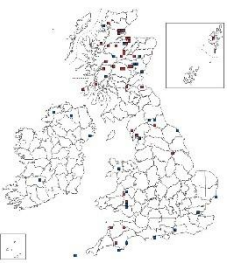


Thallus diffuse, rarely slightly delimited, especially when growing on moss cushions, pale blue-grey to greenish cream, granules 0.04–0.2 (–0.3) mm diam., with a soft surface, usually with only shortly projecting hyphae to *ca* 40 µm long; medulla absent. Thallus C+ faint yellow or pink, K+ yellow, KC+ pink, Pd+ yellow to orange (three chemotypes: I alectorialic, and protocetraric acids, II alectorialic, psoromic, and 2′-*O*-demethylpsoromic acids, III alectorialic acid only). **BLS 1713**.

On slightly calcareous siliceous rock or on limestone or brick, often overgrowing bryophytes, occasionally on more or less basic bark. Widespread in Britain and Ireland, locally abundant, still under-recorded.

Pale, diffuse thalli on slightly calcareous rock suggest the presence of this species, but TLC is necessary to confirm an identification; *L. diffusa* is similar and can occur in similar habitats. Specimens stain collection paper red-brown after some years, due to alectorialic acid. *L. neglecta* also contains alectorialic acid, but the thallus is granular and grows on rain-exposed montane rocks. The chemotypes of *L. eburnea* cannot be separated reliably by spot tests.

Lepraria elobata Tønsberg (1992) **NE**



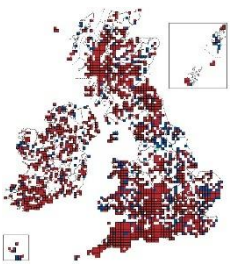
Thallus diffuse, pale blue-grey to dull blue-grey, granules 0.03–0.12 mm diam., with a fairly firm appearance, projecting hyphae absent or very short. Medulla absent. Thallus C–, K+ yellow, Pd+ orange, UV– (stictic and constictic acids, zeorin, atranorin). **BLS 0833**.

On acid rock and bark in semi-natural woodland, on conifers in plantations, and on soil banks. Widespread in Britain and Ireland but under-recorded, locally frequent. The distribution is poorly known due to confusion with *L. finkii*.

Very similar in appearance to *L. incana*, which is Pd–, UV+ bluish white (divaricatic acid); some specimens of *L. elobata* are paler than *L. incana*, but others are the same colour. *L. finkii* has a similar chemistry to *L. elobata*, but the thallus is soft and spongy. *L. humida* differs in the presence of rangiformic acid; reports of fatty acids in *L. elobata* are due to mixed stands of these species.

Host to the lichenicolous fungus *Rhymbocarpus neglectus*.

Lepraria finkii (B. de Lesd.) R.C. Harris (1985) **NE**



Lepraria lobificans auct. br., *non* Nyl. (1873)

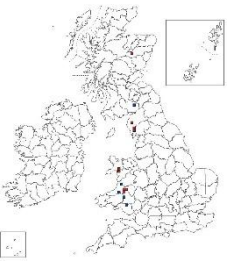
Thallus diffuse or with a slightly delimited margin, bright, pale green, bluish white to pale blue-grey, soft and spongy in texture; granules often ill-defined, especially in humid situations, 0.12–0.36 mm diam., comprising loose aggregations of smaller granules; free hyphae (not associated with algae) abundant in the thallus, forming a spongy network connecting the granules, and often predominating in the lower part of the thallus to form a more
or less distinct white medulla. Thallus Pd+ orange, K+ yellow, C–, UV– (stictic, and constictic acids, zeorin, atranorin). **BLS 1629**.

On bark, wood, siliceous rock, limestone, mortar and soil, on surfaces sheltered from rain, on a wide range of rock types and phorophytes, but avoiding very acid substrata. Widespread and often abundant.

Recognized in the field by the pale blue-grey thallus with a soft and spongy texture and white medulla. *L. elobata* has a similar chemistry, but the thallus is composed of firmer granules, and is not spongy, and the species prefers more acidic substrata.

Host to *Arthonia neglectula* (q.v.), as well as *Monodictys epilepraria* Kukwa & Diederich (2005), *Rhymbocarpus pubescens* (Etayo & Diederich) Diederich & Etayo (2000) and the plurivorous *Paranectria oropensis* subsp. *oropensis* (Ces.) D. Hawksw. & Piroz. (1977).

Lepraria humida Slavikova & Orange (2006) **NE**

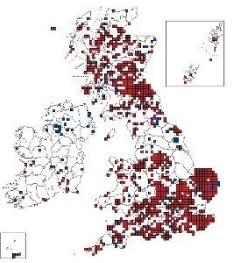


Thallus diffuse, bluish white to pale blue-grey, powdery, granules 0.4–0.1 (–0.16) mm diam; medulla absent; hyphae below the thallus usually sparse, pale orange-brown. Thallus C–, K+ yellowish, Pd± yellow, UV– (jackinic/rangiformic acid, atranorin), hyphae below thallus K+ purple-red (anthraquinones). **BLS 2458**.

On acidic rocks in deciduous woodlands, often on moist faces or associated with bryophytes, also on upland cliffs and block scree; local. Wales, Cumbria, Scotland (Cairngorms).

Similar to *L. jackii*, but containing jackinic/rangiformic acid instead of roccellic and jackinic acids, and with anthraquinones associated with the sparse hyphae below the thallus. *L. elobata* differs in the presence of stictic acid and the absence of fatty acids, and the thallus is often slightly darker. Morphologically and chemically identical specimens occur in other parts of Europe, but some may represent cryptic species and need more study.

Lepraria incana (L.) Ach. (1803) **NE**



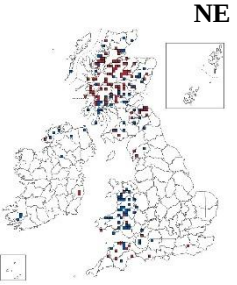
Thallus diffuse, pale to usually dull blue-grey, occasionally with dull pale orange patches, granules 0.05–0.12 mm diam. (rarely marginal ones to 0.2 mm), projecting hyphae usually absent or very short, giving a fairly firm appearance to the granules. Medulla absent. Thallus C–, K–, Pd–, UV+ bluish white (divaricatic and nordivaricatic acids [trace], zeorin), frequently also containing parietin, often irregularly distributed in the thallus and then K+ purple, UV+ pale orange. **BLS 1974**.

On acid rock, walls, bark and soil, on surfaces sheltered from direct rain, often forming extensive colonies, tolerant of pollution, often abundant. Widespread in Britain and Ireland.

Can often be recognized with experience by the diffuse, powdery UV+ thallus with a characteristically rather dull blue-grey colour. It is probably the most widespread species in the region, but other species are more abundant in certain habitats, such as calcareous areas and oceanic woodland. Specimens with parietin develop minute crystals on the thallus surface during storage. Records under this name made before 1992 have little meaning, as the name was formerly used in a broad sense.

Host to *Psammina stipitata* D. Hawksw. (1979) and the plurivorous *Paranectria oropensis* subsp. *oropensis*.

Lepraria jackii Tønsberg (1992) **NE**



Thallus diffuse, bluish white to pale blue-grey, powdery, granules 0.04–0.60 mm diam; medulla absent; hyphae below thallus often rather abundant in crevices in the substratum, but not forming a hypothallus, white. Thallus C–, K+ yellowish, Pd–, UV– (jackinic acid, usually roccellic acid, atranorin). **BLS 1693**.

On acid bark, frequently on conifers, also on *Betula*, *Alnus*, plant remains or moss over rock; in seminatural woodland but often frequent in conifer plantations. N. and W. Britain, scattered in Ireland especially near the coast.

The pale thallus, fine granules, and occurrence on acid bark are characteristic in the field, but TLC is necessary to distinguish *L. humida* and *L. sylvicola*; these were previously recorded as *L. jackii*, but the three species differ in ecology, chemistry, and ITS sequences. *L. atlantica* is also similar, but is confined to rock and contains porphyrilic acid. *L. jackii* appears to lack the anthraquinones found in the subthalline hyphae of *L. atlantica*, *L. humida* and *L. sylvicola*.

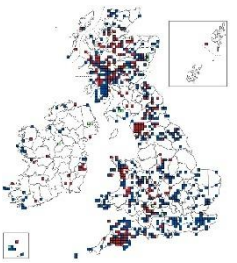
Lepraria membranacea (Dicks.) Vain. (1921) **NE**

Thallus delimited, often forming a coherent membrane, pale grey to cream or yellowish, marginal lobes usually distinct, to 3.5 mm wide, sometimes obscure in older thalli, extreme margin often turned upwards to form a narrow raised rim, but rim sometimes weakly developed; surface of lobes with granules 0.04–0.12 mm diam., older parts often with coarser granules to 0.3 mm diam. Medulla present as a layer of colourless hyphae without photobiont cells, grading downwards into a layer of brown, slightly thicker hyphae forming a grey to brown

hypothallus-like layer. Thallus C+ yellow, K+ yellow to orange, Pd+ orange (pannaric, and roccellic acids, usually atranorin, rarely zeorin). **BLS 1603**.

On shaded vertical acidic surfaces sheltered from rain, on rock and also on acid bark (often *Quercus* or *Alnus*); locally frequent in upland areas, but old records need to be checked; potentially nearly all records from the S.E. lowlands are errors, probably for *Lepraria vouauxii*. Throughout Britain and Ireland.

The membranous thallus with well-defined lobes, often with a yellowish tinge, is usually identifiable in the field. *L. nivalis* differs in the whitish thallus with a less well-defined raised margin, and the lack of a hypothallus, and often but not always occurs on calcareous substrata. Apothecia have been incorrectly reported from this species.

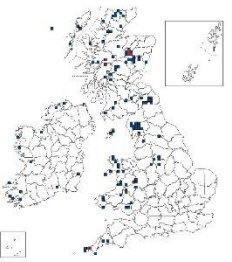


Lepraria neglecta (Nyl.) Lettau (1958) **NE**

Thallus similar in appearance to *L. caesioalba*. Thallus C± orange-pink, K± yellow, KC+ orange-pink, Pd+ yellow (alectorialic and angardianic acids [rarely replaced by rangiformic acid]). **BLS 0822**.

On moss cushions on acid rocks and on stony ground, on unshaded rain-exposed surfaces, montane, mostly above 850 m altitude, rarely down to around 300 m; probably locally frequent in the Cairngorm Mountains (C. Scotland), rare elsewhere; the map probably overstates the distribution (see below).

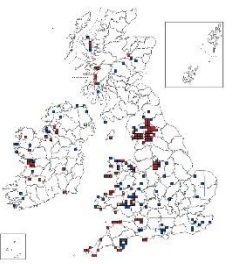
Similar in appearance to *L. borealis, L. caesioalba* and *L. alpina*, differing in the presence of alectorialic acid which is KC+ orange-pink; specimens stain collection packets red-brown after several years' storage. Records under this name made before 1992 mostly refer to the widespread *L. borealis* or *L. caesioalba***.**



Lepraria nivalis J.R. Laundon (1992) **Nb**

Thallus whitish to pale blue-grey, usually with a well-delimited margin except in heavy shade, often forming a coherent membranous crust which in well-developed specimens can be peeled away from the substratum; granules 0.06–0.2 (–0.4) mm, soft in appearance and sometimes poorly defined, medulla present; underside sometimes with sparse, brown hyphae, not forming a hypothallus. Thallus C–, K+ yellow, Pd+ red, UV– (protocetraric, and roccellic acids, atranorin). **BLS 1714**.

On acid to slightly calcareous siliceous rocks, and on limestone, sometimes on soil or overgrowing bryophytes, on surfaces sheltered from rain; often dominant and conspicuous on dry limestone cliffs, only rarely on building stone. Probably widespread in Britain and Ireland, mainly in limestone areas and near the coast, locally frequent.



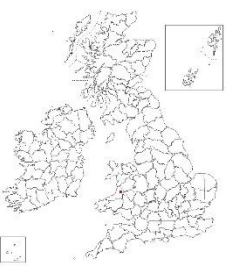
Whitish, membranous, well-delimited thalli on limestone are easily recognized in the field, but some specimens, especially in shade, are less distinctive in appearance and need to be confirmed by TLC. Although this species is often abundant on dry limestone, specimens can also be found on siliceous rocks with no apparent calcareous influence. Chemotypes with fumarprotocetraric, psoromic, stictic and roccellic acids are reported from other parts of Europe. *L. membranacea* has a different chemistry, and the thallus often has a better defined thickened margin, and is often cream in colour.

Lepraria nylanderiana Kummerl. & Leuckert (1995) **DD**

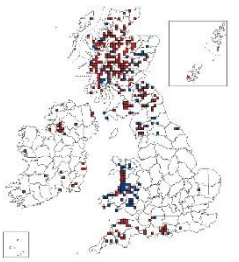
Thallus whitish to pale blue-grey, diffuse or with a weakly delimited and slightly thickened margin; granules 0.1–0.3 mm diam., soft in appearance, often poorly defined; lower part of thallus often with a poorly defined medulla. Thallus C–, K+ bright yellow, Pd+ bright yellow, UV– (thamnolic and roccellic acids, atranorin). **BLS 0936**.

On slightly calcareous cliffs in light or moderate shade in woodland. Wales (Cardiganshire: Coed Rheidol).

Similar in appearance to weakly delimited specimens of *L. nivalis*, which differs in the Pd+ red thallus (protocetraric acid). *L. umbricola* also contains thamnolic acid, but the thallus is diffuse, green, and it grows mainly on acid bark.



Lepraria rigidula (B. de Lesd.) Tønsberg (1992) **NE**



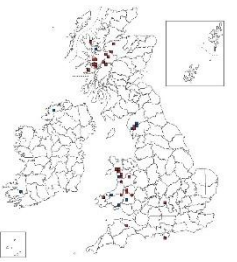
Thallus whitish grey or bluish grey, diffuse, powdery, soft, usually forming a thick, more or less continuous, irregularly spreading crust; granules 0.1–0.2 mm diam., soft in texture, with long projecting hyphae at least 60 µm long. Medulla absent. Thallus C–, K+ yellow, Pd–, UV– (nephrosteranic acid, atranorin). **BLS 1715**.

On acid bark, on a wide range of phorophytes, including both deciduous trees in semi-natural woodland and on conifers in plantations, where it is sometimes conspicuous. Also on acid rock, on surfaces sheltered from rain; frequent, but still under-recorded. Widespread in N. & W. Britain, present in Ireland.

Recognized in the field by the grey colour (less bluish than some species), and the rather coarse granules with long projecting hyphae. *L. jackii* has a similar chemistry, but the soredia (granules) are green and projecting hyphae are not or hardly present.

A host for *Monodictys epilepraria*.

Lepraria sylvicola Orange (2006) **NE**

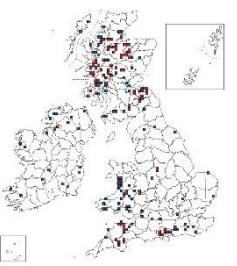


Thallus diffuse, bluish white or greenish white to pale blue-grey, powdery, granules 0.04–0.16 mm diam; medulla absent; hyphae below the thallus usually sparse, white to pale orange-brown. Thallus C–, K+ yellowish, Pd– or Pd+ yellow, UV– (roccellic, and toensbergianic acids, atranorin), hyphae below thallus K+ purple-red (anthraquinones). **BLS 2427**.

On more or less neutral or slightly acidic bark, especially frequent on mature *Quercus petraea* in seminatural woodland, also on *Fraxinus*, *Alnus*, rarely on rock in woodland; locally abundant. Wales, England, W. Scotland, Ireland.

Often the most abundant *Lepraria* in oak woodland in western Britain. *L. jackii* differs in the fatty acid content (roccellic and jackinic acids), the preference for more acidic bark or in upland overhangs, and in the absence of anthraquinones in the subthalline hyphae.

Lepraria umbricola Tønsberg (1992) **NE**



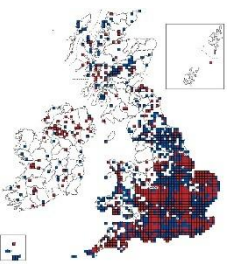
Thallus diffuse, grey-green or green to dull blue-green, finely granular, granules 0.06–0.1 mm, mostly without projecting hyphae. Medulla absent; hyphae below thallus usually sparse, sometimes abundant in cracks in the substratum, white or sometimes in part brown. Thallus and subthalline hyphae C–, K+ bright yellow, Pd+ bright yellow, UV– (thamnolic acid). **BLS 1716**.

On shaded acid bark (mainly *Quercus*, *Alnus* and *Betula*) and wood, less commonly on rocks and soil, on surfaces sheltered from rain; often in crevices and apparently requiring more humidity than other common species of the genus, but sometimes extensive on trunks in high rainfall areas, tolerant of shade. Widespread in Britain, but mainly in the north and west, under-recorded in Ireland. Some published records belong to *L. nylanderiana*.

Recognized in the field by the dull green diffuse thallus on acid substrata. *L. nylanderiana* also contains thamnolic acid, but is grey and also contains roccellic acid.

Host to *Lichenodiplis lecanorae* (Vouaux) Dyko & D. Hawksw. (1979).

Lepraria vouauxii (Hue) R.C. Harris (1987) **NE**



Thallus diffuse or with the margin slightly delimited, powdery, greenish grey, bluish white to pale blue-grey, grey, or pale cream; granules 0.08–0.18 mm diam., surface loose, with or without short projecting hyphae; medulla weakly developed, lower side of thallus often with brown hyphae forming a weakly developed hypothallus. Thallus C+ dirty yellow, K+ dirty yellow to orange, Pd+ orange or orange-yellow, UV– (pannaric acid 6-methylester, trace of pannaric acid, rarely atranorin; roccellic acid and others reported as accessories). **BLS 1604**.

On surfaces sheltered from rain, shaded or unshaded, on siliceous rocks, limestone, mortar, and bark, avoiding very acidic substrata; in semi-natural habitats and on walls. Widespread and frequent in lowland Britain, local in Scotland and Ireland, but probably under-recorded there.

The often slightly delimited margin helps to distinguish this species from others in the field, but TLC is recommended for confirmation.

SQUAMARINA Poelt (1958)

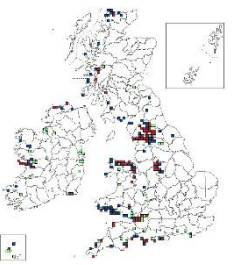
Thallus squamulose with lobed margins, often pruinose. **Cortex** thick, sharply delimited. **Photobiont** chlorococcoid. **Medulla** thick, dense, white. **Ascomata** apothecia, concave to flat or convex. **Thalline margin** distinct at first, often becoming excluded. **Disc** yellow-brown to red-brown. **Epithecium** granular. **Hamathecium** of paraphyses. **Asci** 8-spored, *Bacidia*-type. **Ascospores** aseptate, colourless. **Conidiomata** pycnidia. **Conidia** filamentous, ± curved. **Chemistry**: usnic, β-depsidones and unknown substances. **Ecology**: on soil, over mosses, or directly on rocks, almost exclusively calcicolous.

Easily distinguished from other genera of Stereocaulaceae by the large squamulose thallus.

Literature:
Feige *et al*. (1997), Seaward (2009), Timdal (1983), Zhang *et al.* (2023).

1 Thallus forming regular rosettes, central part densely pruinose; underside pale brown; medulla Pd–; very rare and probably extinct ..... ***lentigera***
Thallus not forming regular rosettes, composed of ± irregular or imbricate lobes, ± pruinose; underside dark brown; medulla Pd± yellow ..... ***cartilaginea***

Squamarina cartilaginea (With.) P. James (1980) **LC**



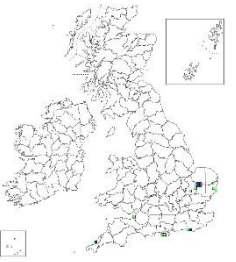
Thallus variable, yellow- to brown-green, of usually irregular to imbricate, concave to highly convex thickish squamules, strongly pruinose or not, loosely to firmly attached; lobes 1.2–2 (–2.5) mm wide. Apothecia 3(–4) mm diam.; thalline margin almost entire, becoming excluded; hymenium *ca* 70 µm tall; disc brownish to reddish brown, concave to flat, becoming irregularly convex; paraphyses slightly widened towards the apices. Ascospores (10–) 12–14 (–15) × (4–) 4.5–6 µm, cylindric-ellipsoidal. Thallus C–, K–, KC+ yellowish, Pd–; medulla Pd± yellow, UV± (usnic, ± psoromic and ± 4-O-dimethylpsoromic acids). **BLS 1337**.

On soil, mosses and hard calcareous rocks, preferring crevices of limestone cliffs and pavements, also on calcareous dunes and serpentine; locally frequent but decreasing, particularly from coastal habitats. Mainly in N. & W. Britain and Ireland.

There are two chemotypes (medulla Pd+ yellow and Pd–; with or without psoromic acid), possibly with different ecology and distribution patterns in our region. Morphs with a Pd+ yellow medulla (psoromic acid) are apparently confined to coastal sites whilst morphs with a Pd– medulla (without psoromic acid) also occur inland.

Host to *Clypeococcum psoromatis* (A. Massal.) Etayo (2010).

Squamarina lentigera (Weber) Poelt (1958) **CR C2 P Eng S8**



Thallus to 6 cm diam., circular, whitish to pale brownish green, of coherent squamules, thinly to densely pruinose, with undulate, crenate edges, upwardly curved and producing distinctive white marginal lobes, flat, 0.8–2.5 mm wide. Apothecia 1.5–2 mm diam.; thalline margin entire, at first thick but becoming thinner and almost excluded; hymenium *ca* 120 µm tall; disc pale brown, concave then convex; paraphyses slightly clavate. Ascospores 9–12 × 4–5 µm, ellipsoidal. Thallus C–, K–, KC+, Pd–, UV– (usnic acid). **BLS 1339**.

On sandy, calcareous soils and dunes; very local, declining rapidly and probably now extinct in Britain. E. England (E. Anglia, Breckland), formerly S. coast and S.W. England (Brean Down and last seen there in 1933).

An unidentified species of *Lichenoconium* has been reported from this host in Breckland.

STEREOCAULON Hoffm. (1796)

Thallus fruticose, but occasionally crust-like. **Primary thallus** crustose, flattened-areolate, squamulose, or variously warted and consisting of basal granules (phyllocladia), in most species disappearing early, in a few, predominant and persistent. **Secondary thallus** of stalked, often richly branched, shrubby, erect, rarely ± prostrate pseudopodetia. **Pseudopodetia** with a solid cartilaginous axis of parallel hyphae surrounded by a lax medulla, corticate or not, covered in wart-like, coralloid or flattened, squamule-like, corticate phyllocladia. **Tomentum** sometimes present on pseudopodetia, with colour varying from white, beige, pinkish to gray, mostly consistent within species. **Primary photobiont** trebouxioid. **Cephalodia** absent to frequent, containing *Nostoc* or *Stigonema*. **Ascomata** apothecia, terminal or lateral; disc usually becoming convex to almost globose, pale to dark brown. **Thalline margin** absent. **Exciple** raised to excluded. **Hypothecium** mostly colourless, occasionally dark brown. **Hamathecium** of paraphyses, unbranched, the apices mainly with a brown cap. **Asci** 8-spored, clavate to cylindrical, with a K/I+ blue outer layer, apical dome K/I+ blue ± with a central darker blue tube, *Porpidia*-like. **Ascospores** colourless, smooth, thin-walled, ellipsoidal, acicular or fusiform, 1- to 13-septate, rarely submuriform. **Conidiomata** pycnidia, occasional, mostly immersed at the tips of phyllocladia, ovoid to spherical, ostiole darkened. **Conidia** aseptate, thread-like to cylindrical, straight or curved. **Chemistry**: atranorin (K+ yellow) present in all species, orcinol and β-orcinol depsides and depsidones, fatty acids present in certain species. **Ecology**: mostly upland on siliceous rocks, particularly recent volcanic rock, on metal-rich spoil heaps (particularly those containing lead), on acid soil, shingle, amongst mosses on the ground and on brick.

There are two groups recognized; (1) with the primary thallus persistent and not producing pseudopodetia and (2) with the primary thallus soon disappearing but with pseudopodetia bearing phyllocladia. There are different types of cephalodia, each species having its own identifiable type. The morphology and coloration of cephalodia in this genus vary, with coloration influenced by the genus of associated cyanobacteria. The specificity of the relationship between cyanobacteria within cephalodia and *Stereocaulon* species is currently under investigation. Phyllocladia can be windowed or not, that is, with a central darkened area of gelatinized and translucent hyphae that presumably functions to allow light into the interior. These are often useful as a species-level character and can be recognized by having darker centres with paler margins, which sometimes become contorted. In the crustose species, particularly in the high-montane areas of late-snow-lie, it is important to seek out well-developed material for identification. Because the quantity of lichen substances varies considerably, chemical spot tests are best performed on filter paper following preliminary extraction with acetone.

Species of *Leprocaulon* (Leprocaulaceae) may be confused with *Stereocaulon* but are distinguished by the leprose primary thallus, the leprose-sorediate, floccose-tomentose granules on the pseudopodetia, the lack of ascomata, the absence of cephalodia and pycnidia, and the chemistry.

Stereocaulon botryosum Ach. (1810) and *S. paschale* (L.) Hoffm. (1796) have been incorrectly recorded from Britain and Ireland.

Literature:
Gilbert *et al.* (2009), Högnabba (2006), Högnabba *et al.* (2014), Ismed *et al.* (2018), Jørgensen & Jahns (1987), Lamb (1977, 1978), McCune *et al.* (2019).

1 Basal thallus persistent, of scattered to confluent phyllocladia or areole-like structures; pseudopodetia short (to 0.5 cm tall), inconspicuous or absent 2
Basal thallus evanescent; pseudopodetia conspicuous, often ± richly branched, sometimes dorsiventral 12

2(1) Basal thallus ± granular, often with ascending, ± fan-shaped phyllocladia, to 0.5 cm tall, the lower surfaces of which are sorediate ..... ***nanodes***
Basal thallus with areole-like structures, or ± granular, sometimes with short, cylindrical phyllocladia.....3

3(2) Basal thallus entirely of areole-like structures; phyllocladia absent; cephalodia absent or reduced 4
Basal thallus granular, with or without short phyllocladia; cephalodia present.....9

4(3) Areoles to 4 mm diam.; soredia absent; apothecia forming blackberry-like aggregates; ascospores 12–20 × 4–6 µm, 1-septate; on soil ..... ***cumulatum***
Areoles mostly ≤ 1 mm diam; soredia present; apothecia simple; ascospores (1-) 3- to 7-septate or submuriform; on rock 5

5(4) Medulla Pd–, soralia UV+ ice-blue (lobaric acid) 6
Medulla Pd+ orange, thallus and soralia UV not ice-blue (sometimes whitish or yellowish; stictic acid) 7

6(5) Thallus developing as small granular areoles, later forming confluent cracked patches, uniformly coloured, mostly without darker centres (not windowed); spores <30 µm long..... ***urceolatum***
Thallus of separate windowed areoles (with darker centres and paler margins), sometimes later becoming compound and convex clusters; spores >30 µm long ..... ***leucophaeopsis***

7(5) Areoles not windowed, mostly simple and separate and uniform in colour; soralia developing marginally or in cracks; ascospores submuriform to muriform, 20–32 × 10–15 µm..... ***plicatile***
Areoles windowed with darker spots, though sometimes these are small and contorted; soralia marginal or involving the whole areole surface; spores transversely septate, 1- to 3-celled 8

8(7) Areoles mostly simple and separate; epithecium POL– ..... ***tornense***
Areoles mostly compound, lobed and strongly convex with punctiform or contorted darker spots (windows); epithecium POL+ ..... ***cephalocrustatum***

9(3) Soredia present on phyllocladia or pseudopodetia; on rock 10
Soredia absent; on soil 11

10(9) Phyllocladia flattened, sorediate below; pseudopodetia to 1 mm tall, without soralia at the tip .. ***nanodes***
Phyllocladia wart-like or cylindrical, rarely branched; soralia absent on the phyllocladia but a terminal soralium present on pseudopodetia; pseudopodetia 2–5 mm tall ..... ***pileatum***

11(9) Cephalodia scabrid, dark reddish brown to blackish brown, containing *Stigonema* ..... ***condensatum***
Cephalodia smooth, pale bluish grey, brownish violet or pinkish white, containing *Nostoc* ..... ***glareosum***

12(1) Phyllocladia peltate, windowed (with a well-defined darker grey-green zone in the centre) 13
Phyllocladia not peltate, without windows 14

13(12) Pseudopodetia erect, to 4 cm high, not dorsiventral, Pd+ orange..... ***vesuvianum***
Pseudopodetia ± prostrate, <1.5 cm high, dorsiventral, Pd± pale yellow ..... ***symphycheilum***

14(12) Soredia present 15
Soredia absent 16

15(12) Pseudopodetia dorsiventral, Pd+ orange; phyllocladia and terminal branches flattened, soredia on lower surfaces and edges ..... ***spathuliferum***
Pseudopodetia thin and fragile, not dorsiventral, Pd± yellow; phyllocladia and terminal branches not flattened; lateral branches often with terminal granular ± globose soralia ..... ***delisei***

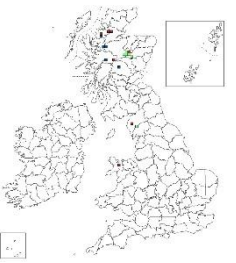
16(14) Apothecia mostly on lateral branches, small and abundant; thallus UV–, Pd+ orange (stictic acid) 17
Apothecia terminal, large, rare or absent; thallus UV+ white, Pd± pale yellow (lobaric acid).....18

17(16) Lower surface of pseudopodetia thickly grey-tomentose; phyllocladia mostly flattened and squamule-like .....***tomentosum***
Lower surface of pseudopodetia usually without tomentum; phyllocladia coralloid-elongate and finger-like .....***dactylophyllum***

18(16) Pseudopodetia without tomentum below; on bare rock .....***evolutum***
Pseudopodetia distinctly tomentose below; terricolous or on humus covered rock 19

19(17) Tomentum ash-grey; cephalodia rare .....***saxatile***
Tomentum pinkish white; cephalodia frequent but often hidden in tomentum .....***alpinum***

Stereocaulon alpinum Laurer (1827) **NT**



Primary thallus evanescent; pseudopodetia to 1(–3) cm tall, dorsiventral, decumbent or erect, sparingly branched, forming low, flat cushions, lower part and undersurface with a distinct pink tomentum; phyllocladia to 0.5 mm diam., whitish grey, granular or finger-like and attached together at the base, flattened, often crowded, particularly towards the apices, but absent on the lower surface; cephalodia frequent on the lower surface concealed in the tomentum, hemispherical, purple, often grey-white tomentose, containing *Nostoc*. Apothecia terminal; disc dark brown, not observed in British material; hypothecium colourless. Thallus K+ yellow, KC+ violet, Pd+ faintly yellow, UV+ white (atranorin and lobaric acid). **BLS 1350**.

On stony ground or short mossy turf on exposed mountain summits and ridges; rare. N. Scotland (Highlands).

Characterized by the pink tomentum and pale cephalodia on the lower surface of the dorsiventral pseudopodetia and the tendency to grow amongst mosses on the ground. Stunted morphs are often difficult to separate from *S. saxatile*, which has a grey tomentum and rarely has cephalodia.

There is some taxonomic confusion about this taxon, with *Nostoc* in cephalodia and pinkish tomentum also appearing in *S. saxatile*.

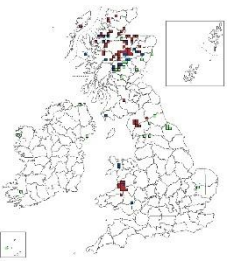
Stereocaulon cephalocrustatum McCune, E. DiMeglio & Tønsberg (2019) **NE**

Primary thallus crustose, areolate, podetia not developed; areoles soon convex or bullate, to 1.0 mm diam but becoming compound and then to 3 mm diam. or more, roundish or irregular, often slightly lobate; upper surface whitish, not pruinose, usually with one or more darker (pale greenish to dark olive) spots (windows) that are punctiform to elongate or irregularly expanded; cortical granules dissolving instantly in K with faint yellow diffusion; algal layer discontinuous; hypothallus not differentiated; soralia sometimes present, laminal or marginal; cephalodia mostly 0.3–1.0 mm diam., blackish, containing *Stigonema*. Apothecia to 1.5 mm diam. or more, roundish, sessile, dark brown to black, the margin initially distinct and raised, exciple dark brown within, somewhat paler near the edge, radiate, POL+; epithecium orangish brown, with brownish POL+ granules; hymenium 90–100 µm tall, colourless; hypothecium dark brown with K+ yellow diffusion, K/I– but bluish above; paraphyses slender, coherent at tips in water, *ca* 1 µm diam, the tips expanded to about 3 µm diam. Ascospores colourless, fusiform, (1- to) 3-septate, (17.5–) 20–25 × 4–6 (–7) µm. Conidiomata not seen. Chemistry: cortex K+ yellow; medulla K+ yellow, C–, KC–, P+ orange, UV ± whitish or yellowish; TLC: atranorin, stictic acid and associated compounds. **BLS 2915**.

On hard siliceous rocks and pebbles and mosses over rocks in areas of late snow lie, montane; rare. N. and W. Scotland (Highlands). Apothecia and cephalodia so far not observed in British material.

Distinguished by typically compound, contorted and strongly convex clusters of areoles to 3(–5) mm diam., convoluted usually with tiny darker patches representing punctiform or contorted windows – these give the distinct impression of tiny brains. When immature, difficult to distinguish from well-developed *S. plicatile* or *S. tornense* as development of windows is not consistent. An entity with smaller spores and POL– apothecia appears morphologically otherwise indistinguishable but with different ITS sequence.

Stereocaulon condensatum Hoffm. (1796) **Nb**



Primary thallus persistent, a basal crust of warted or cylindrical grey or sometimes bluish phyllocladia; cephalodia 0.5–1 mm diam., hemispherical, with a rough surface, dark reddish brown to black, frequently interspersed amongst the phyllocladia, also on pseudopodetia, containing *Stigonema*; pseudopodetia to 1 (–2) cm tall, infrequent or absent, erect, unbranched or sparingly branched, ± tomentose above with ± warted, occasionally incised, squamulose phyllocladia. Apothecia 1–2 mm diam., rather frequent, terminal on pseudopodetia or on basal phyllocladia; hypothecium colourless. Thallus K+ yellow, KC+ violet, Pd+ faintly yellow, UV+ white (atranorin and lobaric acid). **BLS 1351**.

On sandy and gravelly soil in montane situations, also at lower altitudes on acid, coastal heaths and on metal-rich soils; locally common. Scotland (Highlands & N.E. coast), Cumbria and Wales; formerly E. England (E. Anglia, N.E. Yorkshire, Durham).

See also *S. glareosum*. Occasionally infected by *Catillaria stereocaulorum* whose apothecia are smaller with aseptate or uniseptate spores. *Polycoccum trypethelioides* (Th. Fr.) R. Sant. (1960) also occurs on some thalli, and *Paranectria alstrupii* Zhurb. (2009) has been found in Easterness.

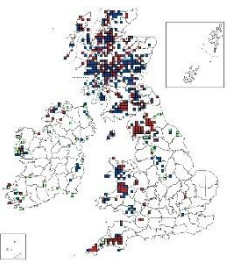
Stereocaulon cumulatum (Sommerf.) Timdal (2002) **Ex**

Thallus squamulose; squamules to 4 mm diam., scattered or forming a continuous crust, flat to weakly convex, crenulate to lobate; upper surface greyish white to medium grey, not pruinose, dull, lacking fissures and pseudocyphellae, edge concolorous with the upper side; upper cortex 20–30 µm thick, poorly developed, packed with crystals which dissolve in K, K+ yellow; lower cortex poorly developed or absent; photobiont zone continuous; medulla containing crystals dissolving in K, K+ yellow; pseudopodetia and cephalodia absent. Apothecia to 0.3 (–0.5) mm diam., marginal on the squamules when young, soon forming large (to 3 mm diam.) agglomerations between the squamules, flat to weakly convex, dark brown, not pruinose; exciple persistent but usually indistinct from above, brown in the inner part, dark brown at the rim, containing crystals dissolving in K, K+ yellow, N–; epithecium brown, lacking crystals, K–, N–; hymenium 40–60 µm tall, colourless to pale brown; hymenium I–. Ascospores 12–20 × 4–6 µm, 1-septate, ellipsoidal to fusiform. Thallus K+ yellow, KC+ violet, Pd+ faintly yellow, UV+ white (atranorin and lobaric acid). **BLS 1419**.

On soils associated with base-rich schistose rocks, montane; possibly extinct in Britain, last collected in the 19th century. N. Scotland (S. Aberdeenshire, Ben Avon).

Distinguished by the blackberry-like fruits and 1-septate ascospores. Resembles *Hertelidea botryosa*, which has a granular-areolate thallus, mostly aseptate, rarely 1-septate, ascospores and occurs on wood and old bark of *Pinus*.

Stereocaulon dactylophyllum Flörke (1819) **LC**



Primary thallus evanescent; pseudopodetia 1–4 (–6) cm in length, erect or horizontally spreading and often forming tufts, irregularly branched, grey to greenish white, usually without a tomentum on the lower surface, very rarely slightly tomentose towards the base of young branches, not dorsiventral; phyllocladia to 1 mm in length, cylindrical, branched and becoming coralloid and elongate, not confluent but occasionally forming crust-like masses; cephalodia to 0.3 mm diam., inconspicuous and infrequent, occasionally absent, rough, brownish grey, containing *Stigonema*. Apothecia frequent, small, terminal on short, lateral branches; disc brown-black; hypothecium colourless. Ascospores 25–32 × 3–3.5 µm, cylindrical to cylindric-fusiform, mostly 3-septate. Thallus K+ yellow, KC–, Pd+ orange, UV– (atranorin, stictic acid, ± norstictic acid). **BLS 1352**.

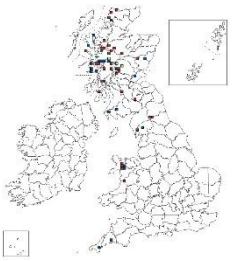
Firmly attached to siliceous, sometimes metal-rich rocks; frequent. Throughout Britain and Ireland, except central, S. & E. England.

Characterized by the finger-like, much-branched phyllocladia, the tendency to form compact cushions covered with brown-black apothecia and the Pd+ orange reaction (stictic acid). For separation from *S. evolutum*, see that species. Occasionally infected by *Catillaria stereocaulorum* whose apothecia are smaller with aseptate or uniseptate spores, as well as by *Polycoccum trypethelioides*.

S. dactylophyllum var. **occidentale** (H. Magn.) Grummann (1963) [map right, **BLS**

1353] forms small, tight cushions of dark grey, flattened phyllocladia with rounded margins on siliceous rocks and walls in E. Scotland. It seems to be rare, and its status is not properly understood.

Stereocaulon delisei Bory ex Duby (1830) **NT IR**

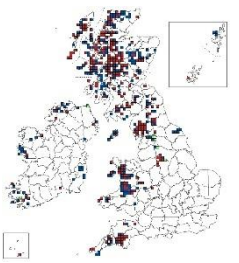


Primary thallus evanescent; pseudopodetia 1–1.5 (–3) cm tall, thin, fragile, not dorsiventral, whitish grey, loosely tufted, often forming patches a few cm in diam., sparingly branched above, sometimes slightly tomentose; phyllocladia infrequent, flattened, ± squamulose, soon becoming sorediate; terminal, granular sorediate masses frequent; cephalodia and apothecia rare. Thallus K–, KC–, Pd± yellow, UV– (atranorin, rangiformic and norrangiformic acids). **BLS 1354**.

On siliceous rocks in upland sites, often associated with heavy metals at old mining sites; local. N. and S.W. England, N. Wales, Scotland (especially N. and W.).

Characterized by the conspicuous terminal granular sorediate masses, the flattened phyllocladia and Pd– reaction. Sorediate morphs of *S. vesuvianum* differ in having peltate phyllocladia with darkened centres and are Pd+ red. See also *S. spathuliferum*.

Stereocaulon evolutum Graewe (1865) **LC**



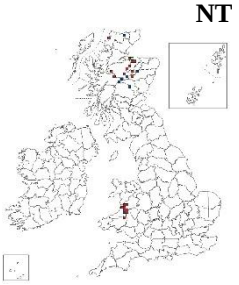
Primary thallus evanescent; pseudopodetia 1–3 cm tall, grey, arched or prostrate at least at the apices, forming compact cushions to 6 cm diam., irregularly branched from the base, dorsiventral; phyllocladia flattened, deeply divided into ± cylindrical extensions, often overlapping and concealing pseudopodetia, the lower surface glabrous; cephalodia indistinct, containing *Stigonema*. Apothecia terminal, large, rare or absent; hypothecium colourless. Thallus K+ yellow, KC+ violet, Pd+ faintly yellow, UV+ white (atranorin and lobaric acid). **BLS 1355**.

Loosely attached to bare siliceous rocks, sometimes amongst mosses; locally frequent. Throughout Britain and Ireland, except central, S. & E. England.

Characterized by the arching, dorsiventral stems, the flattened, deeply divided phyllocladia and the glabrous lower surface. *S. saxatile* has a grey-tomentose lower surface and is mainly restricted to high altitudes on Scottish mountains. When stunted, it can be distinguished from stunted morphs of *S. dactylophyllum* by the Pd–, KC+ violet reactions (best carried out on an acetone extract on filter paper).

Host to *Arthonia stereocaulina* (q.v.), *Catillaria stereocaulorum* and an unidentified *Sphaerellothecium* (from Easterness and Sutherland).

Stereocaulon glareosum (Savicz) H. Magn. (1926) **NT**



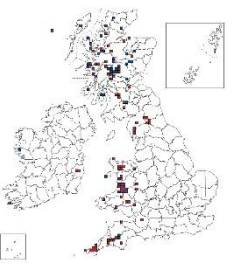
Like *S. condensatum* but usually taller (to *ca* 2.5 cm), with conspicuous, sparingly branched pseudopodetia which are grey-tomentose on their lower surfaces and have smooth, pale bluish brown, brownish violet or pinkish white cephalodia (containing *Nostoc*) amongst basal phyllocladia and on pseudopodetia. Apothecia rare; hypothecium colourless. Thallus K+ yellow, KC+ violet, Pd+ faintly yellow, UV+ white (atranorin and lobaric acid). **BLS 1356**.

On sandy or gravelly soil; rare. Mid Wales, Scotland (N. & C. Highlands).

Characterized by the smooth, pale cephalodia that contain *Nostoc*, but otherwise often difficult to distinguish from *S. condensatum*.

Host to *Catillaria stereocaulorum* and *Polycoccum trypethelioides*.

Stereocaulon leucophaeopsis (Nyl.) P. James & Purvis (1985) **Nb**



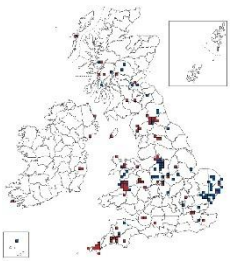
Primary thallus crustose, areolate, the areoles scattered to contiguous, to 1 mm diam., grey, spreading, with slightly tumid margins and a darker central area, remaining conspicuous especially when wet; soralia, when present, usually confined to the margins of the areoles; pseudopodetia and cephalodia absent, but cyanobacteria are often abundant between the areoles. Apothecia rather frequent, developing from between the thalline areoles; disc to 1.5 mm diam., black; epithecium brown, POL+; hypothecium dark brown. Ascospores (25–) 30–38 (–40) × 6–7 µm, 3- to 5-septate, cylindric-clavate with one end ± tapered, rarely fusiform. Thallus K+ yellow, KC+ violet, Pd+ faintly yellow, UV+ ice-blue (atranorin and lobaric acid). **BLS 1639**.

Usually on metal-rich rocks, occasionally on calcareous substrata, upland; very local. Mainly W. Britain, with a few records from Ireland.

Characterized by the basal peltate areoles with dark centres which resemble the basal phyllocladia in young material of *S. vesuvianum*, which, however, produce pseudopodetia. Distinguished from *S. tornensis* in the restriction of soredia to the margins of the areoles and the presence of lobaric acid and atranorin giving Pd+ pale yellow, UV+ ice-blue reactions.

An unidentified *Arthonia* has been reported on this host from Ceredigion (apothecia 0.1–0.15 mm diam.; hypothecium dark brown; spores 1-septate, 8.5–10.7 × 4–4.5 µm).

Stereocaulon nanodes Tuck. (1859) **Nb**

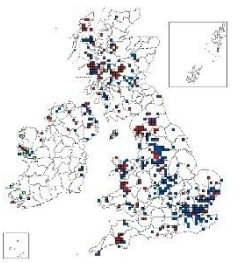


Primary thallus persistent, of ascending to erect flattened phyllocladia, to 0.5 cm tall, grey, scattered or forming swards, at first widened at the apices and appearing fan-shaped, later becoming irregularly branched in one plane; lower surface sorediate; pseudopodetia to 1 cm tall, rather rare, sparingly branched, the branches flattened, sorediate below; soredia occasionally delimited in ± globular soralia; cephalodia infrequent, bluish grey, on pseudopodetia and amongst basal phyllocladia. Apothecia very rare; hypothecium colourless. Thallus K+ yellow, KC+ violet, Pd+ faintly yellow, UV+ white (atranorin and lobaric acid). **BLS 1357**.

On sheltered rocks, often in rather damp situations, particularly frequent on old mine spoil heaps associated with lead and zinc deposits, also on roadside walls in urban areas and associated with iron railings in churchyards; rather frequent. Throughout Britain except for the far north of Scotland, a few records from Ireland.

Characterized by the persistent, basal, ± erect and flattened phyllocladia, which have sorediate lower surfaces. *S. pileatum* has wart-like basal phyllocladia and the short pseudopodetia bear terminal globose soralia.

Stereocaulon pileatum Ach. (1810) **LC**

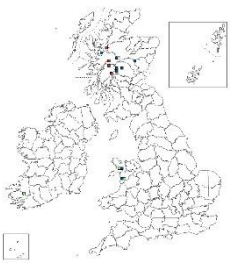


Primary thallus persistent, of grey ± wart-like granular basal phyllocladia to 3 mm diam., spreading irregularly on rock; soredia absent; pseudopodetia 2–5 mm tall, mostly unbranched, with a terminal globose soralium; phyllocladia infrequent, wart-like or cylindrical, sometimes branched; cephalodia forming granular to hemispherical warts, grey- to violet-brown, amongst basal phyllocladia and on pseudopodetia, containing *Stigonema*. Apothecia rare, disc red-brown; hypothecium colourless. Thallus C–, K+ yellow, KC+ violet particularly the sorediate tips, Pd+ faintly yellow, UV+ white (atranorin and lobaric acid). **BLS 1359**.

On damp, siliceous rocks, particularly on loose stones, often on mine spoil heaps, also on basalt, brick and road-side walls in industrial and urban areas; rather frequent. Throughout Britain and Ireland.

Characterized by the persistent wart-like basal phyllocladia and small pseudopodetia with terminal, globose soralia. *S. nanodes* has flattened phyllocladia, which are sorediate below.

Stereocaulon plicatile (Leight.) Fryday & Coppins (1996) **NT IR**



Thallus crustose, thin, areolate, areoles 0.2–0.6 mm diam., confluent to scattered, whitish to grey, matt to slightly glossy, a few rarely with darker centres; prothallus rather indistinct, black; soralia arising from cracks, discrete, somewhat confluent, pale green to bluish-green or brown; pseudopodetia absent, cephalodia also absent (at least in British material). Apothecia (0.2–) 0.6–1.2 (–1.6) mm diam., ± sessile, developing from between the thalline areoles, blackish with a brownish tinge (especially when wet), not pruinose, orbicular, persistently flat to slightly convex; exciple persistent, brownish black in the rim, inner part paler brown, containing crystals dissolving in K, pigment K–, upper edge POL+; epithecium brown, K–, POL+; hymenium colourless but slightly I+ blue around the asci; hypothecium dark brown, K–. Ascospores 20–32 × 10–15 µm, submuriform to muriform with 3–7 transverse septa and 1 (very rarely 2) longitudinal septum, remaining colourless. Conidia 14–18 (–22) × 0.5–0.7 µm, colourless, filiform, curved. Medulla K+ yellow, KC–, Pd± faint yellow; soralia K+ yellow, Pd+ orange, UV– (atranorin and stictic acid). **BLS 1269**.

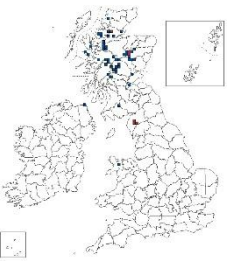
On hard siliceous rocks and pebbles, montane; rare. N.W. England (Cumbria), N. Wales (Snowdon range), N.

Scotland (Highlands).

Distinguished by the persistently areolate primary thallus and colourless, ± muriform ascospores. When sterile, difficult to distinguish from *S. tornense*.

Merismatium coccisporum (Norman) Vouaux (1913) has been reported on this host from Glen Coe.

Stereocaulon saxatile H. Magn. (1926) **Nb**

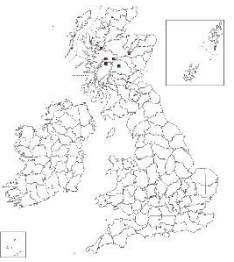


Primary thallus disappearing; pseudopodetia 1–2 cm long, ± firmly attached, forming dense, prostrate colonies to 7 cm across, stout, dorsiventral, with ash-grey to pinkish tomentum towards the apices, richly branched in the upper part; phyllocladia abundant, dark grey, sometimes confluent, almost completely covering pseudopodetia, flat to convex, deeply incised at the margins, appearing ± digitately squamulose; cephalodia rare, inconspicuous, containing *Stigonema* or *Nostoc*. Apothecia rare, terminal; hypothecium colourless. Thallus K+ yellow, KC+ violet, Pd+ faintly yellow, UV+ white (atranorin and lobaric acid). **BLS 1360**.

On gravelly soil in high gullies, on mountain summits or associated with areas of late snow lie; locally frequent. N. England (Cumbria), N. Scotland (Highlands), single records from N. Wales and N. Ireland.

Characterized by the dorsiventral pseudopodetia covered in a grey tomentum and the flattened, digitate, squamule-like phyllocladia. *S. tomentosum* also has a grey tomentum, but is Pd+ orange. Further taxonomic work is required to clarify the circumscription of this species, especially in Britain and Ireland in relation to *S. alpinum*.

Stereocaulon spathuliferum Vain. (1909) **NT**

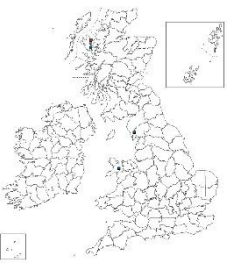


Primary thallus evanescent; pseudopodetia 1–3 cm tall, dorsiventral, irregularly branched, terete and thickened basally with ± flattened, mainly decorticate, pale grey-white side branches; phyllocladia wart–like or flattened, with spathulate apical extensions, the lower surface often coarsely granular-sorediate, occasionally terminal, ± globose soralia may also occur, the upper surface usually with some phyllocladia spreading over the surface of pseudopodetia in interlocking areoles; cephalodia mostly distinct, bluish grey, usually stalked and uneven, containing *Nostoc*. Apothecia terminal, not observed in British material; hypothecium colourless. Thallus K+ yellow, KC–, Pd+ orange, UV– (atranorin, stictic acid). **BLS 1361**.

On damp rocks in the vicinity of waterfalls or by persistent snow patches in montane situations; very rare. N. Scotland (Highlands).

Differs from *S. delisei* which is Pd± yellow, has globular, terminal soralia on lateral branches and in which the pseudopodetia are not dorsiventral.

Stereocaulon symphycheilum I.M. Lamb (1961) **EN**



Primary thallus evanescent; pseudopodetia to 1.5 cm, ± prostrate, dorsiventral, sparingly branched, firmly attached to rock, without tomentum; phyllocladia on the upper side of pseudopodetia, grey-green, peltate, with pale wavy and swollen margins and a darker centre, often concave; soralia terminal, ± globose; cephalodia dark brown-black, with a roughened surface, containing *Stigonema*, commonly on the lower surface of the pseudopodetia and on the substrate between basal phyllocladia. Apothecia terminal, rare; hypothecium colourless. Thallus K+ yellow, KC+ violet, Pd+ faintly yellow, UV+ white (atranorin and lobaric acid). **BLS 1680**.

On rocks often containing heavy metals, in montane situations; rare. N.W. England (Lake District, Coniston), Wales (Snowdonia), N.W. Scotland (Skye).

British specimens are poorly developed, lacking well-defined terminal soralia. Characterized by the flattened phyllocladia with darkened centres and the presence of lobaric acid (Pd− or pale yellowish, UV+ white). *S. vesuvianum* tends to be more erect, is Pd+ orange, UV– and does not have basal, ± flattened phyllocladia bearing soredia, frequently interspersed with cephalodia.

Stereocaulon tomentosum Fr. (1824) **Ex**

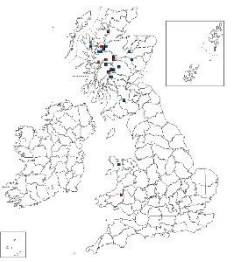
Primary thallus evanescent; pseudopodetia to 3 cm tall, prostrate or erect, loosely attached, dorsiventral, the lower surface thickly grey-tomentose; phyllocladia wart-like or flattened and ± squamulose, grey without darkened

centres, overlapping and thickly covering the pseudopodetia; soredia absent; cephalodia indistinct, containing *Nostoc*, concealed in the tomentum of the lower surface. Apothecia 0.3–0.6 mm diam., rather frequent, on short side branches; hypothecium colourless. Thallus K+ yellow, KC–, Pd+ orange, UV– (atranorin, stictic and ± norstictic acids). **BLS 1362**.

In gravelly situations in heaths; extinct in Britain and Ireland. Formerly at several sites in E. Scotland (Angus and Fife).

Characterized by the dorsiventral podetia, grey tomentose lower surface and abundant small apothecia. The Pd+ orange reaction distinguishes it from *S. saxatile*.

Stereocaulon tornense (H. Magn.) P. James & Purvis (1985) **NT**



Primary thallus crustose, areolate; areoles scattered or confluent, to 0.5 mm diam., grey, with tumid, raised margins and a small darker central area which is sometimes obliterated by the margins even when wet; soralia, when present, involving the whole surface of an areole; pseudopodetia and cephalodia absent, although cyanobacteria are often abundant between the areoles. Apothecia rather frequent, developing from between the thalline areoles; disc to 1.5 mm diam., black; epithecium brown, POL–; hypothecium dark brown, POL–. Ascospores (18–) 21–25 (–30) × 5–8 µm, (1-) 3-septate, regularly fusiform with equally rounded apices. Medulla K+ yellow, KC–, Pd± faint yellow; soralia K+ yellow, Pd+ orange, UV– (atranorin and stictic acid). **BLS 1681**.

On pebbles in turf, especially associated with persistent snow patches; rare. Wales (Snowdonia, Cardigan), N. Scotland (Highlands).

Characterized by the swollen areoles with dark centres. Distinguished from *S. leucophaeopsis* by the tendency of individual areoles to dissolve into convex, finely granular soralia (somewhat resembling those in the apices of the pseudopodetia of *S. pileatum*) and the Pd+ orange (not yellow), UV– thallus.

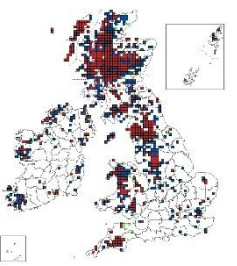
Stereocaulon urceolatum (P.M. Jørg.) Högnabba (2006) **NE**

Primary thallus crustose, areolate, with individual areoles granular, convex and often confluent into cracked patches up to 5 mm diam., dispersed over the substratum, and with thallus subtended by an extensive cyanobacterial hypothallus-like mat; upper surface of areoles breaking into crater-like sorediate patches. Apothecia rare, developed from between areoles under a small flap of tissue, breaking open with a star-like opening when young (angiocarpic), disc up to 0.5 mm wide, becoming urceolate with a raised margin, black; upper part of subhymenium brown, K+ intensifying, resting on a colourless obconical-shaped hypothecium; paraphyses with brown-capped, externally pigmented apical cells to 3–5 µm diam.; ascospores 1- to 3-septate, 20–28 × 6–8 µm. Cortex K+ yellow (atranorin), medulla K–, P–, UV+ ice-blue (lobaric acid). **BLS 2910.**

On siliceous moist rocks or rock walls, known mainly in lowland sheltered humid habitats; rare. Scotland (Eigg).

In other parts of this species range, it is known from sheltered rock walls and moist woodlands up to 800 m, where sorediate forms are more likely in exposed situations, contrasting with more scattered and less sorediate areoles in shaded sites. The star-like development of apothecia is distinctive.

Stereocaulon vesuvianum Pers. (1811) **LC**

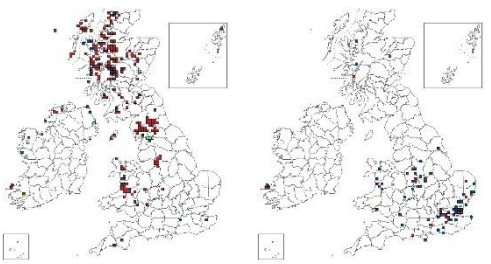


Primary thallus soon evanescent; pseudopodetia to 1.5 (–4) cm tall, erect or decumbent, often forming compact tufts, richly branched or unbranched, ± woody at the base, grey-white, tomentum absent; phyllocladia wart- or shield-like, occasionally becoming flattened or concave, sparse or crowded, at least some, particularly those in shade, with green-grey central parts surrounded by a paler grey-white, often swollen and ± crenulate margin; soredia occasionally present in terminal, ± globose soralia at the apices of erect pseudopodetia which in their upper parts mostly lack phyllocladia; cephalodia rare, verrucose, dark olive-brown to black, containing *Stigonema*, more abundant on lower parts of branches. Apothecia 0.5–1 mm diam., rare, on lateral branches; hypothecium colourless. Thallus K+ yellow, occasionally K+ red forming crystals, KC–, Pd+ orange, UV– (atranorin, stictic and ± norstictic acids). **BLS 1363**.

Mostly firmly attached to well-lit siliceous rocks, including those containing heavy metals, on tarmac, also colonizing walls and brick near towns; frequent, especially in the north and west. Throughout Britain and Ireland.

Very variable and best characterized by the wart-like to peltate phyllocladia with dark grey centres and paler margins (generally best observed on the lower parts of the podetium), though these may be sometimes difficult to find and may be absent. Tolerant of sulphur dioxide pollution and extending to lowland England on man-made substrata. Cephalodia are rare to absent in areas with high nitrogen pollution (esp. England, Wales and Southern Scotland), but apothecia become more frequent in such situations. Sorediate morphs may resemble *S. delisei*, but in that species phyllocladia lack dark centres and are Pd–. *Leprocaulon* species are K–.

In **S. vesuvianum** var. **nodulosum** (Wallr.) I.M. Lamb (1969) [**BLS 1364**; map left] the pseudopodetia are loosely clustered, unbranched, upper parts naked, each terminated with a small globose soralium. On hard siliceous rocks, montane; occasional in England and Wales and there apparently associated with heavy metal-rich rocks. N. & W. Britain and Ireland.



In **S. vesuvianum** var. **symphycheileoides** I.M. Lamb (1975) [**BLS 1598**; map right] the primary thallus is persistent, of pale-edged squamules, pseudopodetia are very short, 2–3 (–4) mm tall, terminated by granular soralia. On wall tops, headstones etc. in urban areas and in mine sites and other post-industrial habitats; locally frequent. England (S.E. & Midlands), Wales, a few records in Scotland and S.W. Ireland.

Literature

Ekman, S. & Tønsberg, T. (2002). Most species of *Lepraria* and *Leproloma* form a monophyletic group closely related to *Stereocaulon*. *Mycological Research* **106**: 1262–1276.

Feige, G.B., Röser, G. & Lumbsch, H.T. (1997). Chemotaxonomic studies of European *Squamarina* species (Ascomycotina: Lecanorales). *Bibliotheca Lichenologica* **67**: 25–31.

Gilbert, O.L., Purvis, O.W. & Smith, C.W. (2009). *Stereocaulon*. In *Lichens of Great Britain and Ireland* (Smith, C.W., Aptroot, A., Coppins, B.J., Fletcher, A., Gilbert, O.L., James, P.W. & Wolseley, P.A. eds): 858–865. London: British Lichen Society.

Hodkinson, B.P. & Lendemer, J.C. (2013). Next-generation sequencing reveals sterile crustose lichen phylogeny. *Mycosphere* **4**: 1028–1039.

Högnabba, F. (2006). Molecular phylogeny of the genus *Stereocaulon* (Stereocaulaceae, lichenized ascomycetes). *Mycological Research* **110**: 1080–1092.

Högnabba, F., Pino-Bodas, R., Nordin, A., Myllys, L. & Stenroos, S. (2014). Phylogenetic position of the crustose *Stereocaulon* species. *Lichenologist* **46**: 103–114.

Ismed, F., Lohézic-Le Dévéhat, F., Guiller, A., Corlay, N., Bakhtiar, A. & Boustie, J. (2018). Phytochemical review of the lichen genus *Stereocaulon* (Fam. Stereocaulaceae) and related pharmacological activities highlighted by a focus on nine species. *Phytochemistry Reviews* **17**: 1165–1178.

Jorgensen, P.M. & Jahns, H.M. (1987). *Muhria*, a remarkable new lichen genus from Scandinavia. *Notes from the Royal Botanic Garden Edinburgh* **44**: 581–599.

Kantvilas, G. (2009). *Hertelidea*. In *Lichens of Great Britain and Ireland* (Smith, C.W., Aptroot, A., Coppins, B.J., Fletcher, A., Gilbert, O.L., James, P.W. & Wolseley, P.A. eds): 429–430. London: British Lichen Society.

Kantvilas, G. & Elix, J.A. (2006). Further notes on the genus *Hertelidea*, with a description of a new species. *Australasian Lichenology* **59**: 30–33.

Kukwa, M. (2006). The lichen genus *Lepraria* in Poland. *Lichenologist* **38**: 293–305.

Lamb. I.M. (1977). A conspectus of the lichen genus *Stereocaulon* (Schreb.) Hoffm. *Journal of the Hattori Botanical Laboratory* **43**: 191–355.

Lamb. I.M. (1978). Keys to the species of the lichen genus *Stereocaulon* (Schreb.) Hoffm. *Journal of the Hattori Botanical Laboratory* **44**: 209–250.

Laundon, J.R. (1992c). *Lepraria* in the British Isles. *Lichenologist* **24**: 315–350.

Lendemer, J.C. (2013). A monograph of the crustose members of the genus *Lepraria* Ach. s. str. (Stereocaulaceae, lichenized ascomycetes) in North America north of Mexico. *Opuscula Philolichenum* **11**: 27–141.

Lendemer, J.C. & Hodkinson, B.P. (2013). A radical shift in the taxonomy of *Lepraria* s.l.: Molecular and morphological studies shed new light on the evolution of asexuality and lichen growth form diversification. *Mycologia* **105**: 994–1018.

McCune, B., Di Meglio, E., Tønsberg, T. and Yahr, R. (2019). Five new crustose *Stereocaulon* species in western North America. *Bryologist* **122**: 197–218.

Nelsen, M.P. & Gargas, A. (2008). Phylogenetic distribution and evolution of secondary metabolites in the lichenized fungal genus *Lepraria* (Lecanorales: Stereocaulaceae). *Nova Hedwigia* **86**: 115–131.

Orange, A. (2020). *Lithocalla* (Ascomycota, Lecanorales), a new genus of leprose lichens containing usnic acid. *Lichenologist* **52**: 425–435.

Orange, A. & Laundon, J.R. (2009). *Lepraria*. In *Lichens of Great Britain and Ireland* (Smith, C.W., Aptroot, A., Coppins, B.J., Fletcher, A., Gilbert, O.L., James, P.W. & Wolseley, P.A. eds): 530–540. London: British Lichen Society.

Orange, A., Earland-Bennett, P.M., Hitch, C.J.B. & Powell, M. (2017). A new leprose *Leprocaulon* (Ascomycota, Leprocaulales) from Great Britain. *Lichenologist* **49**: 183–188.

Printzen, C. & Kantvilas, G. (2004). *Hertelidea*, genus novum Stereocaulacearum (Ascomycetes lichenisati). *Bibliotheca Lichenologica* **88**: 539–553.

Saag, L., Saag, A. & Randlane, T. (2009). World survey of the genus *Lepraria* (Stereocaulaceae, lichenized Ascomycota). *Lichenologist* **41**: 25–60.

Seaward, M.R.D. (2009). *Squamarina*. In *Lichens of Great Britain and Ireland* (Smith, C.W., Aptroot, A., Coppins, B.J., Fletcher, A., Gilbert, O.L., James, P.W. & Wolseley, P.A. eds): 851. London: British Lichen Society.

Timdal, E. (1983). The genus *Squamarina* in Scandinavia. *Lichenologist* **15**: 169–179.

Tønsberg, T. (1992). The sorediate and isidiate, corticolous, crustose lichens in Norway. *Sommerfeltia* **14**: 1–331.

Tønsberg, T. (2002). Notes on non-corticolous *Lepraria* s.lat. in Norway. *Graphis Scripta* **13**: 45–51.

Zhang, Y.-Y., Wang, L., Wang, X.-Y., Printzen, C., Timdal, E. & Wang, L.-S. (2023). *Squamarina subcetrarioides* comb. & stat. nov. (Stereocaulaceae), a separate species from the type species of *Squamarina*. *Lichenologist* **55**: 133–137.