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Lecanorales: Cladoniaceae

Cover image: *Cladonia subulata*, on the ground in fixed sand dunes, Coul Links, Sutherland, Scotland.

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

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to compile new printed editions of the entire lichen biota of Britain and Ireland is extensive, and many parts are out-of-date even as they are published.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

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Lecanorales: Cladoniaceae

including the genera *Cladonia*, *Pilophorus* and *Pycnothelia*

by

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CLADONIACEAE Zenker (1827)

Thallus usually dimorphic, composed of primary and secondary structures. **Primary thallus** evanescent to persistent, crustose or squamulose, lacking rhizoids. **Secondary thallus** (podetia) \pm vertical, usually branched (sometimes in complex patterns), hollow or rarely solid, the apices attenuated (subulate) or of cup-shaped scyphi that are sometimes perforated in the centre. **Soredia** and/or **squamules** often present, **isidia** very rare. **Photobiont** green algae (*Asterochloris* or *Chlorella*), cephalodia present only in *Pilophorus*. **Ascomata** apothecia, entire to lobate, biatorine, without a fully differentiated exciple, sometimes brightly coloured, sometimes proliferating. **Interascal tissue** of sparsely branched and anastomosed paraphyses. **Asci** cylindric-clavate, thickened at the apex, with a K/I+ blue apical cap and usually a K/I+ blue gelatinous outer layer. **Ascospores** usually aseptate and colourless. **Anamorphs** coelomycetous, pycnidial, with aseptate \pm filiform to falcate spermatial conidia.

The Cladoniaceae contains eighteen genera (Stenroos *et al.* 2019), of which *Cladonia* is by far the largest and most complex. Only three genera occur in our region, *Cladonia*, *Pilophorus* and *Pycnothelia*. Morphological structures in *Cladonia* (especially) are highly varied. Most species occur on soil, or some on rotten wood, and may form dominant mats in boreal and austral ecosystems. The Stereocaulaceae has been shown as closely related to the Cladoniaceae, and the two families were merged by Kraichak *et al.* (2018) on the basis of likely dates of phylogenetic divergence. However, they are kept separate here, following Stenroos *et al.* (2019) and Lücking (2019), as both families are monophyletic and easily distinguishable on both morphological and molecular terms.

Literature

Ahti (2000), Ahti & Stenroos (2013), Burgaz & Ahti (2009), Burgaz *et al.* (2020), Kraichak *et al.* (2018), Stenroos *et al.* (2019), Wedin *et al.* (2000).

- | | |
|------|--|
| 1 | Primary thallus squamulose, persistent or evanescent, or crustose and evanescent <i>Cladonia</i> |
| | Primary thallus crustose, always persistent 2 |
| 2(1) | Podetia hollow, swollen; cephalodia absent..... <i>Pycnothelia</i> |
| | Podetia solid, not swollen; cephalodia present <i>Pilophorus</i> |

CLADONIA P. Browne (1756)

Primary thallus squamulose (*Cladonia* morphotype), or crustose and soon evanescent (*Cladina* morphotype). **Basal squamules** (where present) closely appressed or ascending to erect, rounded to elongate, entire or variously indented, involute, occasionally sorediate, persistent or evanescent, occasionally dominant. **Upper surface** usually corticate, the cortex dense, of \pm vertical hyphae. **Lower surface** without rhizines, not corticate, usually finely arachnoid or sorediate. **Photobiont** *Asterochloris*. **Medulla** usually two-layered, the outer white, of \pm loose hyphae, containing algal cells, the inner glassy or white, cartilaginous, with conglutinate hyphae surrounding a central canal. **Secondary thallus** \pm erect, richly branched (especially the *Cladina* morphotype) or not (*Cladonia* morphotype), consisting of usually hollow podetia, growing from the margins or upper surface of primary squamules, blunt, pointed or with cup-shaped scyphi, unbranched or branched (Fig. 1); outer surface mostly corticate (not

so in species with the *Cladina* morphotype and some others), often with \pm non-corticate areas, corticate granules, soredia, microsquamules or outgrowths, or more rarely peeling, occasionally areolate; apices, scyphi and axils closed or perforate. **Ascomata** apothecia, at the apices of podetia, on cup rims or rarely \pm sessile on basal squamules. **Thalline margin** absent. **True exciple** often becoming excluded. **Hymenium** red, pale or dark brown. **Asci** elongate, clavate, thickened at the apex, 8-spored, with a K/I+ blue tholus and K/I+ strongly blue outer gelatinous sheath. **Ascospores** aseptate, colourless, fusiform, oblong or ovoid. **Conidiomata** pycnidia, at the apices of podetia, cup rims or on basal squamules, sessile or short-stalked, cylindrical to top-like. **Conidia** cylindrical to falcate, thread-like, curved, rarely straight. **Chemistry**: depsides, depsidones, dibenzofurans, terpenes, aliphatic acids and quinone pigments. **Ecology**: on soil, over mosses, on bark, wood, or soil in rock crevices, several species often forming complex, extensive communities, as on heathlands; mainly on acid humus-rich substrata, a few species on calcareous substrata.

Table 1. Characteristics of the various clades within the genus *Cladonia*. Information primarily abstracted from Stenroos *et al.* (2019). Only about 60% of species have been sequenced, and the phylogenetic relationships of those without molecular data cannot always be confirmed.

Major clade	Subclade	Morphological characteristics of GBI species	British and Irish species
<i>Arbuscula</i>		Cladina morphotype ; dichotomous or trichotomous branching, presence of perlatolic and usnic acids	<i>arbuscula</i> , <i>mitis</i>
<i>Borya</i>		Uncialis morphotype ; fairly well branched, lacking soredia and podetial squamules, chemically diverse, with terpenoid crystals at the tips of podetia	<i>zopfii</i>
<i>Cladonia</i>	<i>Ascyphiferae</i>	Cladonia morphotype ; podetia pointed or scyphose; many species with fertile podetia having split and flattened areas; chemically diverse; fumarprotocetraric acid and atranorin most common.	<i>conista</i> , <i>cyathomorpha</i> , <i>furcata</i> , <i>humilis</i> , <i>peziziformis</i> , <i>scabriuscula</i> , <i>stereoclada</i>
	<i>Callosae</i>	Cladonia morphotype ; podetia not or slightly branched, with inconspicuous fissures; contains grayanic acid.	<i>callosa</i>
	<i>Cladonia</i>	Cladonia morphotype ; species subulate or with centrally proliferating scyphi; rarely sorediate; fumarprotocetraric acid and atranorin most common	<i>caespiticia</i> , <i>cervicornis</i> , <i>pulvinata</i> , <i>subulata</i> , <i>trassii</i> , <i>verticillata</i>
	<i>Firmae</i>	Cladonia morphotype ; well-developed primary thallus, scyphose, with fumarprotocetraric acid and atranorin	<i>firma</i> , <i>subcervicornis</i>
	<i>Foliaceae</i>	Cladonia morphotype ; large primary squamules prominent and sometimes forming large rosettes or cushions; also species with dominant scyphose podetia that often produce fairly large podetial squamules; usnic acid present, also members of the fumarprotocetraric acid complex	<i>foliacea</i> , <i>phyllophora</i> , <i>ramulosa</i>
	<i>Graciles</i>	Cladonia morphotype ; with tall and slender podetia, or with broad well-developed scyphi; sorediate or fully corticate, sometimes granular; basal squamules persistent or evanescent. Fumarprotocetraric acid commonly present, also found are atranorin, homosekikaic, physodalic, psoromic, cryptochlorophaeic, paludosic, grayanic, merochlorophaeic and quaesitic acids	<i>asahinae</i> , <i>chlorophaea</i> , <i>coniocraea</i> , <i>cornuta</i> , <i>chryptochlorophaea</i> , <i>fimbriata</i> , <i>gracilis</i> , <i>grayi</i> , <i>maxima</i> , <i>merochlorophaea</i> , <i>novochlorophaea</i> , <i>ochrochlora</i> , <i>pocillum</i> , <i>pyxidata</i> , <i>rei</i>
<i>Helopodium</i>	Cladonia morphotype ; fissured/striate podetia, scyphi absent, with a persistent well-developed primary thallus; chemically diverse, atranorin, norstictic and psoromic acids are common.	<i>cariosa</i> , <i>symphyrcarpa</i>	

Major clade	Subclade	Morphological characteristics of GBI species	British and Irish species
	<i>Macropus</i>	Cladonia morphotype ; podetia with or without scyphi, basal squamules persistent, psoromic or fumarprotocetraric acids	<i>asahinae</i> , <i>macrophylla</i>
	<i>Rangiformes</i>	Cladonia morphotype ; with large, often somewhat deformed primary squamules (evanescent in <i>C. rangiformis</i> itself); podetia richly branched, squamulose. Atranorin as their major substance, rangiformic acid common	<i>rangiformis</i>
<i>Crustaceae</i>		Cladina morphotype ; podetia with anisotomic branching, either tetrachotomous or dichotomous; fumarprotocetraric acid complex and usnic acid	<i>ciliata</i> , <i>rangiferina</i> , <i>stygia</i>
<i>Erythrocarpae</i>	<i>Subglaucescentes</i>	Cladonia morphotype ; apothecia red; podetia with or without scyphi, basal squamules persistent or evanescent; with dibenzofurans and thamnolic, barbatic and didymic acids, occasionally zeorin, quite often usnic acid	<i>bellidiflora</i> , <i>borealis</i> , <i>coccifera</i> , <i>deformis</i> , <i>digitata</i> , <i>diversa</i> , <i>floerkeana</i> , <i>macilenta</i> , <i>pleurota</i> , <i>polydactyla</i> , <i>sulphurina</i>
	<i>Incrassatae</i>	Cladonia morphotype ; small, abundantly soresiate primary squamules, cylindrical and ascyphose podetia, containing usnic, didymic and squamatic acids	<i>incrassata</i>
<i>Impexae</i>		Cladina morphotype ; podetia with dichotomous or trichotomous branching patterns, with perlatolic and usnic acids	<i>mediterranea</i> , <i>portentosa</i>
<i>Ochroleucae</i>		Cladonia morphotype ; morphologically variable but with pale ochraceous apothecia; almost all soresiate or squamulose, primary squamules persistent, inconspicuous; most with usnic and barbatic acids	<i>botrytes</i> , <i>carneola</i>
<i>Perviae</i>		Cladonia morphotype ; with open podetial tips and axils, sometimes very wide and forming funnel-like scyphi with central holes; often squamulose or soresiate. Most species with squamatic and/or thamnolic acid, barbatic acid also common.	<i>cenotea</i> , <i>crispata</i> , <i>glauca</i> , <i>parasitica</i> , <i>squamosa</i> , <i>strepsilis</i>
<i>Unciales</i>		Uncialis morphotype ; podetia stiff and spiky, dichotomously or polychotomously branched, the branches abruptly tapered, containing usnic and squamatic acids or only usnic and rarely hypothamnolic acids	<i>uncialis</i>

The so-called ‘reindeer-moss lichens’, with a soon evanescent, granular, crustose primary thallus, have sometimes been assigned to a separate genus *Cladina* or as a subgenus within *Cladonia*. However, molecular phylogenetic analysis has demonstrated that this morphological type has evolved on at least three separate occasions (Stenroos *et al.* 2019), and no fewer than thirteen clades can be distinguished. The same work also shows that *Cladonia* as traditionally circumscribed is a monophyletic entity, and there is no good justification for splitting it into multiple genera.

The British records of *Cladonia acuminata* (Ach.) Norrlin (1875), *C. amaurocraea* (Flörke) Schaerer (1823), *Cladonia stellaris* (Opiz) Pouzar & Vězda (1971) and *C. turgida* Hoffm. (1796) are based on material collected last century which is now known to originate from outside the British Isles; only *C. amaurocraea* is considered likely to occur here.

Many *Cladonia* spp. are now rarer and more localized due to the disappearance or widespread degradation of heathland as well as the overall increase in eutrophication in lowland areas of Britain and Ireland.

Most species of *Cladonia* are notably polymorphic and are often difficult to identify especially in a juvenile or environmentally stressed state. Although the most relevant morphological features to

identify the species are associated with the podetia, it is also important to consider: the overall habit, dominance of either basal squamules or podetia, the extent and nature of the cortication of the podetia (e.g. *C. coniocraea*, *C. cornuta*, *C. humilis*), the presence and position of perforation of the podetia (e.g. *C. cenotea*, *C. crispata*, *C. glauca*, *C. squamosa*), and the nature of the propagules – finely sorediate (e.g. *C. fimbriata*, *C. humilis*), granular sorediate±corticate (*C. chlorophaea*, *C. scabriuscula*), or coarsely corticate-granular (*C. diversa*, *C. pyxidata*). In a few species (e.g. *C. bellidiflora*, *C. squamosa*) the algae are first contained in the cortex of the podetium which eventually peels away to form the squamules; in most other species the squamules are direct outgrowths from the podetia, containing algae at the outset. Species with red apothecia usually have a yellowish to dirty orange (K+ purple) pigment towards the base of the lower side of the squamules. Such observations given above, as well as habitat, should be combined with basic chemical tests and UV analysis, and preferably also by TLC analysis which will identify the lichen substances present. UV tests should be made on cut or abraded surfaces as cortical pigments, e.g. usnic acid, can mask UV+ bluish or white reactions. Beware of stray white light generated by the UV lamp reflecting off the very white medulla of some species; *Cladonia coniocraea* is an example where this phenomenon can be seen.

See Pino-Bodas *et al.* (2017a), Zhurbenko & Pino-Bodas (2017) and Diederich *et al.* (2018) for information on and a key to the many lichenicolous fungi inhabiting *Cladonia* species. The species known from Britain and Ireland are included in Table 2 at the end of the genus account, as almost all are not specific at species level.

Literature

Ahti (1998, 2000), Ahti & Hammer (2002), Ahti & Stenroos (2013), Athukorala *et al.* (2016), Burgaz & Ahti (2009), Burgaz *et al.* (2020), Fontaine *et al.* (2010), James (2009), Kotelko & Piercey-Normore (2010), Orange (1992), Pino-Bodas & Stenroos (2020), Pino-Bodas *et al.* (2010a, 2012a, b, 2013a, b, 2015a, b, 2017a, b, 2018), Steinová *et al.* (2013), Stenroos *et al.* (2015, 2018), Zhurbenko & Pino-Bodas (2017).

1	Some squamules present, either scattered or forming a ± continuous, persistent basal thallus and/or dispersed on podetia (<i>Cladonia</i> morphotype)	2
	Squamules present at extreme juvenile stages only or reduced to short-lived, coarse, crust-like areoles (<i>C. uncialis</i> aggr. and <i>Cladina</i> morphotype)	110
2(1)	Apothecia red, K+ purple; undersides of squamules often ± suffused orange-brown towards the base, and then K+ purple	3
	Apothecia flesh-coloured (rarely pinkish) to brown-black, K–, or absent ; undersides of basal squamules pale, grey-black or yellow-green, never K+ purple	20
3(2)	Undersides and/or margins of squamules densely sorediate	4
	Undersides and margins not sorediate	5
4(3)	Basal squamules large, >5 mm long, ± horizontal with ± ascending entire margins, underside ± strongly orange-tinted towards the base; apothecia on well-developed podetia; podetia with scyphi; K+ yellow, Pd+ yellow-orange, UV–	<i>digitata</i>
	Basal squamules small, <4 mm long, mostly erect, very crowded, margins crenate-incised; undersides pale, orange pigmentation faint or absent at the point of attachment; apothecia sessile or on short podetia (< 5 mm long) as pin-like extensions of basal squamules; K–, Pd– (very rarely Pd+ yellow), UV+ blue-white	<i>incrassata</i>
5(3)	Undersides of squamules entirely cottony-arachnoid (×20 lens), pale yellow	<i>luteoalba</i>
	Undersides of squamules smooth, whitish or yellow-green	6
6(5)	At least some podetia with well-developed scyphi	7
	All podetia subulate, scyphi absent	15

- 7(6) Podetia pale grey (usnic acid absent); scyphi often very irregular, often proliferating from the margin, entirely sorediate 8
Podetia yellow-green (usnic acid); subulate or with regular, rarely proliferating scyphi 9
- 8(7) Thallus K+ yellow→orange, Pd+ orange, UV- (thamnolic acid) *polydactyla*
Thallus K-, Pd-, UV+ white (squamic acid) *umbricola*
- 9(7) Podetia to 5 cm tall, subulate or with scyphi, surface finely sorediate, smoothly corticate at the base 10
Podetia <2 cm tall, with wide regular scyphi, subulate podetia absent; surface with corticate granules or squamules, farinose soredia 11
- 10(9) Podetia deformed, with a conspicuous lacerate fissure at the apex; with irregular scyphi and some subulate podetia; UV+ white *sulphurina*
Podetia with regular scyphi, without fissures, always with cups; UV- *deformis*
- 11(9) Podetia smoothly corticated, with corticated flat plates in and on the scyphi; with barbatic acid *borealis*
Podetia covered by granules or squamules; when corticated with verrucose cortex; without barbatic acid 12
- 12(11) Surface of podetia covered with microsquamules 13
Surface of podetia granulose or verrucose 14
- 13(12) Podetia UV+ white or K+ yellow, often with black areas at the base *straminea*
Podetia UV- & K-, without black areas at the base *diversa*
- 14(12) Podetia granulose-sorediate with cortex restricted to the base *pleurota*
Podetia corticate, cortex verrucose *coccifera*
- 15(6) Podetia partially to totally sorediate 16
Podetia not or rarely very sparingly sorediate 19
- 16(15) Podetia yellow-green (usnic acid), apices conspicuously lacerate *sulphurina*
Podetia grey (usnic acid absent), apices not, or rarely obscurely lacerate 17
- 17(16) Podetia to 4 (-5) cm tall, unbranched or bifurcate, variably sorediate especially towards the apices, some corticate granules also present; montane, rare *alpina*
Podetia 1-2.5 (-3) cm tall; thallus Thallus K+ yellow→orange, Pd+ orange 18
- 18(17) Podetia ± farinose sorediate throughout *macilenta*
Podetia coarsely sorediate throughout *polydactyla*
- 19(15) Podetia to 5 cm tall, densely coated with numerous, ± yellow-green, peeling squamules; UV+ white, variably fertile *bellidiflora*
Podetia 1-2.5 cm tall, grey, partly ecorticate, granular-corticate or squamulose; UV- or ± pale blue; frequently fertile *floerkeana*
- 20(2) Basal squamules dominant; podetia absent or poorly developed and amongst the squamules 21
Basal squamules not dominant, numerous to very sparse or restricted to the lower part of the podetia only; podetia dominant 43
- 21(20) Squamules C+ emerald green *strepilis*
Squamules C- 22
- 22(21) Squamules minutely red-dotted (×20 lens); medulla pink *norvegica*
Squamules without red dots; medulla pale 23

23(22)	Squamules yellowish below	24
	Squamules white, darker, grey-violet or blackish toward the base	25
24(23)	Squamules ± cottony-arachnoid below (×20 lens), Pd–	<i>luteoalba</i>
	Squamules smooth below, Pd+ yellow-orange	<i>foliacea</i>
25(23)	Squamules sorediate below or at least with the margins coralloid-sorediate	26
	Squamules not sorediate below	28
26(25)	Squamules large, >10 mm diam., ± horizontal, ± rounded, with raised margins, K+ yellow, UV–	<i>digitata</i>
	Squamules small, <5 mm in length, crowded, ± erect; margins coralloid-isidiate to sorediate; K+ purple or K–	27
27(26)	Thallus yellow-green, K–, UV± white; pycnidia and apothecial initials red, K+ purple; often on soil	<i>incrassata</i>
	Thallus grey-green, K+ yellow, UV–; pycnidia and apothecial initials brown, K–; mainly on decorticated wood	<i>parasitica</i>
28(25)	Apothecia brown, sessile or on very short, colourless, decorticate podetia	<i>caespiticia</i>
	Apothecia absent or, if present, on corticate or sorediate podetia	29
29(28)	Squamules K+ yellow, orange or red	30
	Squamules K–	34
30(29)	Squamules ± erect, apices frequently recurved, pale to deep grey-violet below; mainly coastal	<i>firma</i>
	Squamules white below, sometimes darkened towards the base, mainly inland	31
31(30)	Squamules 0.5–2.0 cm tall, becoming grey-black and ± necrotic towards the base on the lower surface	<i>subcervicornis</i>
	Squamules to 0.5 cm tall, sometimes tinged yellow-ochre, without black necrotic bases	32
32(31)	Squamules green above, starkly white below, K+ red (crystals) or K+ yellow, on basic soils in rock clefts and on limestone	33
	Squamules blue-grey above; lower surface sometimes tinged yellow-ochre (K+ purple) at the base of underside; K+ yellow to orange (no crystals); on acid humus	<i>polydactyla</i>
33(32)	Squamules very small (1-3 mm long), mainly erect; K+ yellow	<i>cariosa</i>
	Squamules > 3 mm long, ± horizontal with recurved margins; K+ red	<i>symphycarpa</i>
34(29)	Squamules Pd–, UV+ mauve or white	35
	Squamules Pd+ red, UV–	37
35(33)	Medulla reddish, K+ mauvish in part, otherwise white and K–, UV+ bluish; squamules with superficial red spots (×20 lens), spots K+ purple (rare)	<i>norvegica</i>
	Medulla white, K–, UV–; squamules without red spots	36
36(35)	Cushion-forming or dispersed, not noticeably fragile; squamules UV+ vivid white.....	<i>squamosa</i>
	Sward-forming, very fragile and easily broken; squamules UV+ vivid mauve.....	<i>callosa</i>
37(34)	On bark or wood, rarely soils	<i>coniocraea</i>
	On mosses on soil or rocks, or directly on soil	38
38(37)	Squamules mostly spreading horizontally, rosette-forming, ± imbricate; often on base-rich substrata	<i>pocillum</i>
	Squamules mostly ascending or erect, tufted or scattered, not rosette-forming; on acid rocks or associated soils	39

- 39(38) Squamules thin, often delicate and notably brittle, not recurved at apices when dry; lower surface white *ramulosa*
Squamules thick, often tough, curved at apices when dry; lower surface white-grey or veined40
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Thallus Pd+ yellow *pulvinata*
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Podetia not yellow tinged (without usnic acid)53
- 46(45) Podetia not sorediate, with scattered to contiguous coarse corticate granules or ± partly squamulose
(see also *C. bellidiflora*) [*coccifera* s.lat.]..... 47
Podetia mostly or entirely farinose-sorediate50
- 47(46) Podetia mostly covered with minute squamules; scyphi rather narrow48
Surface of podetia smooth, areolate or granular; scyphi usually rather broad49
- 48(47) Podetia pale greenish yellow, without blackened areas, UV- *diversa*
Podetia dark green, some parts blackened (especially the scyphus margins); mostly UV+ white. *straminea*
- 49(47) Podetia smoothly corticate or with flat plate-like areoles, hardly granular *borealis*
Podetia irregularly corticate, verrucose, granular in the upper parts *coccifera* [s. str.]
- 50(46) Podetia with a short corticate zone at the base, densely sorediate above; apothecia absent or,
if present, red51
Podetia entirely farinose-sorediate; all podetia with goblet-shaped scyphi, margins dentate,
rarely proliferating; apothecia often present, pale brown to pale flesh-coloured *carneola*
- 51(50) Podetia tall (to 4–6 cm), sometimes apically fissured; soredia farinose52
Podetia shorter (1–3 cm), not fissured; soredia granulose to farinose *pleurota*
- 52(51) Podetia distinctly yellowish; scyphi narrow and irregular, perforated and often deformed, often
longitudinally split; UV+ white..... *sulphurina*
Podetia yellowish grey; scyphi broader and more regular in form; longitudinal splits rare; UV-... *deformis*
- 53(45) Podetia without granules or soredia54
Podetia entirely or at least partly sorediate or with delimited convex corticate granules66
- 54(53) Podetia ± perforate, subulate or with very irregular scyphi; squamules deriving from
peeling outgrowths of the podetia (see also *C. bellidiflora*) *squamosa*
Podetia rarely perforate, subulate or with regular scyphi55
- 55(54) Podetia regularly proliferating from the centre of the scyphi, forming tiers.....56
Podetia not proliferating or else proliferating from margins of scyphi58

- 56(55) Thallus K+ yellow; associated with late snow patches*trassii*
Thallus K-; rarely associated with late snow patches57
- 57(56) Podetia slender, with regular scyphi, abruptly tapered; basal squamules small and rounded
(< 6 mm long) with the lower surface white *verticillata*
Podetia robust, gradually tapered; basal squamules longer and indented (to 12 mm long),
lower surface tinged grey *cervicornis*
- 58(55) Podetial squamules present, often auricular; K+ yellow; associated with late snow patches*trassii*
Podetial squamules absent; K-; rarely associated with late snow patches59
- 59(58) Scyphi inconspicuous, often reduced to 3-6 short points surrounding a central rounded gaping
perforation; UV+ white *crispata* var. *cetrariiformis*
Scyphi mostly conspicuous, very rarely centrally perforate; UV± white60
- 60(59) Scyphi conspicuous, centrally perforate (forming funnels), with long subulate proliferations;
UV+ white.....*crispata* var. *crispata*
Scyphi not centrally perforate; UV-61
- 61(60) Podetia >6 cm tall; basal and podetial squamules often very sparse or absent62
Podetia <2 cm tall; basal and podetial squamules usually numerous and well-developed63
- 62(61) Podetia rather swollen, 2-3 mm diam., blue-green, brownish at apices and yellowish at base,
never with squamules; boggy alluvial grassland, often associated with late snow patches *maxima*
Podetia mostly slender, 0.5-1.5 mm diam., olive-brown, dark brown-black at base,
± sparingly squamulose; widespread *gracilis*
- 63(61) Bases of older podetia marbled, with ± dispersed white or grey areoles on a black decorticate surface64
Podetia with a uniform cortex, or if broken, never becoming blackened at the base65
- 64(63) Thallus Pd+ red, UV-; scyphi without perforations, frequently proliferating from the margins
to form intricate clusters of podetia; the surface often matt, pale grey, subarachnoid*phyllophora*
Thallus Pd-, UV+ bright mauve; scyphi with perforations, not proliferating at the margins except
to form short, ± coralloid extensions bearing apothecia; the surface not subarachnoid *callosa*
- 65(63) Podetia with wide, shallow, mostly regular scyphi; basal squamules with lower surface white,
tinged grey; K- *cervicornis*
Podetia irregular, often turgid-coralloid; lower surface of basal squamules markedly tinged
grey-black towards the base; K+ yellow*subcervicornis*
- 66(53) Podetia and scyphi with either corticate granules or peeling squamules67
Podetia and scyphi ± sorediate70
- 67(66) Scyphi narrow, ± irregular, usually occluded when fertile *ramulosa*
Scyphi wide, ± regular, not occluded when fertile68
- 68(67) Squamules of the primary thallus large, veined below, or even partially corticate, sometimes
sorediate at the margin *cyathomorpha*
Squamules of the primary thallus never partially corticate69
- 69(68) Basal squamules well-developed, forming brownish ± imbricate or contiguous, horizontally
spreading rosettes; on strongly calcareous substrata *pocillum*
Basal squamules-well developed, forming bright green-grey mats, with the squamule ends
upturned to show the white undersides when dry; on non-calcareous soils *humilis* [schizidiate morph]
Basal squamules sparse to abundant, contiguous or dispersed, becoming erect, not
rosette-forming; on non-calcareous soils (if yellow-green see *C. coccifera* aggr.)*pyxidata*

- 70(66) Scyphi all centrally perforate (check for especially well-developed *C. glauca*)..... *cenotea*
 Scyphi not centrally perforate71
- 71(70) Pd-, UV+ white *umbricola*
 Pd+ yellow to orange, UV-72
- 72(71) Thallus Pd+ yellow-orange, K+ yellow; basal squamules frequently with orange spots,
 sometimes sorediate below *polydactyla*
 Thallus Pd+ red or rarely Pd-, K- or yellow; basal squamules without orange spots, not sorediate73
- 73(72) Podetia corticate for at least 1-3 mm at the base, frequently extending to the scyphi74
 Podetia entirely sorediate, not or very slightly corticate at base83
- 74(73) Scyphi wide, sessile, or with a short (<1 cm), ± corticate stalk; not proliferating from
 the margins.....75
 Scyphi narrow to wide, with a well-developed stalk (1-3.5 cm), sometimes proliferating
 from the margins [*Cladonia chlorophaea* s.l.]76
- 75(74) Podetia K+ yellow, robust, with a short stalk *humilis*
 Podetia K-, usually ± slender, with a longer stalk *conista*
- 76(74) Scyphi wide in relation to length of podetial stalk; soredia often ± confined to within the
 scyphi [*Cladonia chlorophaea* s.l.]77
 Scyphi narrow in relation to length of podetial stalk; soredia often widespread82
- 77(76) Podetia with farinose soredia; only containing fumarprotocetraric acid; most common on bark
 of living trees, less acid loamy soil and less acid decaying lignum *chlorophaea* [s.s.]
 Podetia with granular soredia, which may be shed exposing a pinkish stem; containing other
 substances, often in addition to fumarprotocetraric acid; most common on soil, acid wood,
 acid bark and detritus [*Cladonia grayi* s.l.]78
- 78(77) Podetia KC+ fleeting but distinct wine red, K+ pink or reddish (slow)79
 Podetia K-, KC-80
 [Observe KC reaction under dissecting microscope: place a small piece of podetium on a microscope slide in a
 small drop of K for a few seconds, then add a small drop of C]
- 79(78) Cryptochlorophaeic acid present *cryptochlorophaea*
 Merochlorophaeic and 4-*O*-methylcryptochlorophaeic acids present *merochlorophaea*
 [use TLC or microcrystal test]
- 80(78) Rangiformic acid present; podetia often slender, with a squamulose stalk *asahinae*
 Rangiformic acid absent81
- 81(80) Sekikaic and sometimes homosekikaic acid present *novochlorophaea*
 Grayanic acid present *grayi*
- 82(76) Scyphi ± regular, abruptly expanded; soredia greenish white; cortex green; Pd+ orange red,
 UV- *coniocraea*
 Scyphi irregular, gradually tapered to podetial stalk; soredia and cortex brownish;
 Pd- or slowly orange, UV+ white *rei*
- 83(73) Podetia green to grey, goblet-shaped; scyphi wider than podetial stalk, rather regular
 with denticulate, little-proliferating margins *fimbriata*
 Podetia subulate, dull grey-green, antler-like, mostly with pointed apices; scyphi narrow, 0
 irregular, often with marginal proliferations *subulata*

- 84(44) Podetia \pm longitudinally lacerate and fenestrate, rarely with a single longitudinal slit85
Podetia entire, not obviously longitudinally lacerate88
- 85(84) Podetia 0.3–1 cm, sparingly lacerate; margins of basal squamules entire; apothecia always present*peziziformis*
Podetia 1–3 (–5.5) cm, conspicuously lacerate; margins of squamules crenate-incised; apothecia present or absent86
- 86(85) Podetia 2–4 (–5.5) cm, verrucose or coarsely corticate-granular or with numerous peltate squamules; K–, Pd+ yellow*macrophylla*
Podetia 0.5–2 cm with scattered areoles; K+ yellow to orange, Pd \pm yellow87
- 87(86) Basal squamules prostrate, brownish toward the margins, Pd+ yellow; podetia < 1cm in length, robust*symphycarpa*
Basal squamules \pm erect, no brownish margins, Pd– or Pd+ red; podetia < 2cm tall, strongly fissured*cariosa*
- 88(84) Podetia entirely or partially sorediate.....89
Podetia not sorediate, smooth, scabrid or granular-corticate.....96
- 89(88) Lower half of podetia corticate90
Podetia entirely sorediate, or corticate for only a few mm at the base91
- 90(89) Podetia brownish-green, to 5 cm tall, basal squamules small.....*cornuta*
Podetia grey-green, <3.5 cm tall, basal squamules longer [*ochrochlora* morph]..... *coniocraea*
- 91(89) Thallus Pd+ orange or red92
Thallus Pd–94
- 92(91) Podetia Pd+ red, K–93
Podetia Pd+ orange, K+ yellow to orange *macilenta*
- 93(92) Podetia <2 cm, often curved, the apices mostly pointed and unbranched *coniocraea*
Podetia 2–6 cm, often branched towards the apices and becoming antler-like *subulata*
- 94(91) Podetia without a longitudinal fissure ($\times 10$ lens), often unbranched; UV– *macilenta*
Podetia with a terminal or obscure, single longitudinal fissure at one side, seen as a shallow depression ($\times 10$ lens); UV+ white95
- 95(94) Podetia yellow-green, apices often conspicuously lacerate *sulphurina*
Podetia pale grey, apices not lacerate but with single, narrow, longitudinal fissure \pm midway down the podetium*glauca*
- 96(88) Podetia <10 mm; apothecia frequent97
Podetia >10 mm; apothecia infrequent100
- 97(96) Podetia yellowish green; apothecia pale cream to pale brown; generally on recently cut pine stumps*botrytes*
Podetia grey; apothecia dark brown or red, widespread on different substrata98
- 98(97) Podetia smooth, weakly fissured, without granules or attached squamules; apothecia brown; basal squamules ear-shaped.....*peziziformis*
Podetia rough, not fissured, often with granules or squamules; apothecia brown or red; basal squamules various99

- 99(98) Podetial surface verrucose-scabrid; apothecia red; Pd-*floerkeana*
Podetial surface areolate-squamulose; apothecia brown; Pd+ red*ramulosa*
- 100(96) Podetial surface rough; squamules derived from peeling cortical scales (if yellow-green
see *C. bellidiflora*)101
Podetial surface smooth; squamules, if present, derived from outgrowths of cortex103
- 101(100) Podetia ± dichotomously branched, upper part ± scaly-sorediate; Pd+ rust-red*scabriuscula*
Podetia mainly unbranched or with irregular branching, not sorediate; Pd± orange102
- 102(101) Basal squamules indented but not greatly dissected to coralloid; podetia regular, 2–5 cm tall ..*squamosa*
Basal squamules greatly dissected, often coralloid-branched; podetia very short, irregular,
to 0.5 (–2) cm tall*parasitica*
- 103(100) Podetia perforate at apices104
Podetia not perforate at apices106
- 104(103) Basal squamules numerous, mat-forming; UV+ mauve; finely tomentose below*callosa*
Basal squamules few or absent; UV+ white; smooth below105
- 105(104) Terminal perforations surrounded by ± well-developed, proliferating cups*crispata* var. *crispata*
Terminal perforations surrounded by 3–6 points, spine-like, surrounding a central rounded,
gaping hole*crispata* var. *ctrariiformis*
- 106(103) Podetia simple, sometimes branched towards base; incipient scyphi sometimes present107
Podetia branching at all levels; scyphi absent108
- 107(106) Podetia K+ yellow, yellowish at base; associated with late snow patches*maxima*
Podetia K–, brownish white at base; widespread*gracilis*
- 108(106) Podetia solid, translucent or ± grey-black*stereoclada*
Podetia hollow109
- 109(108) Branching markedly divergent; algae forming ± dispersed, raised, green areoles (×10 lens)
especially in older parts of the thallus; usually Pd– (occasionally Pd+ red), K+ yellow*rangiformis*
Branching weakly divergent; algae ± continuous or forming a mosaic intersected by thin white
decorticate lines or dispersed in scattered (not raised) clusters (×10 lens); often with scattered,
white concretions or nodules in calcareous habitats; Pd+ rust-red, K–*furcata*
- 110(1) Podetia finely corticate; branches abruptly tapered at the apices; thallus stiff and spiky111
Podetia not corticate; very richly branched, the branching sympodial; branches not abruptly
tapered at the apices; often forming extensive and elegant tufts113
- 111(110) Podetia silver-grey; surface opaque, evenly coloured with the algae clusters not visible but
forming verrucose lumps; thallus decumbent, the branches widely divergent, with closed axils;
apices long-pointed and not darkened.....*zopfii*
Podetia yellow-green to pale grey-green; surface translucent with the algae clusters visible giving
a ‘giraffe’ pattern, smooth, somewhat glossy; thallus erect, the branches moderately to closely
divergent with some open axils; apices abruptly pointed, darkened at the tip112
- 112(111) Podetia ± regularly dichotomously branched, often some tridichotomous branching in robust
thalli; inner surface of hollow podetia white-powdery*uncialis* subsp. *biuncialis*
Podetia predominantly tri-, tetra- or polychotomously branched; surface of central canal
not powdery*uncialis* subsp. *uncialis*

- 113(110) UV+ bright blue, with perlatolic acid; terminal branchlets may be recurved but not in the same direction across the whole podetium 114
 UV-, without perlatolic acid; terminal branchlets often recurved in the same direction across the whole podetium 115
- 114(113) Branchlets tri- or tetrachotomous, particularly at the tips, often with perforate axils *portentosa*
 Branchlets dichotomous, particularly at the tips, often with closed axils (Lizard, Cornwall) *mediterranea*
- 115(113) Branchlets tri- or tetrachotomous 116
 Branchlets usually bifurcate *ciliata*
- 116(115) Podetial surface finely cottony-tomentose, white to grey (without usnic acid), the apices often ± suffused brown-mauve; K+ yellow 117
 Podetial surface smooth, sometimes ± uneven; yellowish (with usnic acid); K- 118
- 117(116) Podetial base pale, translucent, to grey, scattered areoles not obvious; upper parts of podetia pale grey; pycnidial gel colourless *rangiferina*
 Podetial base blackened, with starkly contrasting scattered white areoles; upper parts of podetia brownish; pycnidial gel red *stygia*
- 118(116) Podetia Pd-; branchlets weakly orientated, not forming dense clusters *mitis*
 Podetia Pd+ red or yellow; branchlets markedly orientated and forming dense clusters *arbuscula*

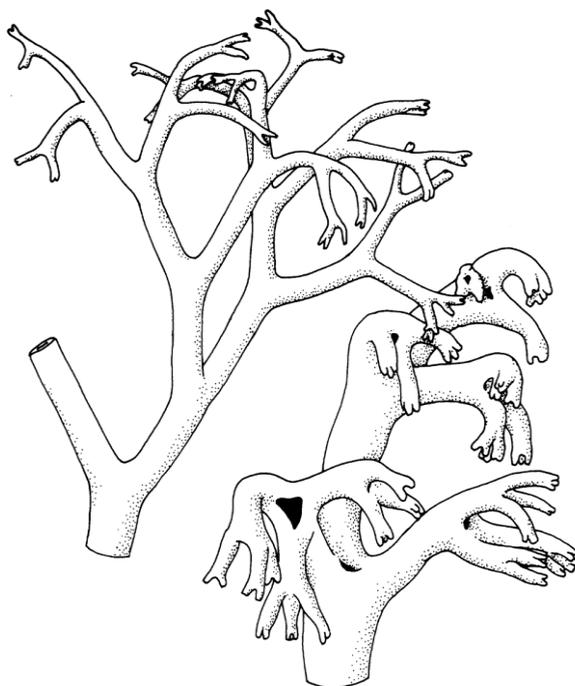


Fig. 1. *Cladonia* branching types. (left) Dichotomous (*C. ciliata*); (right) trichotomous (*C. arbuscula*).

Cladonia alpina (Asahina) Yoshim. (1968)

Resembles *Cladonia macilenta* but the podetia are distinctly taller, up to 4 (–5) cm in height, usually bifurcate or sparingly dichotomously branched in the upper part. Podetia are partially corticate or sorediate throughout, or ± corticate with soredia only towards and at the tips; soredia farinose to subgranular. Basal squamules 1–2 mm long, crenulate or incised. Apothecia red, rather rare. Pycnidia on the apex of podetia, pycnidial jelly red. Thallus C–, K–, KC–, Pd– (or rarely P+ yellow), UV– (barbatic and porphyrylic acids, also thamnolic acid, ± frequent). **BLS 0322**.

On soil rich in humus and on lignum, also on soil over rocks and walls and on *Betula* trunks; rare. N. and S. Wales, England (Lake District), Scotland (W. Ross).

A member of the Erythrocarpae: Subglaucescentes clade based on ITS sequences, which are similar or identical to those of *C. floerkeana*, *C. macilenta* and *C. polydactyla*. The presence of porphyrylic acid has been claimed to be diagnostic for this species, but according to Ahti & Stenroos (2013) some non-European collections do not contain this chemical. British material needs re-evaluation.

**Cladonia arbuscula** (Wallr.) Flot. (1839)

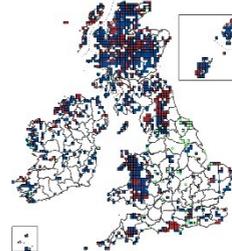
Cladonia arbuscula subsp. *squarrosa* (Wallr.) Ruoss (1987)

Primary thallus crustose, evanescent. Podetia 4–10 cm tall, yellow-green, richly branched, surface ± uneven-roughened; terminal branches notably recurved and markedly orientated in one direction, branching predominantly trichotomous (Fig. 1b) or tetrachotomous at the apices; young apices <2 mm diam., blunt. Apothecia brown, inconspicuous, rather rare. Pycnidial jelly colourless. Thallus C–, K–, KC+ yellow, Pd+ rust-red (fumarprotocetraric and usnic acids) or rarely Pd+ yellow (psoromic and usnic acids), UV–. **BLS 0273**.

In montane and lowland heathlands and acid dunes, on nutrient-poor and often ± boggy soils, rather local. Throughout Britain and Ireland, but rare in C. & E. England and there decreasing due to the loss of suitable habitats and overall eutrophication.

The central species of the *Arbuscula* clade. Characterized by the richly branched, yellow-green podetia with recurved branchlets with tri- and tetrachotomous endings. The similarly coloured *Cladonia portentosa* (*Impexae* clade) has terminal branchlets which are not recurved and diverge in all directions forming broccoli-like tufts; *C. ciliata* (*Crustaceae* clade) differs in the dichotomous branching, and more slender, strongly recurved branchlets. See also *C. mitis*, which is more slender, the branchlets less recurved and contains rangiformic (usually), usnic and, very rarely, also fumarprotocetraric acid.

Often treated as a species complex, including several infraspecific taxa. The dominant morph in our region may be referred to *Cladonia arbuscula* subsp. *squarrosa* (Wallr.) Ruoss (1987) [**BLS 0360**], which is PD+ rust-red (fumarprotocetraric acid) and is claimed to be less profusely branched than the type subspecies. *C. arbuscula* subsp. *arbuscula* is very poorly known, and has not been sequenced; it contains psoromic rather than fumarprotocetraric acid (and is thus Pd+ yellow rather than Pd+ rust-red). There is only one confirmed British record, from coastal dunes in N.E. Scotland (Angus). Molecular data for European populations are sparse, but a study focusing on North American samples (Piercey-Normore *et al.* 2010) did not support them as monophyletic. It is treated here as a single polymorphic species, following Ahti & Stenroos (2013) and Burgaz *et al.* (2020).

**Cladonia asahinae** J.W. Thomson (1977)

Similar to *Cladonia grayi*, but the often slender podetia are covered irregularly with finer granules and soredia, and with small ± persistent squamules with crenulate margins at their base. With similar spot reactions but different chemistry. Thallus C–, K–, KC–, Pd+ red, UV– (rangiformic, norrangiformic and fumarprotocetraric acids). **BLS 1747**.

On peaty soil and on the base of a *Salix* trunk; reported from Wales (Merioneth) and Scotland (Perth, W. Ross).

Part of the *Cladonia grayi* complex; see under that species for more information. It could well be under-reported, and identification using TLC or sequencing is recommended. Populations elsewhere have varied chemotypes (Brodo & Ahti 1996), and *C. asahinae* could be a species complex in itself.

**Cladonia bellidiflora** (Ach.) Schaer. (1823)

Podetia 3–4 (–5) cm tall, grey-green to yellow-green, straight or somewhat curved or twisted, pointed at the apices, unbranched, the surface often entirely densely peeling-squamulose, especially towards the base, often becoming

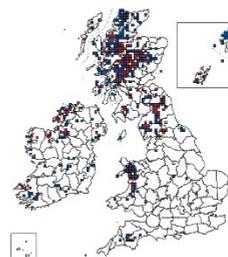
LC

corticate-granular or \pm decorticate and paler towards the apices, never sorediate. Basal squamules small, often inconspicuous, 1–3 mm long, upper surface dull grey-green \pm tinged yellow, deeply indented, yellowish brown towards the base on the lower surface. Apothecia occasional, red, sessile or on short projections at the apex of podetia, often becoming clustered. Thallus C–, K–, KC+ yellow, Pd–, UV+ white (\pm usnic and squamic acids, \pm yellow pigment). Populations elsewhere contain other substances (Stenroos *et al.* 1992). **BLS 0362.**

Amongst *Calluna* and mosses between rocks, blanket bog and particularly on stabilized scree on moorland and montane areas. Chiefly Scotland, also extending locally to N. England, Wales and S.W. England (Devon, Dartmoor). Widely distributed but scarce in Ireland.

A distinctive species which, though often stunted in southern localities, is characterized by the unbranched, pointed podetia, the yellow-green colour, the often dense, peeling squamules, absence of soredia or granules and the red apothecia and pycnidial jelly. When sterile it is distinguished from *Cladonia squamosa* by the yellow colour (usnic acid), \pm presence of orange pigmentation (K+ purple) at the base of the undersides of the basal squamules and absence of perforations in the podetia; entirely grey specimens, lacking usnic acid, are rarely encountered.

Phylogenetically close to *Cladonia polydactyla* according to Stenroos *et al.* (2019), but that species is clearly distinct in morphological terms and is K+ yellow-orange, Pd+ orange and UV–.



Cladonia borealis S. Stenroos (1989)

Similar to *Cladonia coccifera*, but the surface of podetia (which are frequently fertile) are uniformly smooth to shallowly areolate-corticate, without granules or minute squamules, with flat corticated plates outside and inside the scyphi. Thallus C–, K–, KC+ yellow, Pd–, UV– (usnic and barbatic acids). **BLS 1748.**

On peaty soil, mostly in montane heaths. Wales (Snowdonia), Highland Scotland (especially Cairngorm region and Shetland but likely to be widespread elsewhere in the Highlands); rare in England (New Forest, Cornwall) and Ireland.

Placed in the *Cladonia coccifera* aggregate by James (2009), and sister to a clade that includes *C. deformis* and *C. pleurota* (Stenroos *et al.* 2019).

Nb



Cladonia botrytes (K.G. Hagen) Willd. (1787)

Podetia to 0.5 cm tall, yellow-green, without scyphi, usually unbranched or occasionally sparingly branched towards the apices when well developed; surface smoothly corticate, becoming \pm verrucose-areolate and sometimes longitudinally fissured. Basal squamules small, scattered, rather inconspicuous, \pm erect and incised. Apothecia flesh-coloured to pale brown, terminal on podetia even when these are young, sometimes also on small lateral branches near the apices. Pycnidia often present on basal squamules, with colourless gel. Thallus C–, K \pm yellow, KC \pm pale yellow, Pd–, UV– (usnic and barbatic acids). **BLS 0363.**

On relatively recently cut surfaces of *Pinus* stumps, more rarely on *Picea* and on dead *Calluna* stems; ephemeral, rather rare and very local. N. Scotland (Cairngorm region); possibly overlooked elsewhere due to lack of focus on its specialized habitat.

A member of the *Ochroleucae* clade, along with *Cladonia carneola* (Stenroos *et al.* 2019). The small size, yellow-green colour, absence of scyphi and pale brown to pinkish apothecia are diagnostic. *C. carneola* has similarly pale coloured apothecia, but always has well-developed, \pm entirely finely sorediate, regular scyphi. The affinity of *C. botrytes* for recently cut (4–10 years) stumps of conifers is of particular note; populations are vulnerable due to decay of the substrata (Yahr *et al.* 2013), with more than 90% of individual mats of thalli not persisting more than three years.

CR



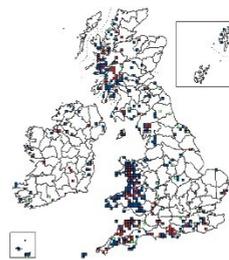
Cladonia caespiticia (Pers.) P. Gaertn., B. Mey & Scherb. (1802)

LC

Podetia to 0.3 cm tall (often absent), decorticate, \pm translucent when wet or sometimes with a yellowish tinge, devoid of algal cells. Basal squamules dominant, 2–7 mm long and to 1.5 mm wide, often irregularly incised, crenulate and \pm erect, often well-developed and forming dense, low cushions; upper surface greyish or brownish green; lower surface white, not sorediate. Apothecia usually present, inconspicuous, brown, single, rounded or \pm tuberculate, sessile or on short podetia. Pycnidia brown-black, on the upper surface of the basal squamules, with colourless gel. Thallus C–, K–, KC–, Pd+ red, UV– (fumarprotocetraric acid). **BLS 0364.**

On mossy tree trunks, stumps and earth banks chiefly in sheltered situations, often in long-established, mature woodlands; widespread but rather local, easily overlooked and often sterile, when it cannot be identified with confidence. S. & W. Britain and Ireland, scattered in E. England and E. Scotland.

A member of the core *Cladonia* subclade, along with *C. cervicornis*, *C. subulata*, and *C. verticillata*. Characterized by the tendency to form \pm compact cushions, the numerous small clusters of incised squamules bearing pycnidia as well as apothecia, the latter either sessile or on very short algal-free \pm white pellucid stalks when wet. The rapid Pd+ red reaction is helpful for identification. Resembles the predominantly lignicolous *C. parasitica* in habit, which also has crowded basal squamules but these bear coralloid-sorediate granules at their margins and the podetia are conspicuously elevated, 0.5–2 cm tall and \pm corticate, K+ orange (thamnolic acid).

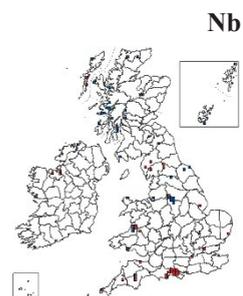


***Cladonia callosa* Delise ex Harm. (1907)**

Podetia to 1.5 cm tall, irregular, \pm often branched, sometimes irregular cup-like around a \pm central perforation at the apices, smooth or wrinkled, \pm completely unevenly corticate or with a mosaic of grey areoles on a white decorticate surface, with scattered, mostly inconspicuous fissures, becoming more decorticate and notably blackened when older, especially towards the base. Basal squamules 1–3 (–5) mm long, 0.5–1 (–2) mm wide, \pm elongate, erect, incised, sometimes upwardly recurved, scattered or forming \pm compact, continuous mats, very brittle and fragile; upper surface grey, sometimes bronze- or brown-tinged, white and finely tomentose on the undersides. Apothecia ca 0.2 mm diam., brown, contiguous in terminal clusters towards and at the apices of podetia, sometimes on short projections from the squamule surface. Pycnidia dark brown, on basal squamules. Thallus C–, K–, KC–, Pd–, UV+ bright mauve-white (grayanic acid). **BLS 0388.**

On acid, sometimes waterlogged peaty or humic soils, at edges of peat hags, path edges and other recently bared ground, in lowland and montane heathlands, quarries and mine spoil heaps, rarely mossy woodland floors and damp lignum; probably a widespread, but extremely under-recorded pioneer species of acid bare ground. S. and S.W. England (esp. New Forest), W. Wales, N. England and Scotland. Very scattered records from Cheshire to Shetland, but recent sampling suggests it is actually frequent in this area.

Often present only as brittle basal squamules, which can be identified by the unique combination of very bright mauve-white UV fluorescence and the white and finely tomentose undersides of the squamules. The most similar squamules are those of *Cladonia crispata*, but these are paler UV+ blue-white and have smooth white undersides. When olive or bronze-green in colour the squamules may be somewhat reminiscent of small morphs of *C. strepsilis*, which is C+ emerald green (strepsilin) and has tougher, more coriaceous squamules. *C. callosa* may resemble morphs of *C. ramulosa* in lowland habitats which may also have brittle, but smaller, squamules, but is Pd+ red (fumarprotocetraric acid) and is UV–. It appears to have no close relatives, and occupies an isolated position at the base of the *Cladonia* clade (Stenroos *et al.* 2019).



***Cladonia cariosa* (Lilj.) Spreng. (1827)**

Podetia 0.5–1.5 (–2) cm tall, grey-green, sometimes tinged brownish; scyphi absent, often sparingly branched above, the surface partly decorticate, distinctly longitudinally fissured with large, gaping cracks, often net-like, \pm covered with numerous small corticate granules, sometimes with scattered squamules; soredia absent. Basal squamules mostly rather small, 1–3 mm long, \pm erect, the margin entire or incised, with dark brown pycnidia on the upper surface, often grey-tinged below. Apothecia usually abundant, dark brown, at apices of podetia and branches, usually larger than the width of branches, often clustered and \pm corymbose. Three chemotypes occur in Britain and Ireland: C–, K+ yellow, KC–, Pd–, UV– (atranorin), widespread but local; C–, K+ yellow, KC–, Pd+ rust-red, UV– (atranorin, fumarprotocetraric acid), rare; C–, K \pm yellow, KC–, Pd–, UV– (atranorin, rangiformic acid), very rare. **BLS 0366.**

In sandy situations, especially moderately calcareous heaths and mine spoil-heaps; rare but widespread. Throughout Britain and Ireland.

The *Cladonia cariosa* complex was investigated by Pino-Bodas *et al.* (2011); it is readily recognized by the longitudinally multi-fissured podetia and large, clustered, terminal brown apothecia. It is chemically variable, as many as nine chemotypes have been described (Osyczka & Skubała 2011). Populations with norstictic acid are rare



in *C. cariosa* s.l. (Pino-Bodas *et al.* 2011, Ahti & Stenroos 2013). The variation indicates that undescribed species probably exist within this complex. *C. symphyrcarpa* is similar but has larger squamules and broader podetia (these rarely seen), and tends to occur on more strongly calcareous substrata.

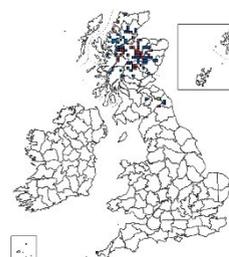
Cladonia carneola (Fr.) Fr. (1831)

Podetia 0.5–1.5 (–2) cm tall, pale yellow-green, appearing ± translucent when wet; scyphi 3–6 mm diam., abruptly tapered to a long narrow stalk, ± regular with finely denticulate scyphi with ± even rims which rarely proliferate; surface within and outside the scyphi entirely farinose-sorediate. Basal squamules often rather small and inconspicuous. Apothecia pale yellow-brown or pale flesh-coloured, rather rare; pycnidia dark brown; both apothecia and pycnidia on rim of scyphi. Thallus C–, K–, KC+ yellow, Pd–, UV– (usnic and ± barbatic acids, ± zeorin; all British material contains barbatic acid, but its presence in this species is less frequent elsewhere). Needle-like crystals of zeorin develop on the surface of specimens in dried collections. **BLS 0367.**

On rotting conifer stumps, more rarely on peat and *Calluna* stems, in ancient Caledonian pine woods, more rarely on moorland and blanket bog above 600 m; locally frequent. Almost confined to Scotland (especially the Cairngorm region) and rare in the Cheviot Hills, recorded once from N. Wales (Denbigh).

Related to *Cladonia botrytes*, which has similarly coloured apothecia and occurs in similar habitats; that species does not have scyphose podetia. In the absence of apothecia, it may be mistaken for the morphologically similar *C. fimbriata* which is Pd+ red (fumarprotocetraric acid) and is grey, not yellowish green. The chemically and morphologically similar yellow-green *C. pleurota* has podetia which are ± corticate at the base and thus usually lacking soredia there, but has red rather than pale brown apothecia.

Nb



Cladonia cenotea (Ach.) Schaer. (1823)

Podetia 1–2.5 cm tall, greyish or greenish brown, often clustered, unbranched or sparingly branched above, with narrow, notably perforate scyphi which irregularly proliferate from the margins, surface farinose-sorediate throughout, sometimes with small squamules, particularly at the base. Basal squamules small, indented, often rather inconspicuous. Apothecia brown, rare, at the apices of podetia. Thallus C–, K–, KC–, Pd–, UV+ white (squamic acid). **BLS 0368.**

On rotting conifer stumps and humus amongst *Calluna*; mostly confined to ancient Caledonian pine woodlands where it is not uncommon. Scotland (especially the Cairngorm region).

Distinguished by the clearly and consistently perforated scyphi, a feature absent in all other brown-fruited, sorediate, ± unbranched species with scyphi, e.g. *Cladonia fimbriata*, *C. chlorophaea*. When the scyphi are narrow and the podetia elongate, *C. cenotea* may be difficult to distinguish from the otherwise similar *C. glauca*, which can rarely have small scyphi. *C. cenotea* appears to be polyphyletic (Stenroos *et al.* 2019).

NT



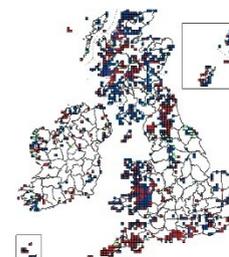
Cladonia cervicornis (Ach.) Flot. (1849)

Podetia to 1 cm tall, with shallow ± regular scyphi, corticate, areolate, often sparingly squamulose and proliferating irregularly from the centre, sometimes forming several tiers of proliferation, without soredia. Basal squamules often dominant, often well-developed, 2–3 (–5) mm long, ± rounded, the margins indented, reflexed when dry, mostly contiguous and forming cushions; upper surface grey-green to grey-brown; lower surface white, often tinged grey; soredia absent. Apothecia rare, brown, on scyphus margins. Pycnidia frequent, brown, on scyphus margins. Thallus C–, K–, KC–, Pd+ red, UV– (fumarprotocetraric acid, rarely ± atranorin). **BLS 0369.**

On mildly acid and basic soils, particularly on coastal dunes and heathland; common. Throughout Britain and Ireland.

A member of the *Cladonia* subclade. Two related species, *C. pulvinata* and *C. verticillata*, were treated as subspecies of *C. cervicornis* by James (2009), but they are distinct in molecular terms and the current consensus is that they are separate species (Pino-Bodas *et al.* 2010a, Ahti & Stenroos 2013, Stenroos *et al.* 2019). *C. pulvinata* can be distinguished easily from *C. cervicornis* by its Pd+ yellow rather than Pd+ red reaction (psoromic rather than fumarprotocetraric acid). Morphological differences were also described by Van Herk & Aptroot (2003). *C. verticillata* differs by the rounded and short basal squamules and podetia with narrower and more regular scyphi

LC



with up to seven layers of proliferation, but well-developed *C. cervicornis* can form several layers of proliferation and the simple presence of tiers is not a reliable separation. The longer, more indented basal squamules of *C. cervicornis* provides a more definitive separation, combined with the less elegant proliferations.

Cladonia cervicornis is distinguished from the unrelated *C. subcervicornis* by the much smaller, more rounded, grey-green basal squamules, the undersides of which are not conspicuously blackened towards the base, and by the K– reaction. See also *C. firma* and *C. symphycarpa*.

Cladonia chlorophaea (Flörke ex Sommerf.) Spreng. (1827)

Podetia 0.5–2.5 (–4) cm tall, greenish grey, sometimes slightly browned; scyphi 3–6 (–12) mm diam., gradually tapered to the stalk, sometimes ± regular but often proliferating (sometimes repeatedly) from the margins, patchily corticate below, becoming granular to ± sorediate above as well as within scyphi, the soredia often mixed with corticate granules and microsquamules. Basal squamules often small and inconspicuous, ± erect, sometimes incised. Apothecia and pycnidia brown, frequent; apothecia stalked or sessile on scyphus margins. Thallus C–, K–, KC–, Pd+ red, UV– (fumarprotocetraric acid). **BLS 2356**.

Probably common throughout Britain and Ireland, but much confused formerly with other members of the *Cladonia chlorophaea* complex [see below]. The map contains only those records definitely identified as *C. chlorophaea* s. str.

Cladonia grayi and its relatives [see below] have previously been included in a morphological assembly with *C. chlorophaea* (e.g. James 2009), and the complex (as *C. chlorophaea* s.lat. **BLS 0371**) is accepted as a pragmatic recording unit by some lichenologists. However, molecular data are incomplete, but *C. chlorophaea* occupies a different phylogenetic branch to the *C. grayi* aggregate, and is close to *C. fimbriata* within the *Cladonia* subclade *Graciles* (Stenroos *et al.* 2019). Ahti & Stenroos (2013) observe that *C. chlorophaea* tends to occupy somewhat less acidic habitats than *C. grayi* s. lat. These include less acid bark and lignum, decaying worked timber, acid grassland and loamy banks; it is largely replaced by *C. grayi* s. lat. in heathland and moorland and on acid bark and lignum.

Cladonia chlorophaea podetia are usually greenish with any exposed medulla being white and it lacks K+ or C+ spot tests or UV fluorescence. In contrast *C. grayi* s. lat. taxa are typically browner and have pink-brown tinged exposed medulla, and can have K+ or C+ spot tests or UV fluorescence, but TLC is required for definitive separation. Microcrystal tests (Orange 1992, Orange *et al.* 2010) are also powerful tools for identification in this group.

Cladonia chlorophaea and *C. grayi* s. lat. are also frequently confused with *C. fimbriata*, which has more abruptly tapering, goblet-shaped scyphi and is entirely farinose-sorediate. Also similar is *C. pyxidata* which has gradually tapered scyphi almost to the base and covered with distinctly coarse, corticate granules, present even in juvenile material and lacking any granular soredia.

Summary of the chemistry of the *Cladonia chlorophaea* morphological complex. Populations outside of Britain and Ireland may show different chemotypes. Data taken from James (2009) and Ahti & Stenroos (2013).

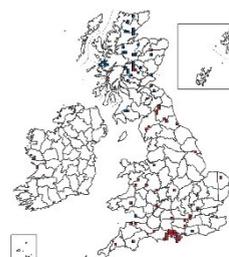
	C	K	KC	Pd	UV	chemistry
<i>asahinae</i>	–	–	–	+ red	–	fumarprotocetraric, rangiformic, norrangiformic acids
<i>chlorophaea</i>	–	–	–	+ red	–	fumarprotocetraric acid
<i>cryptochlorophaea</i>	± yellow	yellow → red	wine red	orange-red	pale yellow	cryptochlorophaeic, fumarprotocetraric, paludosic acids
<i>grayi</i>	–	–	–	± red	+ mauve-white	grayanic, ± fumarprotocetraric acids
<i>merochlorophaea</i>	± red	–	wine red	± orange-red	+ faint blue	merochlorophaeic, 4-O-methylcryptochlorophaeic, ± fumarprotocetraric acids
<i>novochlorophaea</i>	± red	–	–	± orange-red	± white	sekikaic, homosekikaic, ± fumarprotocetraric acids

Cladonia ciliata Stirt. (1888)

Cladonia ciliata var. *tenuis* (Flörke) Ahti (1993)

Primary thallus crustose, evanescent. Podetia 3–6 cm tall, grey-white, lacking green coloration, or greenish grey to yellowish due to the presence of usnic acid, upper part often suffused with a distinct purple-brown colour towards

LC



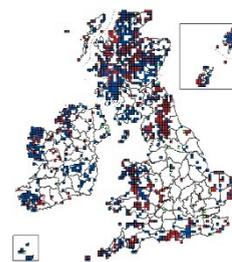
the tips, richly-branched; terminal branches \pm downturned, distinctly orientated in one direction, the branching predominantly dichotomous at the apices (Fig. 1a), axils rarely perforated; young tips slender, to 0.8 mm diam. Apothecia brown, inconspicuous, rather rare. Pycnidial jelly red. Thallus C $^-$, K $^-$, KC $^-$, Pd $^+$ red, UV $^-$ (fumarprotocetraric and \pm usnic acids). **BLS 0372**.

On montane and lowland heathlands, in woodland, especially western woods and acid dunes; local. Throughout Britain and Ireland.

Cladonia ciliata belongs to the *Crustaceae* clade, along with *C. rangiferina* and *C. stygia*. It differs from *C. rangiferina* in the predominantly dichotomous terminal branching, much more delicate habit, smooth not cottony-arachnoid surface, red pycnidial jelly and chemistry.

Large, coarse specimens containing usnic acid with terminal branches not strongly orientated may resemble *Cladonia portentosa* which is, however, KC $^+$ yellow, Pd $^-$, UV $^+$ pale blue; *C. arbuscula* is always coarser with a strongly emphasized orientation of the terminal branchlets and has tri- and tetrachotomous branching.

Collections containing usnic acid (and then with greenish grey to yellowish thalli) have frequently been separated at form or varietal level (e.g. as *Cladonia ciliata* var. *tenuis* (Flörke) Ahti (1993) by James 2009, or *C. ciliata* f. *flavicans* (Flörke) Ahti & DePriest (2001) by Ahti & Stenroos 2013). James (2009) noted that intermediates may be found with low concentrations of usnic acid, and distributions and habitat requirements are largely similar. Molecular data are not extensive, but do not support the monophyly of both chemotypes (Athukorala *et al.* 2016, Stenroos *et al.* 2019). Burgaz *et al.* (2020) treat *C. ciliata* as a single polymorphic taxon. The two morphs are best considered as chemotypes, pending further investigations.



Cladonia coccifera (L.) Willd. (1787

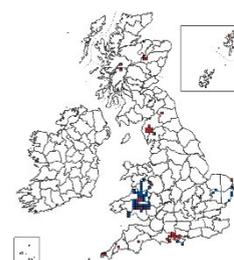
Podetia to 3.5 cm tall, yellow-grey to yellow-green; scyphi broad, gradually tapering to the base with only a short stalk (*C. pyxidata*-type), usually regular, rarely proliferating from the margins; surface \pm corticate but \pm areolate throughout, with conspicuous coarse bullate corticate granules, especially within the scyphi, sometimes \pm squamulose at the base; soredia usually absent. Basal squamules to 2 mm diam., very variable, \pm rounded and sparingly indented; lower surface often yellow- to orange-brown, K $^+$ purplish towards the base, \pm dispersed or occasionally forming \pm compact cushions. Apothecia and pycnidia frequent, on the margins of scyphi, the apothecia red and pycnidia black or reddish and containing red gel. Thallus C $^-$, K $^-$, KC $^+$ yellow, Pd $^-$, UV $^-$. In dried collections, needle-like crystals develop on the surface of collections of the complex containing zeorin. **BLS 2357**.

Mainly in upland heath and species-rich lowland heath; occasional, but the distribution needs further study due to confusion with other members of the *Cladonia coccifera* aggregate. Scottish Highlands, Cumbria, Wales, S.W. England and the New Forest.

The *Cladonia coccifera* aggregate as treated by James (2009) forms a broadly monophyletic group within the Subglaucescentes clade along with *C. deformis* and *C. sulphurina*, but some of the component species are varied in sequence and hybridisation may have taken place (Steinová *et al.* 2013, Stenroos *et al.* 2019). Spot tests are mostly unhelpful for distinguishing taxa within this group (see table below) but TLC may be useful for identification in some cases. Subtle morphological distinctions remain important for species delimitation. Sterile specimens of this and other members of the aggregate are separated from *C. pyxidata* by their yellow colour (usnic acid), Pd $^-$ reaction and chemistry.

In *Cladonia coccifera* s. str., podetia are regular, continuously corticate but often irregularly granular in the upper part. Squamules are few, and granules \pm flattened.

DD



Summary of the chemistry and morphology of the *Cladonia coccifera* complex. Populations outside of Britain and Ireland may show different chemotypes. Data taken from James (2009) and Ahti & Stenroos (2013).

	C	K	KC	Pd	UV	chemistry	Morphology
<i>borealis</i>	-	-	yellow	-	-	usnic and barbatic acids, \pm 4-O-demethylbarbatic and rhodocladonic acids	Podetial surface smoothly corticate with flat plates outside and inside the scyphi
<i>coccifera</i>	-	-	yellow	-	-	usnic acid, \pm isousnic acid, \pm porphyritic acid, rhodocladonic acid, zeorin	Podetial surface corticate to areolate with bullate granules inside the scyphi

		C	K	KC	Pd	UV	chemistry	Morphology
<i>deformis</i>		–	–		–	–	usnic, isousnic and rhodocladonic acids, zeorin, bellidiflorin	Podetial surface with farinose soredia
<i>diversa</i>		–	–	yellow	–	–	usnic acid and zeorin, ± conporphyritic, isousnic and porphyritic acids, skyrin (rare)	Podetial surface with microsquamules and granules
<i>pleurota</i>		–	–	yellow	–	–	usnic, isousnic and ± porphyritic acids, rhodocladonic acid, zeorin	Podetial surface sorediate then completely corticate
<i>straminea</i>	I	–	–		–	white	usnic, didymic, rhodocladonic and squamatic acids	Podetial surface corticate with numerous squamules and microsquamules
	II	–	yellow		yellow	–	usnic, didymic, rhodocladonic and thamnolic acids	Podetial surface corticate with numerous squamules and microsquamules, basal part blackish

Cladonia coniocraea (Flörke) Spreng. (1827)

Cladonia ochrochlora Flörke (1828)

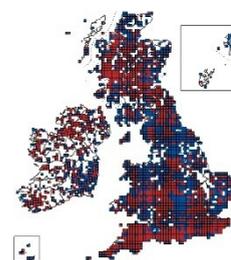
Podetia 1–3.5 (–5) cm tall, grey-green, green when wet, mostly pointed at the apices, unbranched, often ± curved, sometimes bearing small, abruptly expanded terminal scyphi (1–3 mm long) that may hardly exceed the breadth of the podetium, predominantly farinose-sorediate but usually with a persistent corticate zone at least at the base, which may extend upwards only for 1–2 mm but in other populations sheathe much of the lower surface and also extend into the scyphi. Basal squamules dull green above, brighter green when wet, pale below, very variable and often sorediate in the lower part. Apothecia brown, rare, on tips of podetia. Pycnidia brown to black, on tips of podetia or margin of scyphi, with colourless gel. Thallus C–, K–, KC–, Pd+ rust-red, UV– (fumarprotocetraric acid). **BLS 0375.**

Chiefly on acid bark of living, or recently dead, trees and wood, less often on heathland peaty soils; common and very widespread. Throughout Britain and Ireland.

Belongs to the *Cladonia* clade, subclade *Graciles*. James (2009) considered *C. ochrochlora* a separate species and that opinion was supported by Ahti & Stenroos (2013), but molecular data provided by Pino-Bodas *et al.* (2012a) and Stenroos *et al.* (2019) did not distinguish sufficiently between the two taxa. In morphological terms *C. coniocraea* has more slender, hardly corticate podetia that rarely produce scyphi, while *C. ochrochlora* has relatively robust podetia that may be corticate at the base and scyphi are present though hardly broader than the podetia. These differences were considered as adaptations to local environmental conditions (Schwerdtner & Cordes 1992). Juvenile material is very difficult to assign to one or other taxon.

Cladonia coniocraea is tolerant of SO₂ pollution, but less so of eutrophication. It often occurs with morphs of *C. polydactyla* lacking scyphi, which may be recognized by its overall blue-grey tinge (± unchanged when wet) and Pd+ orange (thamnolic acid) or Pd– (barbatic acid) reaction.

LC



Cladonia conista (Nyl.) Robbins (1930)

Morphologically similar to *Cladonia humilis*, but tending to have slightly narrower and less abruptly flared scyphi with slightly longer stalks and smaller soredia, and with a different chemistry. Thallus C–, K–, KC–, Pd+ red, UV– (bourgeanic and fumarprotocetraric acids). **BLS 0156.**

On turf between basic boulders and on wall tops, Scotland (E. Lothian, Mull) and Wales (Ceredigion).

The species is commoner than *Cladonia humilis* in Scandinavia according to Ahti & Stenroos (2013), and could be more widespread in northern Britain, but the distribution is not well-known because TLC is necessary to distinguish it from *C. humilis*. They observe that morphs of *C. fimbriata* with corticate podetial stalks may be confused with *C. conista*, but are generally more robust and longer-stalked. The species was considered a chemotype of *C. humilis* by James (2009) but is now considered to be distinct (Pino-Bodas *et al.* 2012b); see under that species for more information. Lendemer (2008) considered that the name *C. conista* was invalidly published and replaced it with *C. innominata* Lendemer, but Pino-Bodas *et al.* (2012b) considered that it was nomenclaturally justifiable to maintain that name.

NE



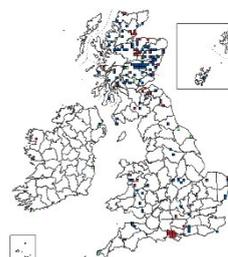
Cladonia cornuta (L.) Baumg. (1790)

Podetia 1–5 cm tall, grey to brownish green, smooth and ± faintly pale areolate-corticate in the lower half, grey-green to grey-white and densely farinose-soresiate in the upper half, the apices pointed, unbranched, rarely with narrow scyphi; a few squamules occasionally present towards the base. Basal squamules rather small, ± rounded, scarcely indented. Apothecia brown, very rare, at apices of podetia. Pycnidia on the tips of podetia, with colourless gel. Thallus C–, K–, KC–, Pd+ red, UV– (fumarprotocetraric acid). **BLS 0378**.

On peat and rotting wood in moorlands, especially montane lichen heaths; widespread and common in Scotland; local and rare elsewhere.

Part of the *Cladonia* clade, subclade *Graciles*, and probably most closely related to *C. gracilis* (Fontaine *et al.* 2010, Pino-Bodas *et al.* 2012a, Stenroos *et al.* 2019). Some partially corticate morphs of *C. coniocraea* can be confused with this species, but in general terms the half-corticate and half-soresiate, pointed, usually brownish, unbranched podetia are diagnostic for *C. cornuta*.

LC

**Cladonia crispata** (Ach.) Flot. (1839) var. **crispata**

Differs from the commoner *Cladonia crispata* var. *ctrariiformis* (see below) in having obvious, more well-developed, clearly perforated scyphi with shorter, subulate proliferations and tiers of more squat, sturdy podetia. Thallus C–, K–, KC–, Pd–, UV+ white (squamic and ± barbatic acids). **BLS 1575**.

Primarily in coastal, grey dune systems, also inland in mine sites and on forestry tracks; very rare. England (Cornwall, Dorset, Yorkshire), Wales (Anglesey, Carmarthen), E. Scotland (Moray, Mid Perths.).

Part of the *Perviae* clade (Stenroos *et al.* 2019), but the species is apparently polyphyletic and further studies are needed. *Cladonia crispata* var. *ctrariiformis* could be separable at species level, but the necessary combination has not been made to date. In *C. squamosa* the squamules are more abundant.

NE

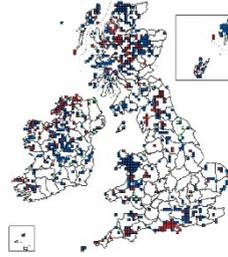
**Cladonia crispata** var. **ctrariiformis** (Delise) Vain. (1886)

Podetia 2–6 cm tall, ± clustered, pale to dark brown-grey to brown-green, unbranched or irregularly branched, particularly in the upper parts, when mature initially terminating in a very narrow cup-like structure consisting of a single perforation surrounded by short spines, subsequently one of these spines may proliferate to form an additional extension, a process which may be repeated several times; surface ± smooth, corticate and ± faintly pale areolate, sometimes partly squamulose. Basal squamules 1–2 mm in size, indented, the underside white and smooth, often disappearing when the podetia mature. Apothecia to 1 mm diam., pale to dark brown, on terminal spines, ± corymbose, rather frequent. Pycnidia dark brown, at apices of podetia, frequent, associated with terminal spines. Thallus C–, K–, KC–, Pd–, UV+ white (squamic and ± barbatic acids). **BLS 0379**.

On peaty soils in lichen-rich *Calluna* heathland in moorland and montane areas; frequent but rather local. Throughout Britain and Ireland.

Characterized by the dark colour (paler in shade morphs), irregular branching, podetia terminating in a single perforation surrounded by short spines (<0.5 mm) and in being Pd– and UV+ white. Immature specimens may resemble *Cladonia furcata* which is Pd+ red and UV–. The coarser and very sparingly branched *C. gracilis* entirely lacks perforations with spines, has a more continuous cortex and is Pd+ red (fumarprotocetraric acid) and UV– (squamic acid absent). Sterile squamules are similar to those of *C. callosa*, but these are UV+ bright mauve and have finely tomentosa under sides.

LC

**Cladonia cryptochlorophaea** Asah. (1940)

A member of the *Cladonia chlorophaea/grayi* morphocomplex. Podetia greyish green with smaller, ± farinose rather than granulose soresia, the exposed medulla pinkish brown and a quite distinct chemistry. Thallus C± yellow, K+ yellow-red, KC+ wine red (fleeting), Pd+ orange-red, UV+ pale yellowish (cryptochlorophaeic and fumarprotocetraric acids); **BLS 0380**.

On humus-rich soil in heaths, moorlands and open woodlands, and on acid lignum and

NE



bark; rarely on soil over siliceous rock. Throughout Britain and Ireland; it appears to be the commonest member of the *C. grayi* group.

The spot reactions for this species are described differently in the literature; James (2009) gives C± yellow and K+ yellow-red (presumably yellow→red). Ahti & Stenroos (2013) and Burgaz *et al.* (2020) give C+ fugitively wine-red (or C+ yellow orange) and K+ wine red, though they note that the K reaction is not always reliable; it may also appear brownish. This may indicate chemical variation, or in part differences of nomenclature. It is difficult to distinguish from other members of the *C. grayi* complex without TLC. It is closely related to the American species *C. cylindrica*.

Cladonia cyathomorpha Stirt. ex Walt. Watson (1935)

Podetia to 0.8 cm tall, gradually tapering to form a scyphus, coarsely corticate-granular within, ± smooth to verrucose outside; marginal proliferations infrequent but intricate and baroque when well-developed. Basal squamules dominant, 5–10 mm diam., ± rounded, indented, sometimes flat, often upwardly recurved at the margins and becoming ± erect when dry; upper surface grey-green; lower surface white with raised, frequently with palmately arranged white to yellow-brown veins radiating from their point of attachment. Apothecia and pycnidia brown, on scyphus rims. Apothecia very rare; pycnidia frequent. Thallus C–, K–, KC–, Pd+ red, UV– (fumarprotocetraric acid). **BLS 0381**.

On damp mossy acid bark of older trees and vertical faces of damp, mossy non-calcareous rocks and walls, mainly in hilly and montane districts, only on older trees in the lowlands; widespread and under-recorded. New Forest and W. England, throughout Wales, W.C. Scotland (mainly Highlands), Channel Islands (Alderney), scattered in Ireland, mostly in the west.

Part of clade *Cladonia* subclade *Ascyphiferae* (Stenroos *et al.* 2019) and included in the *C. humilis* complex by Pino-Bodas *et al.* (2013a). When well-developed, characterized by the large squamules with pronounced radiating ± raised white to yellow-brown venation on the lower surface, veins K± reddish. Differs from *C. pyxidata* in having larger, veined, basal squamules, podetia with smaller granules and (sometimes) an additional unidentified compound along with fumarprotocetraric acid. Stunted material on bark cannot be separated from poorly grown *C. pyxidata*, but the latter is confined to base-rich bark.

Cladonia deformis (L.) Hoffm. (1796)

Similar to *C. sulphurina*, but with ± regular scyphi (despite its name) that tend to be less strongly yellow-pigmented but orange-yellow in necrotic basal parts. Thallus C–, K–, KC+ yellow, Pd–, UV– (usnic acid, zeorin).

On rotting, fallen pine trunks, Cairngorms (Glen Quoich).

See also under the *Cladonia coccifera* aggregate for comparison of chemistry. Zeorin can be detected as needle-shaped crystals on the surface of old dried specimens. Most old records of *C. deformis* need confirmation; they probably refer to *C. sulphurina*.

Cladonia digitata (L.) Baumg. (1790)

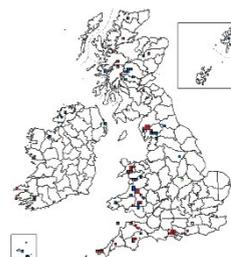
Podetia to 1 cm tall, often ± curved-decumbent, pointed or with irregular, mainly narrow scyphi which occasionally proliferate from their margins, the surface entirely farinose-sorediate or with a few corticate patches towards the base and also within the scyphi. Basal squamules to 1 cm diam., often dominant, ± horizontally spreading, often overlapping, ± rounded and entire, scarcely indented, yellowish green-grey above, densely white farinose-sorediate on the lower surface and on the upturned margins, often with a distinct orange tinge (K+ purple) on the lower surface towards the point of attachment. Apothecia and pycnidia red, occasional, at ends of pointed apices or on short projections from margins of scyphi. Thallus C–, K+ yellow, KC–, Pd+ yellow, UV– (thamnolic acid). **BLS 0383**.

On rotting wood, especially rotting tree stumps of conifers, more rarely on peaty soils, especially in mature woodlands; often locally common. Throughout Britain and Ireland.

Part of a well-supported clade within the species of *Cladonia* with red apothecia, that also includes *C. bellidiflora* and *C. polydactyla* (Stenroos *et al.* 2019).

The only species of *Cladonia* in Europe which is truly densely farinose-sorediate on the lower surface of basal

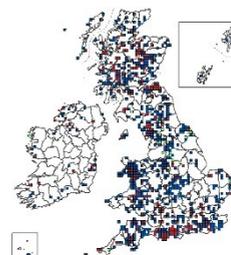
Nb



Nb



LC



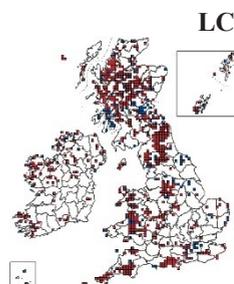
squamules. The squamules in *C. incrassata* and *C. parasitica* are often coarsely granular-sorediate, but are much smaller, deeply incised and compacted. In other species, e.g. *C. polydactyla*, the squamules may be sparsely sorediate, often the result of the shedding of soredia from associated podetia; *C. polydactyla* has smaller, more incised basal squamules and usually more numerous, erect podetia, which are never corticate within the scyphi.

Cladonia diversa Asperges ex S. Stenroos (2012)

Similar to *Cladonia coccifera*, but the podetia are regular to \pm uneven, densely squamulose, with corticate, easily detached granules, microsquamules and scale-like plates in the upper part and within the scyphi. Thallus C-, K-, Pd-, UV- (usnic and porphyritic acids, zeorin). **BLS 1749**.

On soil over rocks and walls, peat and sandy soils in heaths, tree bases and lignum etc., in upland and lowland habitats. Widespread and common throughout Britain and Ireland.

Part of the *Cladonia coccifera* aggregate; see under that species for more information. The minutely squamulose podetia are important in diagnosis (Ahti & Stenroos 2013), and they are generally more slender with narrower scyphi compared with other members of the group.

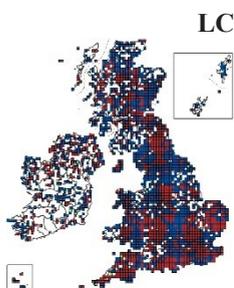


Cladonia fimbriata (L.) Fr. (1831)

Podetia 0.5–1.5 cm tall, greyish to (rarely) brownish green; scyphi to 0.5 cm diam., margins \pm regular, sometimes dentate, not proliferating, abruptly joined to a long stalk and appearing \pm goblet-shaped, farinose-sorediate throughout, including the base and within scyphi. Basal squamules numerous but often rather small and inconspicuous, \pm elongate and often incised. Apothecia and pycnidia brown, infrequent, on scyphus margins; apothecia sessile or shortly stalked. Thallus C-, K-, KC-, Pd+ orange-red, UV- (fumarprotocetraric acid). **BLS 0384**.

Often associated with mosses on recently disturbed sites, on rotten wood, in gardens and on old walls, occasionally in heathlands and dunes, absent from damp montane areas; common throughout Britain and Ireland.

Assigned to clade *Cladonia* subclade *Graciles* (Stenroos *et al.* 2019), and probably closely related to *C. chlorophaea*. Characterized by the abruptly expanded regular goblet-shaped scyphi, the absence of cortication and entirely farinose-sorediate podetia. *C. chlorophaea* has more gradually tapering scyphi, and corticate or \pm non-corticate podetia with coarsely granular soredia. A morph of *C. cryptochlorophaea* with slender podetia is frequent on acid bark and is often mistaken for *C. fimbriata*, but is KC+ wine red (fleeting). See also *C. carneola* and *C. humilis*.

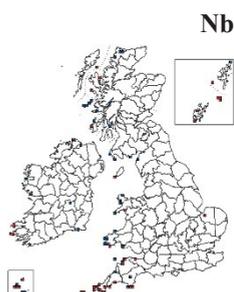


Cladonia firma (Nyl.) Nyl. (1861)

Basal squamules dominant, 0.4–1 cm tall, ascending, \pm elongate, indented, recurved at the apices when dry, contiguous, forming cushions; upper surface grey-green to dark brown with pruinose tips; lower surface white, \pm suffused pale to dark grey-violet. Podetia small, rare, 1–7 mm high, irregular, with shallow scyphi, corticate, somewhat verrucose. Apothecia dark brown, on nodulose extensions. Thallus C-, K+ yellow, KC-, Pd+ red, UV- (atranorin, fumarprotocetraric and \pm rangiformic acids). **BLS 0385**.

On neutral to basic soil, mostly on or near the coast, but has also been confirmed with sequencing from more acid inland sites. Occasional. W. Britain but often overlooked, Channel Islands, New Forest, S. Devon & Isles of Scilly, northwards to Shetland Islands (Unst), W. Ireland.

Related to *Cladonia subcervicornis*, the only other member of clade *Cladonia* subclade *Firmae* (Stenroos *et al.* 2018), which has basal squamules with pure white lower surfaces. Differs from *C. foliacea*, with which it often grows, also by the characteristic grey-violet toning of the lower surface of the recurved basal squamules, and in addition by the presence of atranorin (K+ yellow) and absence of usnic acid. The atranorin can be difficult to detect and the K/UV (dry)+ vivid neon yellow test is recommended. *C. cervicornis* has smaller squamules, and lacks atranorin.



Cladonia floerkeana (Fr.) Flörke (1828)

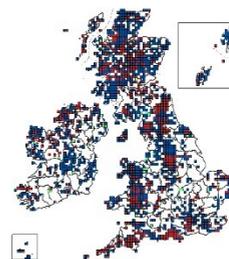
Podetia to 2 cm tall but often shorter, pale to dark grey, \pm tinged brown in exposed sites, without scyphi, unbranched

LC

or occasionally sparingly branched near the apices, \pm entirely corticate or becoming partially decorticate especially towards the apices, rarely granular-soresiate in patches but very frequently with coarse granules, or podetia becoming \pm entirely densely squamulose. Basal squamules small, persistent, inconspicuous, often tinged orange toward the base of the lower surface. Apothecia commonly abundant; hymenium and pycnidia red, terminal on podetia, single or clustered. Thallus C $^-$, K $^+$ yellow (rare) or K $^-$ (orange pigment reacts K $^+$ purple), KC $^-$, Pd $^-$, UV \pm blue (barbatic acid and, rarely, thamnolic acid). **BLS 0386.**

On heathland and moorland, also on mossy scree, well-rotted wood, fence posts and tree stumps in open situations; common throughout Britain and Ireland.

A member of clade *Erythrocarpae* subclade *Subglaucescentes*, closely related to *Cladonia macilenta* (Stenroos *et al.* 2019). Usually an abundantly fertile, and then conspicuous species, but the podetia are variable and may be almost entirely decorticate except for a few scattered corticate granules, or, conversely, densely squamulose throughout. *C. macilenta*, which may occur in similar habitats, is always partly to wholly finely soresiate and K $^+$ yellow. The closely related, but very rare, *C. alpina* has taller podetia, farinose to subgranular soresia and contains porphyritic acid.



Cladonia foliacea (Huds.) Willd. (1787)

Cladonia convoluta (Lam.) Anders (1906)

Cladonia angustiloba Ahti & Aptroot (2009)

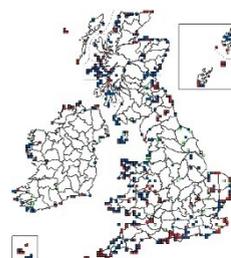
Podetia to 6 mm tall, often absent, smooth, \pm evenly corticate, with a \pm regular scyphus. Basal squamules predominant, elongate, 4–10 (–25) \times 1–3 (–8) mm, very variable, lobate to deeply incised, often ascending, recurved, forming compact mats or \pm straggling clusters; upper surface greyish yellow to yellow-green; lower surface pale yellow with occasional tufts of black, marginal hairs. Apothecia brown, on scyphus rims, very rare. Pycnidia dark brown, frequent on basal squamules. Thallus C $^-$, K $^-$, KC $^+$ yellow, Pd $^+$ red, UV $^-$ (fumarprotocetraric and usnic acids). Other chemotypes are found outside the region (Burgaz *et al.* 2020). **BLS 0387.**

In moss-lichen swards on well-drained \pm basic soils and humus-stabilized sand dunes and shingle, in wind-swept, sunny situations, sometimes in rock crevices in both acid and calcareous soils. Throughout Britain and Ireland, predominantly coastal, more rarely inland; common.

Cladonia convoluta has been distinguished from this species; it was described as having larger squamules (15–25 \times 2–8 mm) and occurring in calcareous habitats (James 2009), but Pino-Bodas *et al.* (2010a) could not find any consistent differences between the two taxa based either on morphological or molecular data. Results were confirmed by Pino-Bodas *et al.* (2018). They also established that *C. angustiloba* (Ahti & Aptroot 2009), recently reported from the Shiant Is (Outer Hebrides), should be treated as a further synonym of *C. foliacea*.

Cladonia foliacea often occurs with *C. firma*, which has squamules which are white, \pm suffused violet-grey, below. *C. luteoalba*, also with yellowish squamules, has \pm rounded, scarcely indented squamules with a pale yellow, cottony-arachnoid lower surface, and is Pd $^-$.

LC



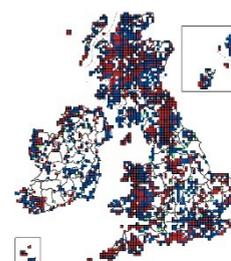
Cladonia furcata (Huds.) Baumg. (1790)

Cladonia furcata subsp. *subrangiformis* (Sandst.) Abbayes (1938)

Podetia 2–5 (–8) cm tall, 0.4–1.0 mm diam., green to dark grey-green or olive-brownish in more open situations, slender, hollow, \pm dichotomously branched, forming \pm spiky, irregular tufts, the apices markedly pointed, without scyphi, the axils closed or sometimes perforate, fertile podetia with longitudinally split tips; surface corticate throughout, smooth, often faintly pale marbled-areolate, occasionally with scattered squamules and cracks. Basal squamules disappearing, rounded, to 3 mm diam.; lower surface white. Apothecia brown, on short lateral branches towards the apices, \pm corymbose, rather frequent. Pycnidia dark brown, terminal, abundant. Thallus C $^-$, K \pm yellow, KC $^-$, Pd $^+$ red, UV $^-$ (fumarprotocetraric acid, rarely traces of atranorin). Other chemotypes are found outside the region (Ahti & Stenroos 2013; Burgaz *et al.* 2020). **BLS 0389.**

On heathlands, dunes, grasslands and lawns, mossy rocks in woodlands and mountain summits, often preferring \pm acid habitats but also in humus and litter on basic rocks where it often occurs with *C. rangiformis*; an ecotype

LC



(see below) occurs on calcareous soils in short turf, particularly on chalk. Common throughout Britain and Ireland.

Very variable, but characterized by the ascending, \pm dichotomously branched podetia with pointed apices and a tendency to form irregular tufts. *Cladonia furcata* subsp. *subrangiformis* was recognized by James (2009) and at species level by Ahti & Stenroos (2013), but a phylogenetic study by Pino-Bodas *et al.* (2016) could not distinguish adequately between the two taxa; the morphological differences may be at least partially habitat-related. It differs in the presence of raised starkly white \pm circular concretion-like spots (of calcium oxalate crystals) towards the base of the olive to dark brown podetia formed by local rupturing of the cortex; the often prostrate and little-branched, worm-like, habit and robust appearance; and the presence of short lateral branches which often arise \pm at right angles from podetia, more frequent in calcareous soils.

Cladonia gracilis is less branched and some podetia develop small scyphi; the juvenile stages of these two species are often difficult to separate. Easily confused with *C. rangiformis*, which is more richly branched, the branches diverging at a wider angle and has a mature cortex which is mosaic-like with raised patches of green areoles on a pale decorticate background ($\times 10$ lens). For differences from *C. scabriuscula* and *C. stereoclada*, see under those taxa.

Cladonia glauca Flörke (1828)

Podetia 1–5 cm tall, pale grey to brownish with pointed apices, or with narrow perforate scyphi, mostly unbranched, or 2- to 3-branched towards the apices, often with a single inconspicuous longitudinal slit-like fissure \pm midway along the main podetium (in branched specimens the axils may also be perforated), often densely squamulose in the lower part, densely and finely sorediate in the upper part, sometimes also with scattered squamules extending upwards from the base. Basal squamules small, often inconspicuous, \pm elongate and incised, greyish green above, white below. Apothecia brown, very rare. Pycnidia brown, on apices of podetia, frequent. Thallus C–, K–, KC–, Pd–, medulla UV+ vivid white (squamic acid) or Pd+ yellow, UV– (thamnolic acid).

BLS 0391.

On old, rotting tree stumps, also on peat in heathlands; widespread. Scattered throughout Britain and Ireland, apparently commoner in Scotland.

Part of the *Perviae* clade, and apparently closely related to *Cladonia cenotea* (Pino-Bodas *et al.* 2010b, Stenroos *et al.* 2019) which has somewhat more robust podetia with more well-developed perforate scyphi; see under that species for further discussion.

When sterile, *Cladonia glauca* may be confused with the red-fruited *C. macilenta*, which has no lateral furrow and is K+ yellow, UV+ pale blue. *C. subulata*, when well-developed, has antler-like branching and is Pd+ red, UV– (fumarprotocetraric acid); claimed distinctions between the two species based on furrowing of the podetia seem to be unreliable. See also *C. rei*.

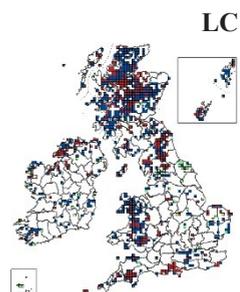
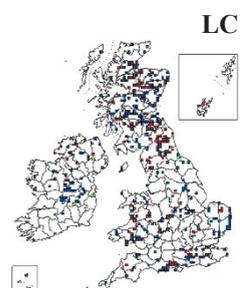
Cladonia gracilis (L.) Willd. (1787)

Podetia 1–6 cm tall, slender, 0.5–1.5 mm diam., greenish grey or often olive to dark brown, often becoming dark brown-black towards the base, unbranched or sparingly branched, pointed at apices or usually some with a terminal, \pm regular, shallow scyphus 1–2 mm in diam., not perforate, often with dentate margins, sometimes proliferating from the rim; surface smooth, corticate, usually conspicuously but finely areolate ($\times 20$ lens), attached squamules usually absent or scarce. Basal squamules to 2 mm, indented, mostly disappearing. Apothecia and pycnidia dark brown, at apices of podetia; apothecia rather rare; pycnidia frequent. Thallus C–, K–, KC–, Pd+ red, UV– (fumarprotocetraric acid).

BLS 0392.

On sandy or acid soil, amongst rocks and more rarely on rotting wood, in heathlands, dunes and in montane situations; frequent. Throughout Britain and Ireland, commoner in the north and west.

Several subspecies are recognized in Scandinavia (Ahti 1980, Ahti & Stenroos 2013), although they are questionably distinct in phylogenetic terms (Fontaine *et al.* 2010, Pino-Bodas *et al.* 2012a); only subsp. *gracilis* is known from Britain and Ireland. Characterized by the slender habit and clustered, smooth, mostly unbranched, erect podetia, some of which are either pointed or terminate in small, non-perforate scyphi. *Cladonia furcata* lacks scyphi and has perforate branch axils; *C. cornuta* has a similar habit but podetia have a sorediate upper half and smooth, corticate lower part; *C. crispata* var. *cetrariiformis* has perforate scyphi, is more branched and is Pd–, UV+ white (squamic acid). See also *C. maxima* and *C. trassii*.



Cladonia grayi G. Merr. ex Sandst. (1929)

Podetia to 2 (–3) cm tall, greenish or pale grey and usually with a distinct brown tinge, sometimes blackened at the base, usually unbranched, the stalk ± corticate, verrucose-areolate, often squamulose; scyphi regular, to 7 mm diam., rarely proliferating, sorediate, the soredia easily eroding and mixed with microsquamules. Basal squamules inconspicuous, soon evanescent. Apothecia rare, ± dark brown, on stalks developing from the scyphus margin. Thallus C–, K–, KC–, Pd± red, UV+ mauve-white (grayanic and ± fumarprotocetraric acids). **BLS 0393**.

On strongly acid peat and sandy soils on banks, pathsides etc. in heathland and moorland, very rarely on acid bark; scattered, certainly under-recorded but always infrequent. Apparently absent from Ireland.

Part of a frequently recognized morphocomplex that traditionally includes *Cladonia chlorophaea* (see above and e.g. James 2009), but that species is phylogenetically distinct and may be separable in morphological terms; the podetia in *C. grayi* s. lat. [**BLS 2810**] are browner and more completely corticate and granulose, rarely with large soredia. It is included in a subclade separate from that containing *C. chlorophaea* within clade *Cladonia* subclade *Graciles* (Stenroos et al. 2019), and seems to be polyphyletic.

Species within the *Cladonia grayi* aggregate include *C. asahinae*, *C. cryptochlorophaea*, *C. merochlorophaea* and *C. novochlorophaea* [see table under *C. chlorophaea* above]. They are difficult to determine using morphology, and are arguably conspecific. TLC is mostly recommended to confirm identification. The presence of grayanic acid (leading to the distinctive bright UV+ mauve-white reaction) is considered to be diagnostic for *C. grayi* s. str., with some populations also producing fumarprotocetraric acid (Pd+ red).

**Cladonia humilis** (With.) J.R. Laundon (1984)

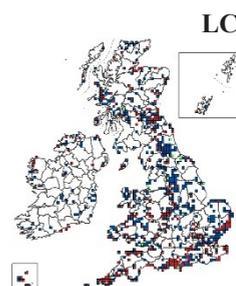
Podetia to 5 (–7) mm tall, grey or rather bright green-grey; scyphi to 6 mm diam., even, regular, only proliferating from the rim when apothecia are developed, abruptly tapered to a short stalk, often sessile, continuously and persistently corticate for a 1–2 mm zone at the base, entirely densely farinose-sorediate above and within scyphi. A morph with large corticate bullate granules replacing the farinose soredia occasionally occurs. Basal squamules often rather large, to 5 mm diam., ± rounded, sparingly incised, often well-developed and forming a continuous carpet, bright green-grey with upturned ends showing bright white undersides when dry. Apothecia and pycnidia brown, rare, on scyphus rim. Thallus C–, K± yellow, KC–, Pd+ red, UV– (atranorin and fumarprotocetraric acids). **BLS 0376**.

Mainly on dry or sandy, less acid but non-calcareous ground, especially on recently disturbed soils, roadsides, sea cliffs, bonfire sites and rockery stones and paths in suburban gardens, absent from montane areas; frequent and widespread. Throughout Britain and Ireland.

Characterized by the sessile short regular scyphi, with farinose soredia and a smoothly corticate surface. The only brown-fruited, sorediate species that contains atranorin in Europe. The K test can be problematic in this species, but soredia show a clear K+ yellow reaction if barely spotted (brushed with a wet pipette tip) with a very small amount of K. However, K– chemotypes are known from elsewhere (Burgaz et al. 2020).

The schizidiate morph with large corticate bullate granules replacing the farinose soredia has been confused with *Cladonia pocillum*, but this has browner imbricate compact rosettes of basal squamules, with recurved squamule tips, is K– and grows on more calcareous soils. The schizidiate morph was considered possibly to belong to the American species *C. pulvinella* or *C. hammeri*, but Pino-Bodas et al. (2013a) showed that such European material clusters with *C. humilis*.

Cladonia conista was considered only as a bourgeanic/fumarprotocetraric acid chemotype of *C. humilis* by James (2009), but is treated as a separate species by Ahti & Stenroos (2013), and Pino-Bodas et al. (2012b, 2013a) showed that there are clear sequence differences between the two taxa. *C. fimbriata* has the podetial surface completely covered by farinose soredia. *C. chlorophaea* has a granulose corticate surface.

**Cladonia incrassata** Flörke (1826)

Podetia mostly 2–5 mm tall, infrequent, often deformed, unbranched or ± distortedly branched, or produced as an extension of a squamule, ± flattened with a partly corticate-granular and sorediate surface. Basal squamules to 4 mm diam., dominant, ± numerous, yellowish grey-green, often contorted, crenulate-incised, usually conspicuously farinose-granular sorediate below, occasionally also above, ± erect, ± tinged orange at the point of attachment (K+

Nb

purple). Apothecia red, frequent, usually sessile on the upper surface and extended margins of the squamules, more rarely on short, sometimes flattened \pm corticate irregular podetia. Thallus C $-$, K $-$, KC $+$ yellow, Pd $-$, UV $+$ white, bluish, or rarely UV $-$ (rarely K $+$ yellow, KC $-$, Pd $+$ yellow). There are three chemotypes: (a) usnic, squamatic and didymic acids; (b) usnic, squamatic and barbatic acids; (c) squamatic, didymic and thamnolic acids. **BLS 0394.**

Very locally frequent on damp soft sandstone and on acid, peaty soil in heathland or on old cut surfaces of peat, more rarely on damp lignum; local but easily overlooked. Scanning with a UV torch makes it easier to spot. From S. England & Wales to W. & N. Scotland (Cairngorms, Sutherland), Shetland, scattered records throughout Ireland, where it is probably frequent on old peat cuttings.

A species without close relatives, the only representative of clade *Erythrocarpae* subclade *Incrassatae* (Stenroos *et al.* 2013). The small \pm sessile red apothecia, yellowish thallus and chemistry are diagnostic. Chemotype (c) is very rare.

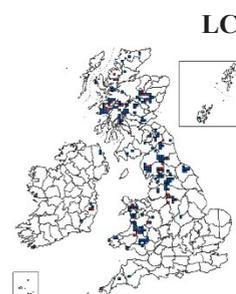


Cladonia luteoalba Wheldon & A. Wilson (1907)

Podetia to 1 cm, rare, decorticate and bluntly subulate or with narrow scyphi, markedly curved, \pm blackened at the base when old, often \pm hidden among squamules. Basal squamules 2–10 mm diam., dominant, greenish yellow above, \pm rounded and entire, scarcely indented, sometimes \pm elongate, the margins ascending, when dry curved upwards exposing a pale yellow, distinctly cottony-arachnoid lower surface ($\times 20$ lens). Apothecia and pycnidia red. Apothecia rare, on margins of narrow scyphi, or sessile on squamules. Thallus C $-$, K $-$, KC $+$ yellow, Pd $-$, UV \pm white (three chemotypes occur: (a) usnic acid, zeorin and \pm porphyritic acid (widespread); (b) usnic and barbatic acids (rare, Isle of Mull); (c) usnic, squamatic and didymic acids (rare, Cairngorm Mountains). **BLS 0395.**

On peaty soils, mossy boulders (sometimes under *Pteridium aquilinum*) and on rock ledges and walls in exposed heathlands and on mountain summits, more rarely on bases and boughs of old trees. N. England (Lake District, Pennines) extending to S.W. England (Cornwall), Wales and Scotland north to Caithness, also S.E. and N.E. Ireland.

Sometimes found growing on other *Cladonia* species (such as *C. coccifera*) and potentially starting life as a parasite. Apparently close in phylogenetic terms to *C. deformis* and *C. pleurota* (clade *Erythrocarpae* subclade *Subglaucescentes*) according to Stenroos *et al.* (2002), but the status of these species is uncertain and more molecular data are needed. Recognized by the conspicuous large curled squamules, pale yellow (K $-$) which are finely cottony arachnoid below ($\times 20$ lens), a feature which distinguishes it from all other species with well-developed basal squamules. The similarly coloured *C. foliacea* has deeply incised squamules, is not cottony arachnoid below, contains fumarprotocetraric acid (Pd $+$) and occurs in different habitats.

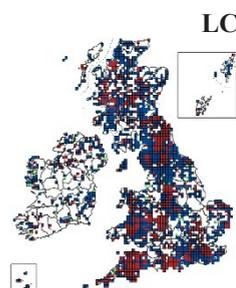


Cladonia macilenta Hoffm. (1796)

Podetia to 1.5 (–3) cm tall, often less, white to pale grey, often tinged orange where abraded, pointed at the apices, without scyphi, usually unbranched or rarely sparingly branched near the apices, often curved and \pm decumbent, usually \pm entirely farinose, at times patchily decorticate, rarely bearing squamules, particularly near the base. Basal squamules small, pale grey above, \pm elongate, much indented, rarely sparingly sorediate below. Apothecia and pycnidia red, at tips of podetia, single or clustered, rather frequent. Thallus C $-$, K $+$ yellow-orange, KC $-$, Pd $+$ yellow, UV $-$ (thamnolic, barbatic and \pm didymic acids). **BLS 0396.**

Mainly on well-lit strongly acid humus and lignum in acid open woodlands and heathlands; localized and infrequent, but much over-recorded for morphs of *Cladonia polydactyla* without scyphi. Probably throughout Britain and Ireland, but much rarer in lowland areas than suggested by the map.

A member of clade *Erythrocarpae* subclade *Subglaucescentes*. Squamulose morphs of *Cladonia macilenta* may be difficult to separate from juvenile, shaded or pollution-stressed morphs of *C. polydactyla* which may develop distinctive scyphi only at a late stage of development. *C. macilenta* can be separated by the farinose soredia on the podetia as opposed to the coarsely granular soredia of *C. polydactyla*. The blue-grey colours, often characteristic of *Cladonia polydactyla*, are not seen in *C. macilenta* which is typically white to pale grey. Specimens reacting C $-$, K $-$, KC $+$ pale yellow or KC $-$, Pd $-$, UV $+$ pale blue or UV $-$ (barbatic and \pm didymic acids), were named as *C.*



bacillaris (Ach.) Genth, but are best considered as chemotypes of *C. macilenta*; when sterile these may superficially resemble *C. glauca* which, however, contains squamatic acid (UV+ vivid white) and usually has a single, obscure longitudinal fissure ± midway down the sides of taller, more slender podetia.

Cladonia macrophylla (Schaer.) Stenh. (1865)

Podetia 2–4 (–5.5) cm tall, grey-green to brown, often contorted, unbranched or sparingly branched particularly in the upper half, without scyphi, the apices ± blunt, the surface often ridged, fissured and gaping-lacerate, with numerous ± discrete crowded rounded to peltate squamules intermingled with grey or black decorticate patches, especially towards the base. Basal squamules 3–6 mm diam., often well-developed, often forming mats, round or elongate, ± incised, the upper surface greenish and the lower surface white. Apothecia and pycnidia brown, frequent, terminal on podetia; pycnidia also on peltate squamules of podetia. Thallus C–, K–, KC–, Pd+ yellow, UV– (psoromic acid). **BLS 0397.**

Montane, on acid peat, especially on scree and amongst mossy boulders, also associated with mine spoil heaps; rare and local. Scotland (Highlands) with outliers (Snowdonia, N. Wales & Dartmoor, Devon).

Included within clade *Cladonia* subclade *Macropus* by Stenroos *et al.* (2019), that only contains two species, both of which produce psoromic acid. It is characterized by the ridged-fissured, partly decorticate podetia with scattered to crowded peltate squamules; the presence of psoromic acid is diagnostic.



Cladonia maxima (Asahina) Ahti (1978)

Like *C. gracilis*, but with more robust, ± swollen and mostly subulate podetia, to 3 mm diam. and 5 cm tall, which are unbranched or 1- to 2-forked towards the apex, and the glaucous tinge, often brownish towards the apex and pale ochre-yellow towards base; surface even, uniform, occasionally with white flecks and lines (×20 lens). Scyphi very rare, narrow, barely wider than the podetium, rim irregularly dentate, occasionally with a single marginal proliferation. Podetial squamules rare, basal squamules absent. Thallus C–, K± yellow, KC–, Pd+ red, UV– (fumarprotocetraric acid and rarely atranorin). **BLS 0398.**

Deeply embedded in boggy alluvial grassland dominated by *Nardus stricta* and moss tussocks above 900 m, often in the vicinity of late snow-lic; rare. N. Scotland (Cairngorm Mountains, W. Inverness, Aonach Mór).

Part of clade *Cladonia* subclade *Graciles*; considered to be monophyletic by Fontaine *et al.* (2010) and Pino-Bodas *et al.* (2012a), but clustering within *C. gracilis* s.l. according to Stenroos *et al.* (2019).



Cladonia mediterranea P.A. Duvign. & Abbayes (1947)

Like *Cladonia portentosa*, but with isotomic or subisotomic branching, predominantly dichotomous (particularly near the tips), and with the surface of the podetia more compact, smooth and matt. Thallus C–, K–, KC+ yellow, Pd–, UV+ bluish (perlatolic, usnic acids). **BLS 0399.**

On ± basic soils associated with serpentine; rare. S.W. England, confined to The Lizard peninsula and the New Forest, where it is uncommon.

The species was studied in detail by Pino-Bodas *et al.* (2015b), and confirmed to be separate from *Cladonia portentosa*, which has a similar chemistry but with predominantly trichotomous branching. ITS sequences were used to compare British and Mediterranean material by Russell *et al.* (2002), confirming the presence of the species in our region, but more detailed phylogenetic analysis would be useful.



Cladonia merochlorophaea Asah. (1940)

Similar to *Cladonia chlorophaea* and *C. grayi*, but greenish-brown with relatively large scyphi and producing rather varied granulate propagules and minute flaking squamules; sometimes entirely without soredia; the exposed medulla pinkish brown. The base of podetia are frequently strongly melanized. Thallus C+ red, K–, KC+ wine red, Pd± orange-red, UV+ faint blue (merochlorophaeic, 4-O-methylchlorophaeic and ± fumarprotocetraric acids). **BLS 0400.**

NE

On acid humic soils, also on rotten wood, roots etc.; scattered but apparently frequent throughout Britain and Ireland. Typically on more acid substrates than the commoner *C. cryptochlorophaea*.

Part of the *Cladonia chlorophaea/grayi* aggregate, differentiated primarily by chemical characteristics; see under those species for more information. *C. merochlorophaea* shares the distinctive KC+ fleeting wine red reaction with *C. cryptochlorophaea*. The C+ red spot test is best seen on damp material. Generally browner and coarser than *C. cryptochlorophaea*, but TLC is recommended for identification.



Cladonia mitis Sandst. (1918)

Cladonia arbuscula subsp. *mitis* (Sandst.) Ruoss (1987)

Like *Cladonia arbuscula*, but more slender, paler grey and the apices less branched. The \pm recurved terminal branches are also less strongly, or not at all, orientated in one direction. Thallus C-, K-, KC+ yellow, Pd- (rarely Pd+ red), UV- (usnic and usually rangiformic acids, rarely, also fumarprotocetraric acid). **BLS 0402.**

On acid dunes and stabilized pebble beaches; very rare, but locally abundant in some dunes in E. Scotland. S.E. England (Dungeness), E. Anglia (Norfolk), E. Scotland.

James (2009) suggested that *Cladonia mitis* might better be treated as a subspecies of *C. arbuscula*, as in central Europe and elsewhere *C. arbuscula* and *C. mitis* were reported to form local populations of intermediates. However, they were considered to be separate species by Ahti & Stenroos (2013). Athukorala *et al.* (2016) and Stenroos *et al.* (2019) showed that *C. mitis* is monophyletic, and the two species are phylogenetically distinct.



NT

Cladonia norvegica Tønsberg & Holien (1984)

Like *Cladonia macilenta*, but thalli with finely divided basal squamules, often with a reddish medulla and blemished with minute ($\times 20$ lens), scattered, superficial red spots, K+ purple, resulting from mite infestation. Apothecia and pycnidia absent in British populations; known to be ochraceous or pinkish in material from other localities. Thallus C-, K-, KC-, Pd-, UV+ bluish (barbatic acid). **BLS 1654.**

On mossy rocks and trunks of old trees, especially *Betula*, in old woodland; rare or overlooked. Somerset (Exmoor), Wales (Cardigan, Snowdonia), Scotland (Kintyre to W. Ross).

It is suggested that the red spotting, a characteristic of this species in our region, is a reaction of this lichen to infestation by mites (probably *Carabodes marginatus*). This characteristic red-spotting is absent in many areas abroad. Molecular data are not available.



Nb

Cladonia novochlorophaea (Sipman) Brodo & Ahti (1996)

Cladonia merochlorophaea var. *novochlorophaea* Sipman (1973)

Close in morphology to *Cladonia chlorophaea*, but the podetia are usually entirely without soredia, dark brown and often blackened at the base, and verruculose. Thallus C+ yellow, K-, KC-, Pd \pm orange-red, UV+ white (sekikaic, homosekikaic and \pm fumarprotocetraric acids). **BLS 2337.**

On peaty soil or decaying wood, and on mine spoil; apparently rare. Reported from England (Cumberland, Shropshire, Surrey) but likely to be under-recorded. A collection from Scotland (E. Inverness) is cited by Stenroos *et al.* (2019).

See under *Cladonia grayi* for a comparison of chemistry between these two taxa. The dark brown verruculose podetia also provide a good indicator for identification.



NE

Cladonia parasitica (Hoffm.) Hoffm. (1796)

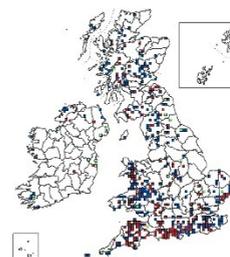
Podetia to 0.5 (-2) cm tall, rather rare, often conspicuously elevated above the basal squamules, without scyphi, irregular, deformed, contorted, sometimes flattened and very irregularly branched, often appearing \pm subcoralloid, often \pm covered in small, isidium-like granules and partly decorticate, with scattered or numerous squamules and granules, fissured with gaping holes when well-developed. Basal squamules to 0.5 cm long, 0.2-1 mm wide, numerous, elongate, greatly dissected, often coralloid-branched, \pm ascending, often coarsely granular-sorediate,

LC

forming crowded, compact, ± continuous spreading mat-like swards; upper surface pale to dark grey, lower surface white. Apothecia small, dark brown, at tips of podetia, often on extended projections, mostly clustered. Pycnidia dark brown-black, on the upper surface of basal squamules; Thallus C-, K+ yellow, KC-, Pd+ yellow, UV- (thamnolic and, restricted to apothecia, ± barbatic acids). **BLS 0404**.

On ± decaying, decorticated wood of branches, trunks, stumps and logs especially of *Quercus* and less frequently on *Pinus* in older woodland, more rarely on consolidated soil of earth banks in woodlands and heathlands. Widespread but rather local throughout England & Scotland mainly in wooded sites, rare in Ireland.

A member of clade *Perviae* (Stenroos *et al.* 2019). Resembles the unrelated *Cladonia incrassata* in habit, which, however, has contorted, flattened yellowish squamules with podetia-like contortions or extensions bearing red apothecia and which contain usnic acid, and is usually strongly UV+ white or bluish. *C. squamosa* has larger, less dissected, peeling squamules and larger podetia, which are often perforate. Poorly grown sterile mats of *C. polydactyla* squamules on wood have the same chemistry, but the squamules are never subcoralloid.



Cladonia peziziformis (With.) J.R. Laundon (1984)

Podetia to 1 cm tall, brownish grey-green, usually unbranched, ± granular-corticate with partly decorticate areas, occasionally fissured and bearing a few squamules; scyphi and soredia absent. Basal squamules small and granule-like or becoming ± rounded or ear-shaped, rather thick, with dark brown-black pycnidia on the upper surface, scattered when mostly horizontal, or forming a ± continuous crust and then ± erect. Apothecia frequent, dark brown, produced mostly singly at the apex and characteristically exceeding the width of the stalk-like podetia, mostly unbranched, but secondary apothecia on short lateral branches are sometimes produced which may fuse with the main apothecium. Thallus C-, K-, KC-, Pd+ red, UV- (fumarprotocetraric and ± ursolic acids). **BLS 0365**.

On mildly enriched acid soils, mainly in coastal heaths but also inland in lowland heathland; requiring short well-lit vegetation, ranging through parched acid grassland, *Calluna*-dominated heath to *Schoenus nigricans* – *Molinia caerulea* – *Ulex gallii* wet heath. In heavily grazed heaths it forms long-lived populations, but in lightly grazed situations it is often a short-lived pioneer colonizer following localized burning; very rare, few recent records, but with a substantial population discovered recently on Ashdown Forest. W. and S. Britain, W. and N.E. Ireland.

Part of clade *Cladonia* subclade *Ascyphiferae* (Stenroos *et al.* 2019). Characterized by the short, longitudinally fissured podetia bearing a single large terminal apothecium. *C. cariosa* is larger, usually has several, proportionately smaller, apothecia in a ± corymbose arrangement on the longitudinally fissured podetia, and contains atranorin.

CR (A)



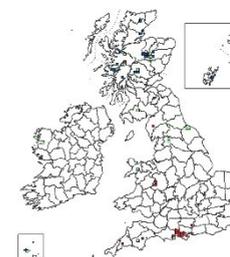
Cladonia phyllophora Hoffm. (1796)

Podetia 1–5 cm tall, the surface in part subarachnoid, ± coarsely areolate especially toward the apices, matt, pale grey-brown, notably appearing more areolate towards the base, with contrasting blackened decorticate areas notably appearing pale-maculated; scyphi irregular, with often extended and uneven proliferation from irregularly dentate margins, which often form extensive ± interlocking tiers; scyphi and lower parts of podetia variously squamulose. Basal squamules mat-forming in young material, becoming ± scattered, small, ± rounded at maturity, greenish grey on the upper side, white below. Apothecia rare; apothecia and pycnidia terminal on podetia, brown. Thallus C-, K-, KC-, Pd+ red, UV- (fumarprotocetraric acid). **BLS 0405**.

On heathland and mossy rocks in montane situations and high-quality lowland heaths; rare and local. S. and S.W. England, Norfolk, Shropshire & N. Scotland; old records from N. Wales. Certainly under-recorded.

Belongs to clade *Cladonia* subclade *Foliacea* (Stenroos *et al.* 2019), forming a monophyletic grouping with *C. ramulosa*. A polymorphic species, usually forming compact turgid interlocked clusters of proliferating, irregular podetia, the lower part with pale areoles on a black necrotic medulla. Sometimes confused with *C. ramulosa* but characteristic pale grey spotting on a black surface of the cortex towards the base of the podetia is absent in that species. It also typically has significant decorticate patches on the podetia that are lacking in *C. phyllophora*. *C. gracilis* has more regular scyphi, a smooth, non-arachnoid cortex and the podetia have uniformly brownish black

NT



bases. *C. trassii* has central proliferations and contains atranorin. *C. cervicornis* also has central proliferations and has brown tinges on the underside of the basal squamules.

Cladonia pleurota (Flörke) Schaer. (1850)

Podetia yellowish or pale green, unbranched, with regular scyphi to 0.7 (–1.5) mm diam.; surface granulose, sorediate inside and on the upper margins of scyphi, continuously corticate below. Basal squamules persistent, lobated to crenate. Apothecia rare (not known in British material), pycnidia black to reddish on margins of scyphi, sometimes stipitate, containing red gel. Thallus C–, K–, Pd–, UV– (usnic, isousnic and porphyrylic acids, zeorin). **BLS 0406.**

On *Racomitrium* heath and rocks near areas of late snow-lie, also upland heathlands; very rare. N. Wales, N.E. Scotland (Cairngorm Mountains), scattered elsewhere.

Similar to the *Cladonia coccifera* aggregate (see that species for more information) but the podetia are regular, broadly cup-shaped, and coated with coarse, granular soredia. Sometimes squamulose and ± corticate at the base. British material needs critical revision and much resembles the unrelated *C. carneola*, which has brown rather than red apothecia and pycnidia.

DD



Cladonia pocillum (Ach.) Grognot (1863)

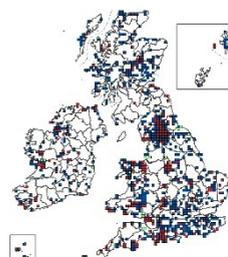
Like *Cladonia pyxidata*, but with particularly well-developed, ± horizontally spreading, thick, contiguous and overlapping basal squamules, which tend to radiate at the margins to form ± imbricate, compact rosettes, white below, softly pulverulent inside. The podetia are coarsely granular-corticate as in *C. pyxidata*. Thallus C–, K–, KC–, Pd+ red, UV– (fumarprotocetraric acid, rarely trace of atranorin). **BLS 0407.**

Mainly on sandy, calcareous soils, old mortar on walls, calcareous dunes and soils overlying calcareous rocks; common. Throughout Britain and Ireland.

Considered by James (2009) possibly to be a calcicole ecotype of *Cladonia pyxidata*, but without apparent intermediates. That hypothesis was tested by Kotelko & Piercey-Normore (2010) using molecular methods, but only American collections were studied and Stenroos *et al.* (2019) considered that *C. pyxidata* s.l. was a polyphyletic entity. The two species are kept separate here, pending more detailed molecular and ecological analyses.

This species is a common primary host for *Diploschistes muscorum*.

LC



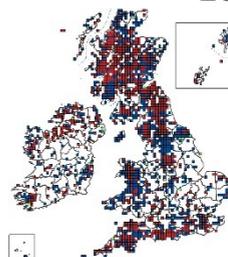
Cladonia polydactyla (Flörke) Spreng. (1827)

Podetia 1–2 (–3) cm tall, pale grey to whitish or greenish grey, pointed at first, later with narrow, usually irregular, abruptly tapering scyphi (to 5 mm diam.), often variously proliferating from margins or remaining dentate, usually unbranched, occasionally sparingly branched near the apices, ± entirely farinose- to coarsely granular-sorediate and mixed with squamules which are particularly frequent near the base, at times patchily decorticate, especially above. Basal squamules small, incised, occasionally ± thinly sorediate below and often with orange pigmented (K+ purple) regions at base. Apothecia and pycnidia red, at apices of podetia, single or clustered, rather frequent. Thallus C–, K+ yellow-orange, KC–, Pd+ yellow, UV– (thamnolic acid). **BLS 0408.**

On rotting wood, also on soil and amongst mosses in woodlands and heathlands in hilly and low-lying areas; often common. Throughout Britain and Ireland.

Part of clade *Erythrocarpae* subclade *Glaucescentes* (Stenroos *et al.* 2019). Very variable, characterized by podetia which bear narrow irregular proliferating scyphi, often with intermixed soredia and squamules. Specimens that are young or from polluted sites lacking scyphi are very common; these can be separated from *Cladonia macilenta* (which always lacks scyphi) by the coarsely granular soredia of *C. polydactyla* as opposed to the farinose soredia of *C. macilenta*. *C. macilenta* has been much over-recorded for stunted *C. polydactyla* lacking scyphi; the latter is generally more widespread than true *C. macilenta* except in strongly acid habitats, especially heathland. In more shady or pollution-stressed sites, *C. polydactyla* without scyphi often occurs with *C. coniocraea* when it may be identified by the coarse soredia and by its characteristic grey-blue colour (unchanged when wet) in contrast to the dark green colour of *C. coniocraea* (brighter green when wet). *C. digitata*, which may occur in similar habitats, has larger rounded squamules with conspicuously and densely sorediate lower surfaces. *C. umbricola*, treated by James (2009) as a variety of *C. polydactyla*, is Pd– and UV+ white (squamic acid). See under that species for more information.

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Cladonia portentosa (Dufour) Coem. (1865)

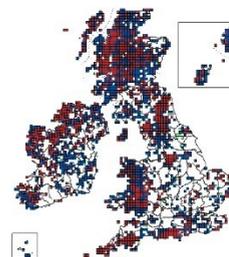
Cladonia azorica Ahti (1961)

Primary thallus crustose, evanescent. Podetia 4-10 cm tall, grey-green and often with a yellowish green tinge, the surface often roughened, areolate particularly towards the base, richly branched; terminal branches mostly \pm erect, not orientated in one direction, forming broccoli-like, rounded heads, the branching predominantly trichotomous at the apices, often with perforated axils. Pycnidial jelly colourless. Thallus C-, K-, KC \pm yellow, Pd- or PD+ red (morphs previously referred to *C. azorica*), UV+ pale blue (perlatolic and usually usnic acid, \pm fumarprotocetraric acid). **BLS 0409**.

On heathlands, moorlands and dunes, also not uncommon on old leaning and fallen trees in open woodland; abundant. Throughout Britain and Ireland.

Belongs to the *Impexae* clade. Characterized by the unorientated terminal branches and distinctive chemistry (especially the presence of perlatolic acid). Very variable, often forming mats of neat tufts amongst low vegetation, sometimes with \pm distorted main branches; \pm inflated-bloated and grossly modified morphs can occur in boggy situations.

Cladonia azorica was differentiated by more delicate Pd+ red thalli with \pm erect, very thin terminal branches that do not form broccoli-like rounded heads, but Pino-Bodas *et al.* (2015b) found that collections identified as this species clustered within the broad *C. portentosa* clade. However, this morph has a distinct ecology in Britain being found on mossy rocks in western woodland, it also more often lacks usnic acid than the typical morph. Pino-Bodas and colleagues also demonstrated that *C. mediterranea* is a related but distinct species (see above).



LC

Cladonia pulvinata (Sandst.) van Herk & Aptroot (2004)

Cladonia cervicornis subsp. *pulvinata* (Sandst.) Ahti (1983)

Similar in morphological terms to *Cladonia cervicornis* but with a different chemistry, containing psoromic rather than fumarprotocetraric acid, and slender podetia. It is further characterized by the broad, \pm vertical basal squamules and often more slender podetia. Thallus C-, K-, KC-, Pd+ yellow, UV-. **BLS 0308**.

On soil in heathland, mine spoil and coniferous woodland. Rarely reported and probably under-recorded, known only from N. England (Cleveland, Cumbria) & C. Scotland (Perth, S. Aberdeen).

Formerly erroneously ascribed to *Cladonia rappii* A. Evans, a widely distributed but primarily American species, which does not occur in Europe. *C. pulvinata* has been shown to be phylogenetically distinct from *C. cervicornis* (Pino-Bodas *et al.* 2010a, Stenroos *et al.* 2019), and probably more closely related to *C. subulata* and *C. verticillata*. The morphological differences among *C. cervicornis*, *C. pulvinata* and *C. verticillata* were studied by van Herk & Aptroot (2003).



NE

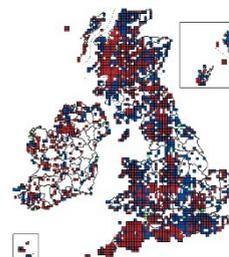
Cladonia pyxidata (L.) Hoffm. (1796)

Cladonia monomorpha Aptroot, Sipman & van Herk (2001)

Podetia 0.5-1.5 (-3) cm tall, grey, occasionally \pm brownish; scyphi 3-10 mm diam., \pm regular, rarely proliferating from the rim, tapering regularly towards the base, stalk very short or hardly present; surface uneven with coarse, smooth, corticate granules, particularly well-developed within the scyphi, often with scattered, partially decorticate pale areas; soredia absent. Basal squamules often rather small, rounded or elongate, with few indentations, sparse or often abundant, becoming \pm erect. Apothecia and pycnidia brown, common, on scyphus rim; apothecia often shortly elevated. Thallus C-, K-, KC-, Pd+ red, UV- (fumarprotocetraric acid). **BLS 0410**.

On mossy rocks, walls, tree trunks and acid soil, chiefly in rather dry habitats; common. Throughout Britain and Ireland. This species has been frequently wrongly identified and many records probably belong to other species.

A variable species within clade *Cladonia* subclade *Graciles*. It is a polyphyletic species, which is in need of revision with further molecular studies (Stenroos *et al.* 2019). *C. chlorophaea* differs in having more slender, gradually tapering scyphi with a short stalk and has powdery, granular granules, more rarely soredia, in the upper part of the podetium and within scyphi. Poorly developed specimens may be impossible to distinguish from *C. pyxidata*. *C. cyathomorpha* is similar but has larger squamules with veins on the underside and the granules on the



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podetia are mainly inside the scyphi, and is found on acid mossy rocks and trees. See also under *C. pocillum*.

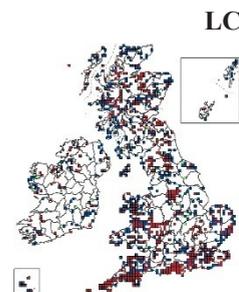
Cladonia monomorpha was included by James (2009) as a possible further British species, but Ahti & Stenroos (2013) considered this a synonym of *C. pyxidata*. The British specimens identified as *C. monomorpha* have conspicuous well-developed, tightly packed \pm vertically aligned squamules, the upper surface of which is a distinctive bright green, especially when moist. Both records are from metal-rich (copper) sites in the Lake District and S. Devon (Tavistock). Their status needs further examination. Material similar to *C. monomorpha* as that described from heathlands in The Netherlands has also been found in similar sand lichen heath in The Brecklands.

Cladonia ramulosa (With.) J.R. Laundon (1984)

Podetia 1–3.5 cm tall, green-brown, very variable, with pointed subulate apices or irregular lopsided poorly developed narrow scyphi, not or sparingly branched towards the apices; surface variously squamulose, in part granular-scabrid or at times partially or almost entirely decorticate, rarely with a few scattered granular soredia. Basal squamules small, often yellowish green-grey when wet, elongate and indented, sometimes densely tufted, fragile (easily broken by rubbing with a finger when dry), the lower surface white, rarely with soralia. Sometimes the thallus may be reduced to a compacted, densely minutely squamulose crust with no, or very few, podetia. Apothecia frequent, brown, somewhat elevated, often turgid when wet and forming convex clusters at the apices of podetia. Thallus C–, K–, KC–, Pd+ red, UV– (fumarprotocetraric acid). **BLS 0359.**

On inland and coastal sandy heathlands, moorlands, rotting tree stumps, fence posts, earth banks, wall tops, thatch and decaying *Armeria* tufts in mainly lowland and coastal sites; frequent. Throughout Britain and Ireland.

A member of clade *Cladonia* subclade *Foliacea*, along with *C. foliacea* and *C. phyllophora* (Stenroos *et al.* 2019); see under those species for diagnostic tips. Very variable and polymorphic, but distinguished by the irregular thalline clusters, often with numerous podetia, which are often partly granular, rarely sorediate, intermixed with brittle squamules, often with \pm decorticate areas and blunt or irregular obscurely scyphose apices with clusters of \pm contiguous apothecia, which become notably swollen pellucid-turgid when wet.

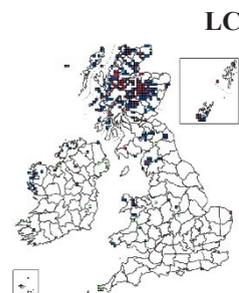


Cladonia rangiferina (L.) F.H. Wigg. (1780)

Primary thallus crustose, evanescent. Podetia 4–10 cm tall, grey-white, the upper part often brown with a \pm purple or bluish grey tinge towards the apices, the surface uniformly decorticate, finely cottony-arachnoid ($\times 20$ lens), richly branched, remaining pale grey towards the base; terminal branches recurved, distinctly orientated in one direction, the branching predominantly tetrachotomous, more rarely trichotomous at the apices; young apices blunt. Apothecia brown, inconspicuous, rare. Pycnidia containing colourless jelly. Thallus C–, K+ yellow, KC–, Pd+ red, UV– (fumarprotocetraric acid, atranorin). **BLS 0411.**

On exposed moss-lichen heaths and moorlands, acid woodlands (especially pinewoods) and in pockets of soil on cliff ledges and rock outcrops in montane to coastal areas; widespread but rather local. N. England, N. Wales, Scotland, Ireland; very rare in lowland England.

Characterized by the even, cottony-arachnoid surface ($\times 20$ lens), white (not yellow-green) colour of the podetia, tetrachotomous branching and the presence of atranorin (K+ pale yellow). *Cladonia ciliata* differs in the roughened, not cottony, surface, thinner branches, dichotomous branching and pycnidia containing red jelly. *C. arbuscula* and many populations of *C. ciliata* are yellowish green due to the presence of usnic acid. *C. stygia* is very similar but has a notably blackened surface towards the base with stark, scattered, white areoles and is browner towards the tips of the branches; its pycnidial jelly is red.



Cladonia rangiformis Hoffm. (1796)

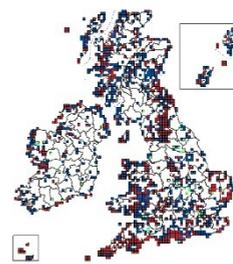
Podetia 2–6 cm tall, grey-white to grey-green, to brownish in sunny areas, richly branched, the branches diverging at wide angles, forming spiky tufts with pointed apices, without scyphi, axils usually closed; upper surface corticate, distinctly mottled-areolate ($\times 20$ lens); attached squamules rather rare; soredia usually absent [a rare sorediate morph has been reported as *C. rangiformis* var. *sorediophora* (Nyl.) Vain. 1887; it has similar chemistry to the type variety]. Basal squamules evanescent, small; lower surface white. Apothecia very rare, brown, at the apices of podetia, sometimes \pm corymbose but never split. Pycnidia brown, at the apices of branches, frequent. Thallus C–, K+ pale yellow, KC–, Pd– (in ca 70% of collections) or Pd+ red, UV– (usually with atranorin and rangiformic acid, more rarely with fumarprotocetraric acid). **BLS 0412.**

LC

On neutral or basic dry grassland, chalk-flint grassland, cliffs and dunes, especially along the coast; often common. Throughout Britain and Ireland, particularly in lowland habitats. *Cladonia rangiformis* var. *sorediophora* has been reported from Somerset and N.E. Scotland.

An unusual species with an evanescent thallus and richly branched podetia with a corticate surface. It is not closely related to species formerly included in *Cladonia* subgenus *Cladina*. It is the only British representative of clade *Cladonia* subclade *Rangiformes* (Stenroos *et al.* 2019). Characterized by the richly branched thallus, the widely divergent branches with pointed apices and the K⁺ yellow reaction. The surface of older parts is distinctly mottled with green areolate patches of algae on a white background. *C. furcata* is often darker or more brownish, the surface not so obviously areolate (crazy-paving effect, best seen when wet), has fewer, less divergent branches and is K⁻.

Diploschistes muscorum is often initially parasitic on the squamules and podetia of this species.



Cladonia rei Schaer. (1823)

Like *C. glauca* or *C. subulata*, but dirty or drab green-brown. Podetia often contorted, rarely branched 1-3 times especially towards the apices, often in part ± entirely farinose to coarsely granular-sorediate, sometimes with minute developing squamules, with a corticate and sometimes squamulose area at the base that sometimes extends towards the apices. Occasional scyphi poorly defined, irregular, often with 1-3 marginal terete extensions. Thallus C⁻, K⁻, KC⁻, Pd⁻ or Pd⁺ slowly yellow-orange, UV± white (homosekikaic and ± fumarprotocetraric, sekikaic acids).

On mineral soil in not very acid woodland, heath and wasteland; rare. S. and E. England.

Belongs to clade *Cladonia* subclade *Graciles*. *C. coniocraea* differs by its small, abruptly expanded, ± regular scyphi which are barely wider than the podetia and is UV⁻ and Pd⁺ quickly rust-red. *C. rei* was considered by some to be a chemical race of *C. subulata* (q.v.), but molecular data (Dolnik *et al.* 2010, Pino-Bodas *et al.* 2020b) show that they are not closely related. *C. glauca* is vividly UV⁺ white (squamic acid) and is also distinguished by a narrow, extended longitudinal slit occurring midway on most podetia.

NT



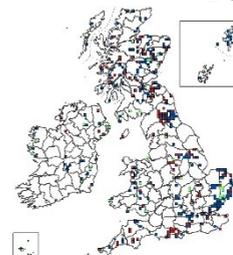
Cladonia scabriuscula (Delise) Nyl. (1875)

Like *C. furcata*, but with a more slender habit, paler greenish white colour and the tendency for the cortex to peel, become partly decorticate and notably scabrid with numerous, small peeling squamules and scattered coarse soredia, particularly towards the apices of the podetia. Thallus C⁻, K± yellow, KC⁻, Pd⁺ red, UV⁻ (fumarprotocetraric acid, rarely traces of atranorin). **BLS 0415**.

On peat in moorlands in montane and lowland situations, old wall tops and heavy metal mine spoil; rather local. Throughout Britain and Ireland.

Sometimes difficult to distinguish from squamulose specimens of *Cladonia furcata* but specimens of *C. scabriuscula* usually have, in part, a matt, scabrid surface especially towards the tips due to an incipient peeling of the cortex. Both species are polyphyletic according to Pino-Bodas *et al.* (2015a). *C. glauca*, characterized by a single inconspicuous vertical furrow along the length of most podetia, is UV⁺ white and ± entirely finely sorediate.

LC

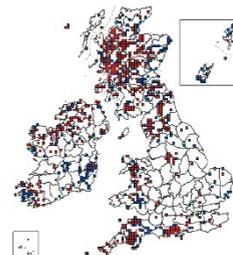


Cladonia squamosa (Scop.) Hoffm. (1796)

Cladonia squamosa var. *subsquamosa* (Nyl. ex Leight.) Vain. (1881)

Podetia 2–5 cm tall, green to grey-brown, the branching irregular, the apices pointed or with an irregular, usually narrow (to 2 mm diam.) perforate scyphus (up to twice as wide with a glossy chestnut interior in well-developed heathland morphs), the scyphi often dentate and proliferating from the rim, the surface scabrid, covered in numerous squamules, particularly at the base, these derived from peeling of the cortex, often leaving extensive decorticate areas (in contrast, large heathland morphs have few peeling squamules). Basal squamules to 2 mm diam., indented, often forming compact mats. Apothecia and pycnidia brown, at the apices of podetia; apothecia rather small, rare, when well-developed often in corymbose clusters. Thallus C⁻, K⁻, KC⁻, Pd⁻, UV⁺ vivid white (squamic acid and ± barbatic acids; chemotype A) or C⁻, K⁺ yellow-orange, KC⁻, Pd⁺ orange, UV⁻ (thamnolic

LC



and \pm barbatic acids; chemotype B). **BLS 0416**.

On heathland, earth banks, rotting wood, old tree stumps, tree trunks and mossy rocks by streams; common. Throughout Britain and Ireland.

A member of clade *Perviae* (Stenroos *et al.* 2019), but molecular data indicate that the species is polyphyletic. Very variable but characterized by the perforate podetia, numerous peeling squamules and absence of soredia. In some morphs the podetia have a \pm intact cortex and a semblance of scyphi, in which case they can resemble *Cladonia crispata*. In these cases the surface of the podetia is nearly always finely roughened and scabrous, a feature absent in the other species.

Populations (common throughout our region) with a more robust and consistently more densely squamulose thallus, which reacts C $-$, K $+$ yellow-orange, KC $-$, Pd $+$ orange, UV $-$ (thamnolic and \pm barbatic acids), have been separated as *Cladonia squamosa* var. *subsquamosa*. This taxon is considered to be a chemotype of *C. squamosa* and not worthy of formal recognition since thamnolic and squamatic acids are very closely related biosynthetically and the morphological distinction is questionable. The distinctive robust heathland morph with wide scyphi with a glossy chestnut interior is mainly the *subsquamosa* chemotype but may vary, sometimes apparently within the same thallus.

Cladonia stereoclada Abbayes (1947)

Like *Cladonia furcata*, but with very thin (0.3–0.5 mm diam.) worm-like flexuose podetia that are only sparingly branched and often entangled, and that are smooth, pale green-grey in shade becoming \pm brownish, unevenly corticate in open situations and are uniquely solid within, the central axis dense, translucent white to \pm grey-black. Thallus C $-$, K $-$, KC $-$, Pd $+$ red, UV $-$ (fumarprotocetraric acid). **BLS 0419**.

On pockets of soil in acid coastal cliffs and mossy boulders; reported from W. Scotland (Oban, Kerrera), S.W. Ireland (Sybil, Clogher & Sleah Heads, Kerry), N.W. Ireland (Crummie's Bay, E. Donegal), N. Ireland (Rathlin) and S.W. England (S. Somerset, S. Devon), likely to be very under-recorded in the west of Ireland at least.

The species appears to form a monophyletic group within the *Cladonia furcata* complex (Pino-Bodas *et al.* 2015a), although only a small number of specimens were sampled. A morph containing bourgeanic acid was found in the Azores (Pino-Bodas *et al.* 2017b), where the species is common.

Nb



Cladonia straminea (Sommerf.) Flörke (1828)

Cladonia metacorallifera Asahina (1939)

Similar to *Cladonia bellidiflora*, but with well-developed scyphi. Podetia are slender, greenish to yellowish grey with narrow, sometimes dentate scyphi that may proliferate marginally, verruculose to densely squamulose apart from at the base, with downward-pointing narrow squamules, medulla of podetia \pm blackened especially toward the base. Pycnidia on the margins of scyphi, containing red gel. Thallus C $-$, K $-$, Pd $-$, UV $+$ white (usnic, didymic and squamatic acids). **BLS 0401**.

On mossy boulders and mossy montane heaths, in \pm sheltered situations; very rare, but probably under-recorded at least in the Highlands. W. England (Shropshire), N.E. & N. Scotland (Cairngorm region, Alladale), Ireland (Mourne Mountains, Co. Down).

Included in the *Cladonia coccifera* complex by James (2009); see under that species for more information.

Most strongly resembles *Cladonia bellidiflora* including the UV $+$ white fluorescence but this for the most part lacks scyphi; it may develop small scyphi on immature podetia. The common *C. diversa* is confused with *C. straminea*; it has paler greenish yellow podetia that are not blackened below and is UV $-$. A chemotype with the squamatic replaced by thamnolic acid has been reported but this has not recorded from Britain yet (thallus C $-$, K $+$ yellow, Pd $+$ yellow, UV $-$).

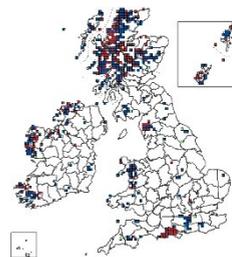
Nb



Cladonia strepsilis (Ach.) Mont. (1839)

LC

Podetia to 1 cm tall, rare, irregular or turgid-branched, \pm uniformly corticate, often squamulose and fissured, sometimes areolate, unbranched or branched near the tips, with perforate axils. Basal squamules dominant, to 4 mm long, rounded or \pm elongate, indented, often contiguous, forming cushions; upper surface bronze-green, white below. Apothecia dark brown, rare. Pycnidia brown, frequent on basal squamules. Thallus C $+$ bright emerald green, K $-$, KC $-$, Pd $+$ yellow, UV $+$ whitish (baeomycesic and squamatic acids, strepsilin). **BLS 0420**.



On poorly drained wet acid sites in open montane situations where it is locally frequent, but less so in low-altitude wetter heathlands. W. & N. Britain and Ireland, extending S. but there local and rare and seriously declining outside of the New Forest, where it is still frequent.

Forming a monophyletic grouping within clade *Perviae* (Stenroos *et al.* 2019). Readily distinguished by the unique C+ emerald green reaction (strep-silin) and tendency to grow in wetter habitats than most other species. Sorediate specimens with stunted podetia and conspicuous yellow-green soralia from the New Forest (S. England, Hants) were erroneously assigned to *Cladonia brevis* (Sandst.) Sandst. but appear to be simply a sorediate morph of *Cladonia strepsilis*. See also *C. callosa*.

Cladonia stygia (Fr.) Ruoss (1985)

Very similar to *Cladonia rangiferina* but differs by being pale grey to strongly brown at the apices, in the intensely blackened decorticate basal area with a mosaic of scattered white areoles at and towards the base of the podetia, and the red pycnidial jelly. Thallus C–, K+ yellow, KC–, Pd+ red, UV– (fumarprotocetraric acid, atranorin). **BLS 0425**.

Moorland, wet bogs and upland woodland, recently in areas of slight snow lie in wind-blown montane heaths; rare, but certainly overlooked. Nineteenth century records from Scottish Highlands (Braemar) and Wales (Merioneth and Snowdonia) and more recently from Wales (Cardigan) and Scotland (E. Perthshire, E. Ross & Caithness).

Molecular studies have proved that *Cladonia stygia* is independent of *C. rangiferina* (Kanz *et al.* 2015).

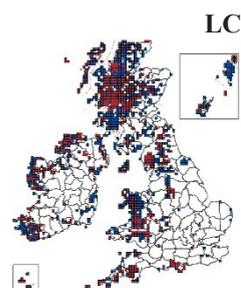


Cladonia subcervicornis (Vain.) Kernst. (1900)

Podetia to 1.5 cm tall, rather rare, with irregular or deformed turgid scyphi, flared from the base, bearing squamules, often irregularly proliferating from rim. Basal squamules dominant, elongate, 0.5–2 cm long, ± erect, with indented margins, mostly contiguous and forming ± compact interlocking cushions; upper surface bluish or lead-grey; lower surface white, usually ± blackened towards the base. Apothecia small, dark brown, on the rim of scyphi, often becoming clustered, rather frequent. Pycnidia dark brown, on the rim of scyphi. Thallus C–, K+ yellow, KC–, Pd+ red, UV– (fumarprotocetraric acid, atranorin). **BLS 0421**.

On humus, particularly pockets in crevices on acid rocks and boulders on moorlands and woodlands in coastal and montane sites, also forming mats on peaty soils in lowland heathland where it had been overlooked until recently. N. & W. Britain and Ireland, extending locally eastwards and southwards. Frequent in the New Forest.

Part of clade *Cladonia* subclade *Firmae* along with *C. firma* (Stenroos *et al.* 2019); that species has squamules that are brownish below. *C. cervicornis* has smaller, less elongate basal squamules, a grey-green upper surface that is not blackened toward the base and more regular podetia, and is K–. *C. symphycharpa*, characteristic of limestone and basic dune systems, contains norstictic acid (K+ red). The atranorin can be difficult to detect but when in low concentration the K/UV (dry)+ vivid neon yellow test can be used.

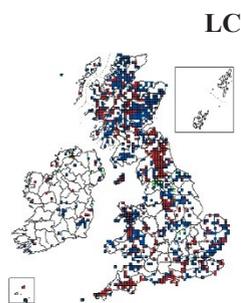


Cladonia subulata (L.) F.H. Wigg. (1780)

Podetia 2–6 cm tall, dull to bright grey-green, sometimes tinged brownish grey, thin, with pointed apices, sometimes with a furrow at the side of the podetium, often irregularly branched or furcate towards the apices and appearing antler-like, occasionally with irregular scyphi which often proliferate from the margins, usually entirely farinose-sorediate throughout, but sometimes ± corticate at the base which may be ± squamulose. Basal squamules inconspicuous or absent, elongate and deeply incised. Apothecia brown, rare, at the apices of podetia. Thallus C–, K–, KC–, Pd+ red, UV– (fumarprotocetraric acid). **BLS 0422**.

In well-drained sandy heathlands and acid dunes, also on earth banks, wall tops and old tree stumps, often amongst *Calluna*; often abundant. Throughout Britain and Ireland.

This is the type species of *Cladonia*. It is phylogenetically related to species with central proliferations in clade *Cladonia* subclade *Cladonia* (Stenroos *et al.* 2019). Scyphose populations can be mistaken for *C. fimbriata* (Burgaz *et al.* 2020), but most have pointed podetia without scyphi. *C. glauca* is more glaucous-grey, contains squamatic acid (Pd–, UV+) and more frequently has a thin narrow ± extended furrow at the side of the podetium. *C. rei* has less branched, often contorted podetia, often with deformed scyphi, which rarely proliferate and contain homosekikaic acid (UV± white).



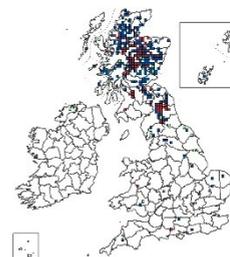
Cladonia sulphurina (Michx.) Fr. (1831)

LC

Podetia to 5 cm tall, yellow to grey- or yellow-green, with \pm pointed apices, unbranched, usually conspicuously longitudinally lacerated, particularly in the upper part, rarely with narrow, \pm regular scyphi, slightly wider than the main podetia, \pm farinose-sorediate throughout, or often with a 1–2 mm corticate area at the base, which is often \pm squamulose. Basal squamules often large, 2–8 mm wide, \pm rounded, the lower surface white, often yellowish to red-brown (K+ purple) towards the base, occasionally sorediate, horizontally spreading or \pm ascending. Apothecia and pycnidia red, at the tips of podetia; rarely fertile. Thallus C–, K–, KC+ yellow, Pd–, UV+ white (usnic and squamatic acids, \pm zeorin, \pm bellidiflorin). **BLS 0423**.

On montane and (less frequently) lowland heaths, also rarely on decaying thatch and well-rotted conifer wood. Much of Scotland, extending locally to S. England and Wales.

Part of clade *Erythrocarpae* subclade *Subglaucescentes*, apparently related to the *Cladonia coccifera* aggregate (Stenroos *et al.* 2019). The tall yellow-green podetia, often conspicuously fissured towards their apices, are particularly diagnostic. Older records of *C. deformis* probably refer to this species; it has UV– thalli.

**Cladonia symphyarpa** (Flörke) Fr. (1826)

Nb

Podetia very rare, small, to 1 cm tall, blunt, \pm continuously corticate, sometimes furrowed. Basal squamules dominant, to 10 mm long, scattered to contiguous, \pm horizontally spreading, with recurved margins when dry; upper surface pale grey-green; lower surface starkly white. Apothecia brown, rare. Pycnidia dark brown-black, frequent on basal squamules. Thallus C–, K+ yellow→red, KC–, Pd+ yellow, UV– (norstictic acid and atranorin). Other chemotypes occur elsewhere. **BLS 0424**.

On coastal limestone, serpentine heath, basic dune systems and montane epidiorite; rare. Centred on S.W. England (Mendips) and Scottish Highlands, very scattered elsewhere in southern England (Dorset, N. Hampshire, Isles of Scilly, Cornwall) and in S.W. Wales.

Part of the small subclade *Helopodium* (clade *Cladonia*; Stenroos *et al.* 2019), along with *C. cariosa* (q.v.). *C. cariosa* has smaller squamules, more fissurate podetia and usually lacks norstictic acid. Easily overlooked in the absence of podetia, this calcicole is distinguished from *C. cervicornis* and *C. pocillum* by the presence of norstictic acid and the occurrence of pycnidia on the basal squamules. In base-rich montane habitats, isolated basal squamules could be confused with *Psora rubiformis*, which is K–. It was referred to incorrectly as *C. symphyarpa* by James (2009).

**Cladonia trassii** Ahti (1998)

VU (D2)

Podetia 0.5–2 cm tall, grey to grey-green, blackened towards the base, sparingly branched above, terminating in narrow scyphi to 1.5 mm wide or with pointed apices, occasionally proliferating from the centre of the scyphus, the surface corticate, \pm smooth with scattered squamules; soredia absent. Basal squamules 3–8 mm long, indented. Apothecia brown, not observed in British material. Pycnidia dark brown, on the rim of scyphi, frequent. Thallus C–, K+ yellow, KC–, Pd+ red, UV– (fumarprotocetraric acid and atranorin). **BLS 1590**.

Associated with areas of late snow-lie in the central Highlands (Cairngorms, Ben Alder).

Characterized by the grey colour, central proliferations from the narrow, indistinct scyphi, the blackened base and K+ yellow reaction. It belongs to clade *Cladonia* subclade *Cladonia* (Pino-Bodas *et al.* unpublished). *C. verticillata* differs in the wider scyphi and unbranched podetia, while *C. phyllophora* has marginal proliferations; both these species are K–. The phylogenetic position of *C. trassii* is uncertain.

**Cladonia umbricola** Tønsberg & Ahti (1980)

Nb

Cladonia polydactyla var. *umbricola* (Tønsberg & Ahti) Coppins (1993)

Similar to *Cladonia polydactyla* but has greener-grey podetia which are usually shorter (1–2 cm), farinose-sorediate to the base, with sparse or no squamules and mostly without corticate patches in the upper parts. The scyphi are rather narrow (to 2 mm diam.) with few or no marginal proliferations and the thallus is C–, K–, KC–, Pd–, UV+ white (squamic acid). **BLS 1750**.

Recorded on decaying wood and bark and amongst mosses on moist rocks, usually in deep shade in Highland Scotland and W. Ireland.

Treated as a variety of *Cladonia polydactyla* by James (2009), but as a separate species by Ahti & Stenroos (2013) and Burgaz *et al.* (2020). It appears to be closely related to *C. polydactyla* but further molecular studies are required considering the polymorphic nature of both taxa. However, there are good chemical distinctions between them – at least when British material is considered.



Cladonia uncialis (L.) F.H. Wigg. (1780)

Podetia to 6 cm tall, without scyphi, yellow-green or greyish green, often brownish towards the abruptly pointed apices, forming ± compact, spiky tufts, the branching divergent, the axils mostly perforate, corticate throughout, the surface marbled in a ‘giraffe-skin’ pattern. Basal squamules absent. Apothecia and pycnidia brown, terminal. Thallus C–, K–, KC+ yellow, Pd–, medulla UV+ white (usnic, ± squamatic acids, ± hypothamnolic acid).

Two subspecies are recognized:

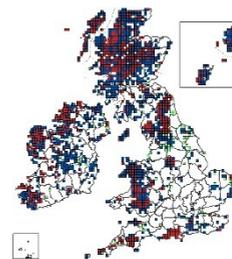
Subsp. *uncialis*: Podetia markedly cushion-forming, predominantly tri- to tetra- or polychotomously branched giving the apices of the podetia a star-like appearance; surface of central canal not powdery. Squamatic acid rarely present. **BLS 1594**. On sand dunes and dry heathlands; rather rare; principally found in E. Scotland (upper map), but with scattered records throughout Britain and Ireland. Pycnidia and apothecia are more frequent in this subspecies.

Subsp. *biuncialis* (Hoffm.) M. Choisy (1951): Podetia ± regularly dichotomously and trichotomously branched; surface of central canal white powdery. Squamatic acid (UV+) usually present. **BLS 0426**. On damp or dry acid soils, particularly on moorlands, at all altitudes; common throughout Britain and Ireland. (lower map). Apothecia are very rare in this subspecies. Characterized by the spiky, entangled tufts, yellow colour, absence of squamules and soredia and UV+ reaction. In boggy situations podetia often become grossly inflated (to 10 mm diam.) and irregular. Dry heathland morphs have narrow (1.5 mm wide) rather richly branched, ± decumbent podetia. Robust upright material is both regularly dichotomously and trichotomously branched and probably accounts for most records of subsp. *uncialis* in the south.

Stenroos *et al.* (2015) conducted a phylogenetic analysis of this aggregate, and concluded that the two morphs described above appear to be monophyletic, but that their distinction was insufficient to treat them unequivocally as separate species. They may be in a process of evolutionary divergence. See also *C. zopfii*.



LC



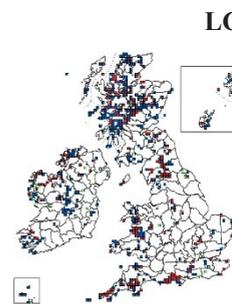
Cladonia verticillata (Hoffm.) Schaer. (1823)

Cladonia cervicornis subsp. *verticillata* (Hoffm.) Ahti (1980)

Similar to *Cladonia cervicornis*, but with smaller rounded basal squamules that are evanescent in mature material, and the podetia with more regular scyphi, to 5 cm tall, which are ± abruptly tapered to the stalk and form proliferating tiers, in 2–3 (–7) levels from the centre of the scyphus. The chemistry is similar. Thallus C–, K–, KC–, Pd+ red, UV– (fumarprotocetraric acid). **BLS 0370**.

A widespread and locally common species, especially in wetter heathland sites and mine spoil-heaps.

This species belongs to clade *Cladonia* subclade *Cladonia* (Stenroos *et al.* 2019). It is polyphyletic and a worldwide study is necessary. *C. cervicornis* has scyphi that may also proliferate, but they are generally less well-organized with fewer verticillate layers. Most critically, it has larger, more elongated and indented basal squamules.



LC

Cladonia zopfii Vain. (1920)

Nb

Like *Cladonia uncialis*, but the silver-grey podetia are usually more decumbent and the branches more widely divergent, with closed axils; surface opaque, evenly coloured with the algae clusters not visible but forming verrucose lumps; apices long-pointed and not darkened. The inner surface of the hollow podetia when split open are longitudinally fibrillose-striate within; it is almost smooth in *C. uncialis*. Thallus C–, K–, KC+ yellow, Pd–,

cortex UV– (usnic acid). **BLS 0427**.

On shallow peat and humic soils in moorland and heathland, often in wet situations, also in disturbed drier acid soils in sand dunes and hollow ways in lowland heaths, rather uncommon but very locally frequent. Scattered throughout Britain and Ireland; more frequently recorded in highland Scotland (but likely still very under-recorded there) and the New Forest.

Apparently the only representative of clade *Borya* from our region (Stenroos *et al.* 2015, 2019).

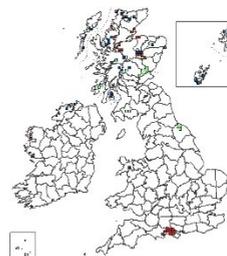


Table 2. Lichenicolous fungi associated with *Cladonia* species. Only those recorded from Britain and Ireland are included.

Species	Host species/comments
<i>Abrothallus cladoniae</i> R. Sant. & D. Hawksw.	<i>C. arbuscula</i> , <i>C. ciliata</i> , <i>C. polydactyla</i> , <i>C. portentosa</i> , <i>C. scabriuscula</i> , <i>C. sp.</i>
<i>Arthonia colombiana</i> Etayo	<i>C. pyxidata</i> , <i>C. squamosa</i> , <i>C. sp.</i> Possibly a lichenicolous lichen.
<i>Arthonia coronata</i> Etayo	<i>C. ochrochlora</i> , <i>C. subulata</i>
<i>Arthonia digitatae</i> Hafellner	<i>C. digitata</i> , <i>C. fimbriata</i> , <i>C. macilenta</i> , <i>C. polydactyla</i>
<i>Arthonia cf. lepidophila</i> (Anzi) Clauzade, Diederich & Cl. Roux	<i>C. cf. cervicornis</i>
<i>Arthrorhaphis aeruginosa</i> R. Sant. & Tønsberg	<i>C. chlorophaea</i> agg., <i>C. coniocraea</i> , <i>C. crispata</i> , <i>C. cyathomorpha</i> , <i>C. digitata</i> , <i>C. diversa</i> , <i>C. fimbriata</i> , <i>C. humilis</i> , <i>C. macilenta</i> , <i>C. polydactyla</i> , <i>C. pyxidata</i> , <i>C. ramulosa</i> , <i>C. verticillata</i> , <i>C. sp.</i>
<i>Bachmanniomyces punctum</i> (A. Massal.) Diederich & Pino-Bodas (<i>B. uncialicola</i> ; anamorph)	<i>C. furcata</i> , <i>C. rangiformis</i> , <i>C. uncialis</i> subsp. <i>biuncialis</i> , <i>C. uncialis</i> subsp. <i>uncialis</i>
<i>Bachmanniomyces punctum</i> (<i>Phaeopyxis punctum</i> ; teleomorph)	<i>C. coccifera</i> agg., <i>C. floerkeana</i> , <i>C. macilenta</i> , <i>C. polydactyla</i> , <i>C. pyxidata</i> , <i>C. sp.</i>
<i>Cercidospora cladoniicola</i> Alstrup	<i>C. arbuscula</i> , <i>C. furcata</i> , <i>C. portentosa</i> , <i>C. (Cladina) sp.</i>
<i>Chaenothecopsis parasitaster</i> (Bagl. & Carestia) D. Hawksw.	<i>C. digitata</i> , <i>C. incrassata</i> , <i>C. polydactyla</i>
<i>Cladoniicola staurospora</i> Diederich, van den Boom & Aptroot	<i>C. pocillum</i> , <i>C. sp.</i>
<i>Cryptodiscus cladoniicola</i> (D. Hawksw. & R. Sant.) Pino-Bodas, Zhurb. & S. Stenroos	<i>C. arbuscula</i> , <i>C. portentosa</i> , <i>C. rangiferina</i>
<i>Didymocyrtis cladoniicola</i> (Diederich, Kocourk. & Etayo) Ertz & Diederich (anamorph)	<i>C. rangiformis</i>
<i>Didymocyrtis foliaceiphila</i> (Diederich, Kocourk. & Etayo) Ertz & Diederich (anamorph)	<i>C. sp.</i> (squamules)
<i>Diploschistes muscorum</i> (Scop.) R. Sant.	<i>C. cervicornis</i> , <i>C. chlorophaea</i> agg., <i>C. coniocraea</i> , <i>C. glauca</i> , <i>C. humilis</i> , <i>C. pocillum</i> , <i>C. pyxidata</i> , <i>C. rangiformis</i> , <i>C. sp.</i> A lichenicolous lichen.
<i>Epicladonia sandstedei</i> (Zopf) D. Hawksw.	<i>C. caespiticia</i> , <i>C. chlorophaea</i> agg., <i>C. cornuta</i> , <i>C. cyathomorpha</i> , <i>C. furcata</i> , <i>C. grayi</i> agg., <i>C. humilis</i> , <i>C. macilenta</i> , <i>C. ochrochlora</i> , <i>C. polydactyla</i> , <i>C. subcervicornis</i> , <i>C. stereoclada</i> , <i>C. subulata</i> , <i>C. sp.</i>
<i>Epicladonia simplex</i> D. Hawksw.	<i>C. furcata</i> , <i>C. pocillum</i> , <i>C. verticillata</i>
<i>Epicladonia stenospora</i> (Harm.) D. Hawksw.	<i>C. chlorophaea</i> agg., <i>C. coniocraea</i> , <i>C. polydactyla</i> , <i>C. pyxidata</i> , <i>C. sp.</i>

Species	Host species/comments
<i>Heterocephalacria bachmannii</i> (Diederich & M.S. Christ.) Millanes & Wedin	<i>C. chlorophaea</i> agg., <i>C. fimbriata</i> , <i>C. foliacea</i> , <i>C. furcata</i> , <i>C. glauca</i> , <i>C. gracilis</i> , <i>C. grayi</i> , <i>C. ochrochlora</i> , <i>C. polydactyla</i> , <i>C. ramulosa</i> , <i>C. rangiformis</i> , <i>C. subcervicornis</i>
<i>Leucogyrophana lichenicola</i> Thorn, Malloch & Ginns	<i>C. ciliata</i>
<i>Lichenocodium erodens</i> M.S. Christ. & D. Hawksw.	<i>C. coniocraea</i> , <i>C. furcata</i> , <i>C. gracilis</i> , <i>C. polydactyla</i> , <i>C. uncialis</i> subsp. <i>biuncialis</i>
<i>Lichenocodium pyxidatae</i> (Oudem.) Petr. & Syd.	<i>C. chlorophaea</i> agg., <i>C. coniocraea</i> , <i>C. macilenta</i> , <i>C. pocillum</i> , <i>C. pyxidata</i>
<i>Lichenocodium usneae</i> (Anzi) D. Hawksw.	<i>C. fimbriata</i>
<i>Lichenosticta alcicornaria</i> (Linds.) D. Hawksw.	<i>C. ciliata</i> , <i>C. coniocraea</i> , <i>C. foliacea</i> , <i>C. furcata</i> , <i>C. ochrochlora</i> , <i>C. pyxidata</i> , <i>C. sp.</i> (squamules)
<i>Milospium lacoizquetae</i> Etayo & Diederich	<i>C. macilenta</i> , <i>C. polydactyla</i> , <i>C. sp.</i>
<i>Niesslia cladoniicola</i> D. Hawksw. & W. Gams	<i>C. azorica</i> , <i>C. ciliata</i> , <i>C. rangiformis</i>
<i>Polycoccum microcarpum</i> Diederich & Etayo	<i>C. cervicornis</i> , <i>C. digitata</i> , <i>C. gracilis</i>
<i>Protothelenella santessonii</i> H. Mayrhofer	<i>C. sp.</i>
<i>Roselliniella cladoniae</i> (Anzi) Matzer & Hafellner	<i>C. cervicornis</i> , <i>C. coniocraea</i> , <i>C. diversa</i> , <i>C. pocillum</i> , <i>C. sp.</i>
<i>Sphaerellothecium cinerascens</i> Etayo & Diederich	<i>C. incrassata</i> , <i>C. parasitica</i>
<i>Sphaerellothecium cladoniae</i> (Alstrup & Zhurb.) Hafellner	<i>C. arbuscula</i> , <i>C. subcervicornis</i> , <i>C. sp.</i>
<i>Taeniolella cladinicola</i> Alstrup	<i>C. arbuscula</i> , <i>C. portentosa</i> , <i>C. strepsilis</i> , <i>C. uncialis</i> subsp. <i>biuncialis</i> , <i>C. zopfii</i>
<i>Talpapellis beschiana</i> (Diederich) Zhurb., U. Braun, Diederich & Heucher	<i>C. coniocraea</i> , <i>C. floerkeana</i> , <i>C. foliacea</i> , <i>C. scabriuscula</i> , <i>C. uncialis</i> subsp. <i>biuncialis</i> , <i>C. uncialis</i> subsp. <i>uncialis</i> , <i>C. zopfii</i>
<i>Tremella cladoniae</i> Diederich	<i>C. ochrochlora</i>
<i>Zhurbenkoa epicladonia</i> (Nyl.) Flakus, Etayo, Pérez-Ortega & Rodr. Flakus	<i>C. pocillum</i> , <i>C. pyxidata</i> , <i>C. sp.</i>

PILOPHORUS Th. Fr. (1857)

Primary thallus crustose, effuse, granular to granular-areolate. **Secondary thallus** of solid short (not hollow) podetia, with a granular to granular-areolate surface. **Cephalodia** present. **Cortex** poorly developed. **Photobiont** *Asterochloris*, with *Nostoc* or *Stigonema* in the cephalodia. **Ascomata** apothecia, almost spherical, terminal on pseudopodetia, immarginate, black. **Thalline margin** absent. **Hypothecium** dark brown. **Hamathecium** of slender, sparingly branched and anastomosed paraphyses, with scarcely swollen apices. **Asci** 8-spored, clavate, *Porpidia*-type. **Ascospores** mostly aseptate, ellipsoidal to fusiform, colourless, without a distinct perispore. **Conidiomata** pycnidia, apical on short pseudopodetia, often surrounded by a collar of granules. **Conidiogenous cells** slender, ± cylindrical.

Conidia sickle-shaped, aseptate, colourless. **Chemistry:** atranorin, \pm zeorin. **Ecology:** mainly on rocks in temperate, montane regions.

Cladonia never has black apothecia and the podetia are usually hollow. *Stereocaulon* has flat, red-brown apothecia producing 2- to 14-celled spores. Cephalodia are uniquely formed in this genus, within the Cladoniaceae.

Pilophorus was confirmed as a member of the *Cladoniaceae* by Stenroos *et al.* (2019), and it appears to occupy an isolated position within the basal clades of the family. Around six species of lichenicolous fungi are known globally from *Pilophorus* species (Diederich *et al.* 2018, Zhurbenko & Triebel 2005), but none has been found to date in Britain and Ireland.

Literature

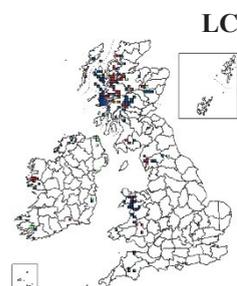
Ahti & Stenroos (2013), Coppins *et al.* (2009), Stenroos *et al.* (2019).

Pilophorus strumaticus Nyl. ex Cromb. (1875)

Primary thallus of whitish or pale grey areoles; areoles granular to minutely squamulose, 0.1–0.3 (–0.5) mm diam., scattered to confluent, or crowded into warty aggregations *ca* 1 mm diam.; photobiont cells 7–14 (–19) μ m diam.; cephalodia scattered, 0.3–1.2 mm diam., dark brown, granular or wrinkled, containing *Stigonema*. Podetia to 2 mm tall, 0.3–0.5 mm diam., pin-like, unbranched, the surface granular-areolate. Apothecia 0.5–1 mm diam., hemispherical to subglobose, epithecium dark olive-green, K–, N+ red; hymenium 70–80 μ m tall, I– (except for I+ blue outer coats of asci); hypothecium dark brown, K–, N–, with underlying tissue of pseudopodetium reddish brown, K+ purple-reddish; paraphyses 1.5–2.5 μ m diam., the apices \pm slightly swollen to 3 μ m diam. Ascospores (14–) 16–21 (–25) \times 6.5–9.5 μ m. Pycnidia 0.26–0.5 mm tall, 0.16–0.4 mm diam., ellipsoidal to elongate-ampulliform or skittle-shaped, black, borne terminally on short podetia to 0.5 mm tall; conidiogenous cells 14–20 \times *ca* 1.5 μ m; conidia 7–11 \times *ca* 0.8 μ m. Thallus C–, K+ yellow, KC–, Pd \pm faintly yellow, UV+ yellowish (atranorin). **BLS 1131.**

On the shaded sides or bases of damp, siliceous rock faces or boulders, less often on upper surfaces of low outcrops or small boulders; local. N. & W. Britain and Ireland.

Characterized by the pin-shaped podetia with terminal black \pm spherical apothecia. Rare morphs of *Micarea lignaria* with stalked apothecia are similar but lack cephalodia, are Pd+ red and have septate ascospores. Occasionally found sterile but can usually be identified by the characteristic cephalodia and rather large, short-stalked pycnidia.



PYCNOTHELIA Dufour (1821)

P. Lambley & O.W. Purvis

Primary thallus persistent, crustose, of non-corticate, rounded granules. **Secondary thallus** fruticose, of podetia, \pm short-cylindrical, hollow, unbranched to richly branched, not forming scyphi, corticate, without squamules or soredia. **Cortex** not differentiated. **Photobiont** *Asterochloris*. **Medulla** outer layer with algal cells forming a persistent pseudocortex; inner layer cartilaginous, variable in thickness, not clearly defined. **Ascomata** apothecia, rare, arising on the tips of the podetia, \pm peltate, often forming apical clusters. **Hamathecium** of paraphyses. **Asci** *Porpidia*-type. **Ascospores** aseptate or 1- to 3-septate, elongate-fusiform. **Conidiomata** pycnidia, frequent, apex red-brown or brown. **Conidia** thread-like, curved. **Chemistry:** β -orcinol depsidones and fatty acids. **Ecology:** on acid peat and sandy soils in open habitats.

Pycnothelia occupies a sister clade to *Cladonia*, along with the small non-European genera *Carassea* and *Metus* (Stenroos *et al.* 2019). There are only three confirmed species.

Literature

Ahti & Stenroos (2013), Lambley & Purvis (2009), Pino-Bodas *et al.* (2020), Stenroos *et al.* (2019).

***Pycnothelia papillaria* Dufour (1821)**

Basal thallus often wide-spreading, of white, grey-white or cream-coloured rounded \pm contiguous granules 0.2–1 mm diam. Podetia to 0.5 (–1.5) cm, scattered or \pm obscuring the primary thallus, \pm cylindrical or cone-shaped, the apices \pm rounded, unbranched to branched-coralloid, \pm swollen, hollow and very fragile, not forming cups, the surface smooth or with scattered rounded granules, pycnidia frequent, dark brown, apical. Apothecia dark red-brown, rare. Ascospores 9–15 \times 2–3.5 μm , 0- to 1-(–3)-septate. Conidia 8–14 \times ca 0.5 μm . Thallus C–, K+ yellow, KC–, Pd–, medulla UV \pm blue-white (atranorin, \pm chloratranorin, d-protolichesterinic, lichesterinic and \pm squamatic acids).

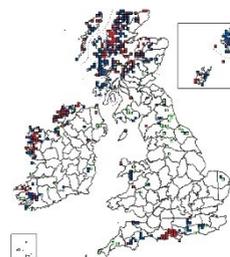
BLS 1211.

On acid peat and on humic layers over leached sandy soil on heathlands; locally frequent. Frequent in the Scottish Highlands, western Ireland and the New Forest, rare and declining in other moorland and heathland areas and absent in the Midlands & E. England.

Characterized by the tooth-like whitish swollen hollow podetia on a thallus of minute, \pm scattered granules.

The only lichenicolous species known from *Pycnothelia* in Britain and Ireland is *Arthrorhaphis aeruginosa*, also reported from a wide range of *Cladonia* species. Interestingly, records of this are so far only from New Forest populations, with no records on *Pycnothelia* from Scotland.

LC



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