Toninia Massal.
(BACIDIACEAE)

After Timdal, 1991

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Thallus crustose, ± immersed, rimosecracked, areolate, or small squamulose to almost foliose or dwarf fruticose, sometimes inflated or lobed at the margin, sometimes absent or in other lichens; upper cortex absent to well developed, often consisting of a layer of dead tissue and a lower, stainable layer composed of anticlinally oriented (periclinal according to Rogers), thin to thick walled hyphae with rounded to narrowly cylindrical lumina; both layers incorporating remnants of the photobiont (seen in chlorzinciodine) and often crystals of calcium ozalate; sometimes with pseudocyphellae; medulla usually well developed, of loosely interwoven hyphae, I, sometimes with calcium oxalate; attached to substrate by medullary hyphae. Algae forming a continuous layer or of ± scattered groups of cells, or sometimes absent and not lichenized, or loosely associated with cyanobacteria. Lower cortex absent to well developed, sometimes developing extensive rootlike branched outgrowths (rhizine strands) penetrating the substrate.

Apothecia sessile, black, often white or graypruinose, usually weakly concave to flat when young, later often becoming convex; disk round; thalline exciple absent; true exciple dark, raised and distinct at first but often finally excluded, of radiating, thickwalled, conglutinated hyphae with rounded to narrowly cylindrical lumina, colorless within with a green or brown outer margin to uniformly dark brown throughout; hypothecium colorless to dark brown, rarely containing crystals of calcium oxalate; hymenium K/I+ blue; paraphyses simple or sparingly branched and anastomsed, not conglutinate, thinwalled, apical cell distinctly swollen and covered by a ± well developed, gelatinous pigment cap; asci clavate, unitunicate, thin walled, surrounded by a gelatinous, I+ blue sheath; tholus well developed, I+ blue, containing a deeper staining tube and a well developed ocular chamber; spores 8, oblong to acicular, simple to 7septate, hyaline, thin walled, ellipsoid, bacilliform to acicular, smooth, without a thickened perispore.

Pycnidia immersed to partly protruding, black; conidogenous cells lining the cavity; fulcrum exobasidial; pycnospores filiform or acicular, curved. Atranorin, nortstictic, stictic, terpenoids, or no substances. Photobiont Trebouxia. Mainly on ± basic rock or soil, in exposed habitats, especially in arid to

alpine areas, often lichenicolous, at least when young, more rarely on mosses, or freeliving from the first; most species, at least when young, associated with cyanophilic lichens.

The following species, with ± conglutinate paraphyses, with or without a swollen apical cell and pigmente cap, asci with or without an ouclar chamber, and different chemistry, may belong elsewhere: T. cumulata, T. lobulata, T. pulvinata, T.squalescens, and T. tumidula.

I. Thallus crustose and areolate, ± epruinose, or not evident (endolithic, or on other lichens); Spores 1septate or 13septate (Also see species of Catillaria, Bacidia and Lecania)

1. Parasitic on other lichens (Lecania) on rock. Spores 1septate, ellipsoid, 1014 x 45.5 um. Epithecium olive green to bright green, K, N+ violet. Hypothecium colorless. Apothecia to 1 mm diam., plane to weakly convex, with narrow and soon disappearing margin. Coastal to inland, California. ..... T. talparum

1. Not parasitic. 2

2. Spores 13septate, 8.516 x 3.55 um, ellipsoid to shortly bacilliform or partly fusiform. Thallus crustose (areolate) to subsquamulose, indeterminate. AReoles to 1(1.5) mm diam., scattered to contiguous, orbicular to angular, plane to weakly convex; upper side medium brown to dark brown,± epruinose, ± matt, smooth; margin concolorous; underside medium brown. Apothecia to 0.6 mm diam., plane and marginate, then weakly to moderately convex and immarginate, ± epruinose. Epithecium gray, K+ violet, N+ violet. Hypothecium pale. No substances. On calciferous rock (limestone or sometimes sandstone), in open situations, Kansas. ..... T. pennina

2. Spores 1septate. (syn. Kiliasia spp.) 3

3. Thallus mainly endolithic, rarely epilithic and rimose to areolate, pale brown to olivaceous or ochraceous brown, epruinose, matt. Apothecia to 0.5 mm diam., plane to moderately convex, wtih a narrow and persistent or often disappearing margin, epruinose. Epithecium olive brown to dark green, K, N+ violet. Hypothecium and inner part of exciple reddish brown to pale brown, K, N+ violet. Apothecia lacking crystals inside. Spores 1septate, 9.512.5 x 45.5 um. No substances. On

calciferous rocks, Colorado and Greenland. ..... T. athallina

3. Thallus epilithic, rimose to areolate, to 4 cm or more across; areoles to 0.8(1.2) mm diam., contiguous, angular, plane to moderately convex; upper side pale yellowish to dark grayish brown or sometimes rusty brown, epruinose. Apothecia to 0.7 mm diam., ± plane and indistinctly marginate, then often becoming becoming convex and immarginate, ± epruinose, matt. Epithecium olive brown to bright green, K, N+ violet. Hypothecium dark reddish brown. Spores 1septate, ellipsoid, 1015.5 x 4.56 um. Usually on calciferous rocks, mainly limestone, in open habitats. Central Rocky Mountains, with apparent disjunct in northern British Columbia. ..... T. philippea

[Note: most squamulose species often overgrow cyanolichens at least when young, but have a distinct thallus of their own]

IIA Thallus squamulose, partly or entirely strongly pruinose; Spores mainly 3 or moreseptate

1. Epithecium (and exciple) gray, K+ violet and N+ violet. Hypothecium pale brown to colorless. Thallus pale gray, regularly rosulate; squamules densely white granular pruinose, not strongly proliferating; surface often shallowly fissured. Spores mainly 3septate, 23.533 x 34 um, narrowly fusiform to acicular. Discs moderately to densely pruinose. Hypothecium colorless to pale yellowish in upper part, colorless in lower part. Proper exciple medium gray in the rim, pale gray to colorless in inner part. No substances, or sometimes faint traces of terpenoids. Mainly on steep, often overhanging, calcareous rock walls in boreal to arcticalpine situations, overgrowing Collema or other cyanolichens when young, 7403290 m, NW Canada, south through Rocky Mountains to New Mexico. ..... T. alutacea (Anzi) Jatta

1. Epithecium green or brown, K and/or N. No substances. 2

2. Epithecium dark reddish brown, K+ red, N. Spores (1)3septate, ±bacilliform, 1220 x 34.5 um. Hypothecium containing calcium oxalate. Thallus indeterminate; upper surface pruinose, pale gray to mediumbrown, matt, deeply and regularly cracked, without pores; margin concolorous or sometimes more densely pruinose; squamules orbicular, to 3(5) mm diam., plane to moderately convex, often with a central depression; underside pale brown to white. Apothecia to 1.3 mm diam., persistently plane and marginate or becoming weakly convex and immarginate, often faintly pruinose. Hypothecium pale brown to colorless, with calcium oxalate crystals. In fissures of calciferous rock, or on soil; usually associated with cyanolichens. Colorado to Mexico. ..... T. lutosa

2. Epithecium dark olivegreen to bright green, K, N+ violet, lacking crystals. Spores usually bacilliform and at least partly 3septate (but sometimes ellipsoid and mostly 1septate), 1222.5 x 45.5 um. Thallus indeterminate; squamules to 4 mm diam., scattered to contiguous, orbicular or usually irregular, weakly concave to weakly convex, usually rugose; upper side pale gray to dark brown, often with green tinge, pruinose or not, matt, without pores or pseudocyphellae but usually with irregular maculae (especially along convex parts); margins concolorous, epruinose; underside paler brown. Apothecia to 1.5 mm diam., ± plane and marginate, ± epruinose. Highly variable. Parasitic on a wide range of crustose lichens, at least when young, on more or less calciferous soil and rock, very rarely on bases of trees.

Widely distributed, mostly borealarctic, but also known from southern California and Mexico. ..... T. aromatica (Sm.) Massal. p.p.

IIb. Thallus squamulose, ± epruinose.
Spores mainly 3 or moreseptate

1. Thallus pale gray, pulvinate; squamules ± epruinose, strongly proliferating. Spores 13septate, narrowly ellipsoid to shortly bacillifrom, 13.520.5 x 3.55 um. Apothecia to 0.5 mm diam., plane to weakly convex, indistingly marginate to immarginate, faintly pruinose. Hypothecium hyaline. Epithecium gray, K+ violet and N+ violet. Hypothecium pale brown to colorless. No substances. On calciferous rock, Lake Superior (known only from type collection). ..... T. superioris Timdal
1. Thallus ± dark brown, completely epruinose. 2

2. Epithecium gray, K+ violet and N+ violet. Hypothecium pale brown to colorless. No substances. 3
2. Epithecium green or brown. 4

3. Thallus crustose (areolate) to subsquamulose. Spores 8.516 x 3.55 um, 13septate. ..... (see T. pennina)
3. Thallus squamulose. Spores 1742.5 x 3.55 um, (1)3septate, ± bacilliform to acicular. Thallus indeterminate; squamules to 3 mm diam., scattered to irregularly imbricate, ± orbicular, soon elongated and proliferating, ± plane; upper side dark olive brown, epruinose, shiny, smooth; margin concolorous; underside pale to medium brown. Apothecia to 1 mm diam, plane to weakky convex, ± persistently marginate, epruinose. Usually on basalt or serpentine, rarely on soil, in ± arid areas of southwestern U.S. and Mexcio. ..... T. submexicana B. de Lesd.

4. Thallus with punctiform pseudocyphellae developing into pores, squamulose, medium to reddishbrown, epruinose,indeterminate; squamules to 5 mm diam., scattered to contiguous, bullate to columnar, simple or branched, often somewhat swollen at tip, matt to shiny. Apothecia to 4 mm diam., weakly concave to weakly convex, usually persistently marginate, epruinose, the outer side of the margin often concolorous with thallus. Hypothecium pale brown to colorless. Epithecium dark brown to bright (sometimes bluish) green, K, N, K+ red and N, or K and N+ violet. Spores acicular, 37septate, 3755.5 x 34 um. Chemistry: usually a series of terpenoids (often only traces). Rather variable. Mainly on soil or among mosses and lichens on acid rock in rather moist situations, often with cyanolichens, Colorado and Mexico. ..... T. bullata (G. Meyer & Flotow) Zahlbr.
4. Thallus without pseudocyphellae or pores. 5

5. Epithecium reddish brown, K+ red, N. Thallus indeterminate; squamules to 5 mm diam., matt to shiny, smooth or sometimes shallowly fissured, without pores; margin concolorous, underside paler brown. Apotheica to 1.5 mm diam., persistently plane and marginate or becoming weakly convex and immarginate, ± epruinose. No substances. 6

5. Epithecium not as above. 7

6. Squamules scattered to contiguous, bullate, medium brown to reddish brown. Spores 13(4) septate. On soil and in fissures of rock in open sites. Coastal, central California to Baja California, rather infrequent. ..... T. ruginosa (Tuck.) Herre ssp. pacifica Timdal

6. Squamules contiguous or forming a ± continuous crust, weakly to moderately convex, dark olivaceous brown. Spores 37(9)septate. On soil and rock, mainly among mosses or in fissures, on calcareous, siliceous, or often ultramafic rocks. Common and widespraed over much of temperate western N. America, especially in California (absent from AZ to TX), with disjuncts in Great Lakes area. ..... T. ruginosa (Tuck.) Herre spp. ruginosa

7. Hypothecium and inner part of exciple pale brown to colorless. 8

7. Hypothecium and inner part of exciple dark brown. 9

8. Spores 37septate, acicular, 2341.5 x 2.54.5 um. Thallus squamulose, indeterminate; squamules to 3 mm diam., but often irregularly proliferating or forming a ± continuous crust, weakly concave to weakly convex; upper side medium brown to dark brown, sometimes grayish, epruinose, matt, often shallowly fissured, without pores; ,margin concolorous,; unerside pale brown. Apotheica to 1.5 mm diam., plane and marginate, later ± convex and immarginate, epruinose. No substances. Variable. Mainly on soil or in rock crevices, usually among mosses, most frequent on somewhat calciferous substrates, widely distributed in temperate western N. America, with disjuncts in Great Lakes region and Alaska; also common in Greenland. ..... T. squalida (Ach.) Massal.

8. Spores 13septate, ellipsoid to bacilliform, 13.530.5 x 34.5 um. Thallus squamulose, indeterminate; squamules to 3 mm diam., becoming contiguous or irregularly imbricate, orbicular to elongated, often deeply lobed, weakly concave to weakly convex; upper side medium to darkbrown, often with olivaceous tinge, matt to slightly shiny, someitmes shallowly and irregularly fissured; margin usually dark gray but sometimes concolorous; underisde

pale to medium brown. Apothecia to 1 mm diam., plane to weakly convex, indistinctly marginate, ± epruinose. Epithecium olive brown to bright green, K, N+ violet. On siliceous and especially calciferous rocks, often over filiform cyanolichens, Arizona. ..... T. cinereovirens (Schaerer) Massal.

9. Epithecium dark olivaceous to bright geeen; squamules pale gray to dark brown, often with a green tinge, usually with irregular maculae. ..... (see T. aromatica)

9. Epithecium dark brown (or sometimes with a green tinge), K, N or faintly N+ violet. Thallus indeterminate; squamules to 2mm diam., scattered to contiguous or partly imbricate, orbicular to elongated, irregularly crenulate, plane to weakly convex; upper side dark brwon or more rarely dark gray, epruinose or partly pruinose, matt or somewhat shiny, often with shallow fissures, lacking pores, without maculae; margin concolorou, usually epruinose; underside dark brown. Apotheia to 1 mm diam., usually persistently plane and marginate, ± epruinose. Spores ellipsoid to bacilliform, 13septate, 10.519 x 3.55 um. No substances. On calcifeorus rock, usually in fissures but also on smooth faces or on soilcovered rocks. Scattered in western N. Am., especially Rocky Mountains, but with disjuncts in coastal CA, northern Canada, Alaska and Greenland ..... T. verrucarioides (Nyl.) Timdal (syn. T. kolax)

IIIa. Thallus Squamulose, Partly or Entirely Strongly Pruinose; Spores (0)1septate

Epithecium gray, K+ violet and N+ violet, and hypothecium pale brown to colorless, in species reported for N. America.

1. Thallus with small, punctiform to shortly linear or irregular pseudocyphellae, without pores, indeterminate; squamules to 3 mm diam., scattered to convex, strongly convex, becoming bullate to columnar, sometimes branched; upper surface dark grayish green to dark brown, usually only weakly pruinose, more rarely densely pruinose, matt to shiny; underside paler than upper side, usually epruinose. Apothecia to 5(10) mm diam., plane to weakly convex, marginate when young, later often becomming immarginate, usually epruinose. Spores broadly fusiform, 1septate, 11.518.5 x 3.55 um. No substances, or sometimes traces of fatty acids. Mainly on soil or sand in opern habitats, often among mosses, more rarely on rock walls. South Dakota and Greenland. ..... T. physaroides (Opiz) Zahlbr.
1. Thallus without pseudocyphellae. 2

2. Upper side entirely covered by white pruina. 3
2. Upper side partly epruinose. 5

3. Thallus regularly rosulate, to 4 cm diam.; pruina farinose; squamules to 5 mm diam., ± scattered when young, later continuous or sometimes slightly imbricate; marginal convex weakly concave to weakly convex, froming ± radiating lobes; central ones more isodiametrical and weakly to strongly convex; upper side pale gray, matt, lacking fissures and pores; margin concolorous, pruinose; underside pale brown to black. Apothecia to 2 mm diam., weakly concave to weakly convex, persistently marginate, densely pruinose. Spores fusiform, 1septate, 1524 x 34 um. Usually no substances. Mainly on steep, often overhanging, calciferous rock walls in ± continental areas (Rocky Mountains and adjacent areas, AZ to Alberta); starting on cyanolichens. ..... T. candida (Weber) Th. Fr.
3. Thallus consisting of scattered to contiguous, more or less isodiametric squamules, indeterminate, sometimes indistinctly rosulate; pruina granular. Almost always containing terpenoids. 4

4. Squamules to 2 mm diam., becoming rather strongly convex; upper side pale gray, smooth to densely granular pruinose, matt, often shallowly fissured, lacking pores and pseudocyphellae; margins concolorous, pruinose. Thallus sometimes indistinctly

rosulate. Chemotype E (terpenoids, with thickest band RF 5 in solvent C) or rarely no substances. Apothecia to 1.5 mm diam., weakly concave to weakly convex, persistently marginate, epruinose to moderately pruinose. Spores fusiform, 1septate, 12.521.5 x 34 um. Hypothecium medium brown to dark redbrown in upper part, to almost colorless below. On soil, often assoicated with cyanophilic lichens. Arcticalpine, Greenland toAlaska, south to Alberta. ..... T. arctica

4. Squamules to 4 mm diam., weakly to moderately convex, pale gray and usually with a green tinge, ± densely granular pruinose, matt, shallowly fissured, withot pores; margins concolorous, pruinose; underside pale gray to medium brown. Apothecia to 1.5(2.5) mm diam., weakly concave to weakly convex, persistently marginate, weakly to moderately pruinose. Spores broadly to narrowly fusiform, 1septate, 14.521 x 3.55 um. Thallus indeterminate; squamules scattered then contiguous, orbicular or with indistinclty radiating lobes. Chemotype D (terpenoids, with thickest band RF just below atranorin in solvent C) or rarely no substances. Squamules larger, not becoming rosulate, less convex. On hard soil or weathered, ± calciferous sandstone in Nfacing or somewhat shaded, steep to overhanging rock walls. Arid parts of western temperate U. S. (AZ, CO, NM, UT). ..... T. subdiffracta

5. Spores 1016.5 x 3.54.5 um, broadly fusiform, 1septate. Squamules weakly to medium convex, to 2 mm diam., usually scattered to contiguous, orbicular or irregularly lobed; upper side usually dark grayish green to dark olivaceous, usually shiny, often with regular but shallow fissures, lacking pores; marginc concolorous; underside pale brown. Thallus indeterminate. Apothecia to 1.5(2) mm diam., plane and marginate when young, later often convex and immarginate, epruinose. Somewhat variable. Chemotype D (terpenoids, with thickest band just below atranorin in solv. C) or rarely no substances. On soil and in fissures of rocks, with cyanolichens. From humid, mediterranean areas to arid temperate areas, S. California dn central Rocky Mountains. ..... T. massata (Tuck.) Herre

5. Spores larger, 1224 x 35 um. Squamules weakly convex to bullate. Chemotype various, rarely D. 6

6. Squamules convex to bullate, partly becoming vertically flattened, often imbricate, to 4 mm diam; upper surface dark olive brown to dark reddsih brown, usualy somewhat pruinose (especially along or near margin on upper and lower sides), somewhat shiny, usually shallowly fissured, lacking pores, concolorous or more desnely pruinose; underside pale brwon to

white. Apothecia to 4 mm diam., weakly concave to weakly convex, ± pruinose or note. Spores medium to narrowly fusiform, 1septate, 1624 x 3.54 um. Chemotype Y (1 thickbanded terpenoid, RF3 in solv. C). On rock and soil, often among mosses, especially in fissures on rock walls, exposed or somewhat shaded, western arctic, south to Alberta. ..... T. opuntioides (Vill.) Buschardt

6. Squamules weakly convex to bullate but not vertically flattened or regularly imbricate. Thallus indeterminate; squamules to 3 mm diam., scattered to contiguous or irregularly imbricate, orbicular or irregularly lobed; upper surface dark olivaceous green to dark brown, usually weakly to densely pruinose (especially in convex parts) orsomeitmes entirely epruinose, ± matt, smooth or shallowly fissured, without pores; margins concolorous, often more densely pruinose; underside pale brown to white. Apothecia to 3 mm diam., weakly convex to weakly convex, marginate then often immarginate, epruinose to densely pruinose. Spores broadly to narrowly fusiform, 1septate, 1224 x 35 um. Chemotype usually C (single phenolic substance, RF 6 in C) or no substances. Variable. On soil and rock, often among mosses, in open to somewhat shady habitats. Very common, throughout most of western N. America, eastward to Greenland in the arctic and to the Great Lakes and New England. ..... T. sedifolia (Scop.) Timdal (syn. T. caeruleonigricans)

IIIb. Thallus ± Epruinose; Spores (0)1septate

1. Epithecium gray, K+ violet, N+ violet. Thallus with pseudocyphellae. ..... (see T. physaroides)
1. Epithecium green or brown, K, N, or either K+ or N+, but not both. 2

2. Thallus indeterminate, with punctiform impressions or pores, lacking pseudocyphellae, squamulose, dark brown. Spores ellipsoid to fusiform, simple to 1septate, broadly ellipsoid to fusiform, variable in size (see subspecies). Squamules to 4(8) mm diam., scattered to contiguous, usually bullate or sometimes horizontally flattened or with an irregular central depression. Upper side castaneous brown to dark brown, sometimes with a green tinge, epruinose, matt or shiny, smooth or shallowly fissured; margin conocolorous; underside pale brown to black. Apothecia to 1.5(4) mm diam., plane to weakly convex, distinctly marginate to immarginate, epruinose. Epithecium bright green to dark brown, K, N+ violet. Hypothecium pale brown, to medium brown above. Containing various series of terpenoids (see subspecies). 3
2. Thallus without impressions or pores; form and color various. 8

3. Epithecium ± bright green. Spores mainly 1septate. Chemotype 5 (with thick band RF 5 in solv. C). On soil or in fissures of rocks, Alaska to Alberta, moderately frequent. ..... T. tristis (Th. Fr.) Th. Fr. subsp. canadensis Timdal
3. Epithecium brown, sometimes green tinged. 4

4. Hypothecium and lumina of many paraphyses, asci and spores containing orange (K+ red) and yellow (K) pigments. 5
4. Hypothecium and lumina without orange and yellow pigments. 6

5. Spores entirely simple [Psora spp. will also key out here]. Chemotype 6 (with thick band RF 6 in solv. C). On limestone, Chiricahua Mts., AZ, known only from the type ..... T. tristis (Th. Fr.) Th. Fr. subsp. arizonica Timdal
5. Spores mainly 1septate. Chemotype 4 (with thick band RF 5 and extra terpenoid RF 2, in solvent C). On soil and in rock fissures, very common, in Rocky Mountains (New Mexico northward), to Alaska, NW Canada and Greenland. ..... T. tristis (Th. Fr.) Th. Fr. subsp. asiaecentralis

6. Spores entirely simple; squamules 2(3) mm diam., bullate to horizontally flattened. Chemotype 3 (with thick band RF 5 in solv. C). On soil, Rocky Mountains (NM to Alberta), moderately frequent. ..... T. tristis (Th. Fr.) Th. Fr. subsp. scholanderi
6. Spores mainly 1septate. 7
7. Squamules to 2(3) mm diam. Chemotype 1 (with thick band RF 6 in solvent C). On soil or in fissures of rocks, calcicolous. Colorado. ..... T. tristis (Th. Fr.) Th. Fr. subsp. tristis
7. Squamules to 3(4) mm diam. Chemotype 5 (with thick band RF 5 in solvent C). On limestone, Coahuila, Mexcio, known only from the type. ..... T. tristis (Th. Fr.) Th. Fr. subsp. coahuilae Timdal

8. Upper surface of thallus pale yellow. Epithecium dark brown, K or + faintly red, N or + faintly violet. Thallus sometimes weakly pruinose, matt, with irregular and often deep fissures, without pores; margin concolorous; underside pale brown. Spores ellipsoid to shortly cylindrical, 1septate, 10.517.5 x 56 um. Thallus indeterminate; squamules to 1.5(3) mm diam., scattered to condtiguous, orbicular to indistinctly crenulate, weakly to strongly convex. Apothecia to 1 mm diam., plane and marginate, later weakly to strongly convex and immarginate, faintly to densely pruinose. No substances, chemotype C (single phenolic substance, RF 5 in solv. C) or D (terpenoids, with thick band just below atranorin in solv. C), occasionally also various unidentified fatty acids. On steep or overhanging faces of calciferous rock, exposed or shaded, in arid areas. Colorado and Utah. ..... T. sculpturata
8. Thallus of different color. Epithecium dull brown (K, N) or olive green to bright or dark green (K, N+ violet). Hypothecium and inner part of exciple pale brown to colorless. Thallus crustose (areolate), saxicolous. ..... (see T. phillipea)

ADD? (listed by Egan; now excluded or synonomized?)

T. caulescens = ?

T. cumulata = ?

T. lobulata = ?

Literature

Baumgrtner, 19 . Toninia.

Galloway, D. 1985. Flora of New Zealand Lichens.

Rogers, 19 . Genera of Australian Lichens.

Timdal, E. 19 . Toninia.

Timdal, E. and P. W. James. 1992. Toninia. In: Purvis, et al., Lichen Flora of Great Britain and Ireland.