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A revised generic classification of the jelly lichens, *Collemataceae*

Mónica A. G. Otálora · Per M. Jørgensen · Mats Wedin

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Abstract Phylogenetic studies have shown the need for a revised circumscription of generic boundaries in the jelly lichens (Collemataceae). Using a four-marker dataset from a recently published phylogeny of Collemataceae, we tested the monophyly of ten morphologically well-characterized groups. To achieve this, we performed Bayesian and maximum likelihood analyses. The monophyly of the ten morphological groups was confirmed. In order to reconcile molecular and morphological data into a formal classification, we here propose new generic delimitations in Collemataceae. *Collema* and *Leptogium* are re-circumscribed and six old generic names are resurrected to accommodate the *Collema* Crispum-group (*Blennothallia*), the *Collema* Tenax-group (*Enchylium*), the *Collema* Cristatum-group (*Lathagrium*), the *Collema* Occultatum-group (*Rostania*), the former small *Leptogium* species (*Scytinium*), and *Leptogium diffractum* (*Pseudoleptogium*). In addition, two new genera are described to accommodate *Collema multipartitum* (*Callome*) and the *Collema* Italicum-group (*Paracollema*). The presence/absence of a eucortex, which was earlier used as the cardinal character to define genera in the family, is still useful, but only in combination with other traits such as thallus habit (size), lobe size, ascospore characteristics, thallus anatomical structure, and habitat preference. A key to the genera is provided. Lectotypes are designated for *Collema marginale* Hoffm., *Synechoblastus nigrescens* (Huds.) Trevis., *Eucollema* (Cromb.) Horw., *Collema* section *Enchylium* Ach., *Collema* section *Lathagrium* Ach., *Collema* sect. *Mallotium* Ach., *Collema* section *Scytinium* Ach., *Collemodium* Nyl. ex Lamy, and *Homodium* Nyl. ex Olivier.

Keywords Classification · Collemataceae · Cyanolichens · Jelly lichens · Test of monophyly

M. A. G. Otálora (✉) · M. Wedin
Department of Botany, Swedish Museum of Natural History, P.O. Box 50007, SE-104 05 Stockholm, Sweden
e-mail: monica.garcia.otalora@gmail.com

P. M. Jørgensen
Department of Natural History, Bergen University Museum, Allégt. 41, Box 7800, 5020 Bergen, Norway

Introduction

Collemataceae ("jelly lichens") is a large family of fungi forming lichen symbiotic associations with cyanobacteria of the genus *Nostoc*. The main characteristic of these lichens is their gelatinous habit, which is due to a polysaccharid matrix around the *Nostoc* colonies that swells and becomes extremely gelatinous when wet. For a long time the family concept was based on the presence of this gelatinous thallus structure together with the ascoma ontogeny and morphology (Henssen 1965, 1981). Henssen (1965) included two genera with septate ascospores (*Collema* F.H. Wigg. and *Leptogium* (Ach.) Gray) and five genera with single-celled ascospores (*Homothecium* A. Massal., *Leciophysma* Th. Fr., *Leightoniella* Henssen, *Physma* A. Massal., *Ramalodium* Nyl. and *Staurolemma* Körb.) in Collemataceae. This family concept was largely accepted until recent molecular phylogenetic studies indicated that the gelatinous thallus structure was not a synapomorphy of a monophyletic group. Most of the gelatinous taxa with septate ascospores formed a distinct group (Collemataceae in a strict sense), while the genera with single ascospores were shown to belong to a different family within the same order, Pannariaceae (Wedin et al. 2009; Otálora et al. 2010). *Collema fasciculare* and related species (Otálora and Wedin 2013), and a recently described species morphologically similar to *Leptogium* (Magain and Sérusiaux 2012) were finally shown to belong to Arctomiaceae in the Ostropomycetideae. Collemataceae currently includes species with a typically non-stratified (homoiomerous) thallus organization, apothecia with a closed

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cupular proper wall (exciple), asci with a distinct internal amyloid tube structure (similar to the *Micarea*-type), septate ascospores, and lacking secondary metabolites visible in TLC. Currently generic delimitations are based on thallus anatomy, where thallus cortex character states define genera. *Leptogium* species have a distinct cortex with at least one well-defined cortical layer (eucortex), while *Collema* species lack a cortex completely, or may develop an indistinct pseudocortex (an irregularly developed structure of small and flattened cells). *Collema* and *Leptogium* are comparatively large genera (with c. 80 and 180 currently accepted species respectively) and include a high morphological and anatomical variation. Several infra-generic classifications have also been proposed in the past. Already Acharius (1810) in his treatment of *Collema* recognized seven sub-generic groups, and subsequently the genus has been split several times since. Gray (1821) divided *Collema* in seven genera which followed Acharius sub-generic classification, including recognizing *Leptogium*. Subsequent authors (e.g. Flotow 1850; Trevisan 1853, 1880; Tuckerman 1872; Lamy 1878; Müller 1882; Oliver 1903; Fink 1918) either suggested further segregates on generic level (i.e. *Blennothallia* Trevis., *Rostania* Trevis., *Collemodium* Nyl. ex Lamy, *Homodium* Nyl. ex Olivier, *Mallotium* (Ach.) Gray, etc.), or described new genera based on newly discovered species (i.e. *Collemodes* Fink). Some of the generic names proposed in the 19th century were recognized as sections of *Collema* or *Leptogium* by different authors (Vainio 1890; Zahlbruckner 1907, 1924, 1926). The infra-generic classifications currently in use were proposed by Degelius (1954, 1974) and Zahlbruckner (1924). Degelius divided *Collema* into 22 informal groups based on habitat, habitus, thallus size and texture, thallus anatomical traits, proper exciple, and ascospore shape. *Leptogium* was subdivided into 7 sections based on presence/absence of cortical hairs (tomentum), spore septation, thallus anatomy and cortex characteristics (Zahlbruckner 1924).

Already Degelius (1954) questioned the monophyly of *Collema* and suggested that different *Leptogium* species could have evolved from different groups of *Collema*. This was recently supported by several Peltigerales phylogenies, where the *Collema* and *Leptogium* representatives did not form monophyletic groups (Wiklund and Wedin 2003; Wedin and Wiklund 2004; Miadlikowska and Lutzoni 2004; Miadlikowska et al. 2006; Wedin et al. 2009; Otálora et al. 2010; Spribille and Muggia 2013). A recent study focussing more specifically on character evolution in the Collemataceae confirmed this reciprocal non-monophyly (Otálora et al. 2013). In that study, a well-resolved and well-supported phylogeny using 4 molecular markers showed that Collemataceae includes 11 well supported monophyletic groups (Fig. 1). The character evolution study showed that the presence of a eucortex have appeared independently several times. This shows that this character, which is currently used as the cardinal trait to define genera, does not characterize monophyletic groups. Nine of the eleven monophyletic groups distinguished are also morphologically distinct enough to be given taxonomical rank. However, the two remaining monophyletic groups (clades B and C; Fig. 1) contain morphologically similar species and lack obvious distinguishing characteristics. If these two clades would be given taxonomic recognition, there would thus be no morphology supporting such a classification. The relationship between these two clades and the clade A, however, did not get significant support in the Otálora et al. (2013) study.

In the present work we use the four marker dataset utilized by Otálora et al. (2013) to test if an alternative topology, where the morphologically similar clades B and C form one group, is significantly worse than the best trees. Such a topology would correspond to a phylogeny where all the monophyletic groups are possible to characterize by morphology, a hypothesis that obviously would be preferable to build a formal classification on. To achieve this we perform Bayesian and maximum likelihood methods for testing alternative topologies. Finally, in order to reconcile morphology and molecular data, we propose a new phylogenetic generic classification for Collemataceae.

Material and methods

Phylogenetic methods The Bayesian and maximum likelihood phylogenies obtained by Otálora et al. (2013) where used as the best topology (i.e. the unconstrained topology, Fig. 1). Alternative topology testing was conducted by creating a constrained topology where clade B and C in Fig. 1 together form one group. Bayesian and Maximum likelihood constrained analyses were performed using this constrained topology and implementing the same dataset, partitioning strategies, and settings, as in Otálora et al. (2013).

To conduct the alternative topology testing we performed two different test; Bayes factor and SH-test. First, to calculate the Bayes factors, marginal likelihoods from constrained and unconstrained Bayesian analyses, performed in MrBayes 3.2.0 (Ronquist et al. 2011), were estimated as the harmonic mean of the sampled likelihoods (Nylander et al. 2004). The Bayes factor corresponds to the ratio of the marginal likelihoods of the two topologies and was calculated as two times the difference between the harmonic mean of the post burn-in log-likelihood of the best topology and the constrained topology. Values >10 are considered to be very strong evidence favouring the best topology (Kass and Raftery 1995). Second, the constrained and the best unconstrained ML trees were used to compute the per-site log likelihood scores for each

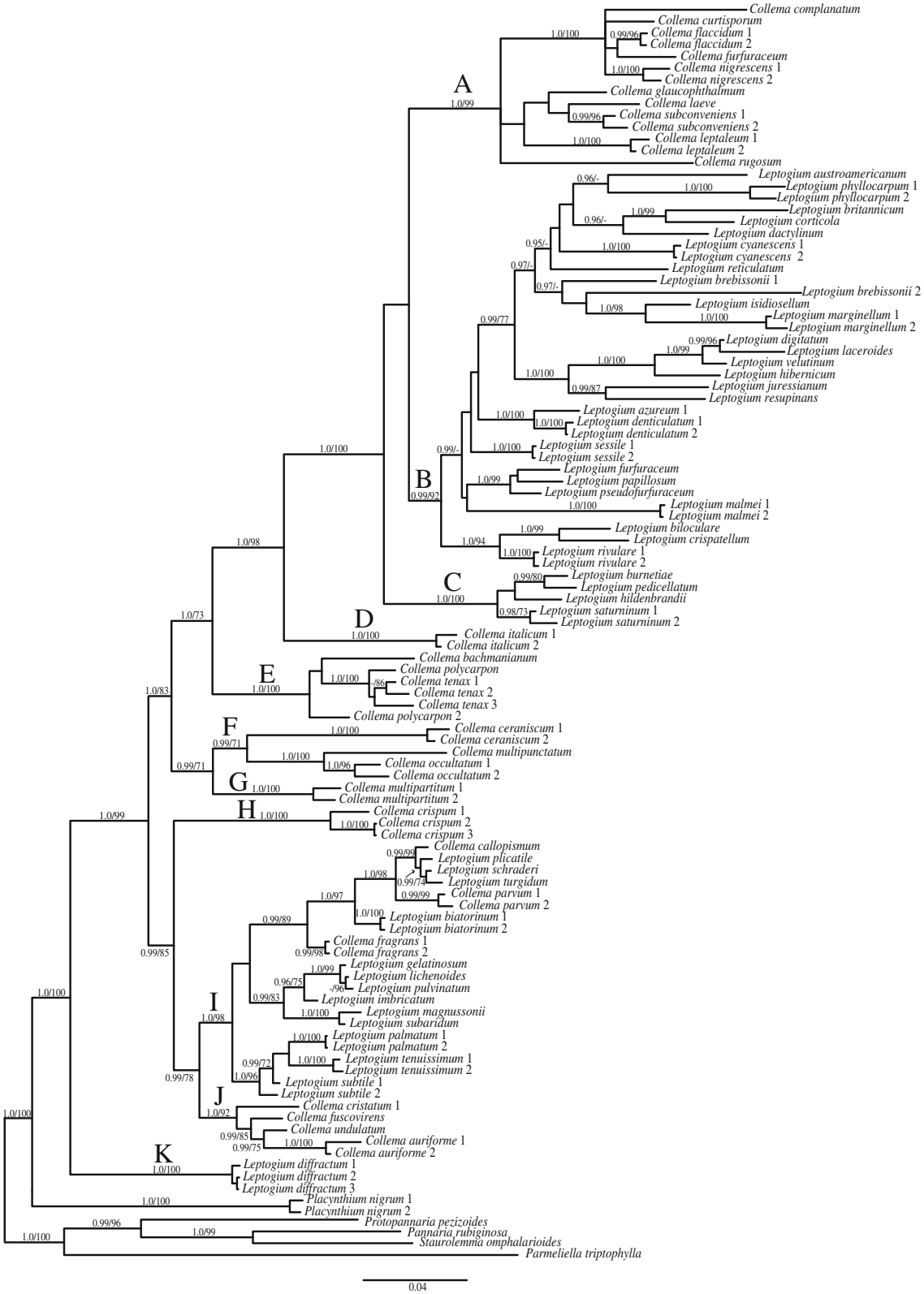

Fig. 1 Collemataceae phylogeny from Otálora et al. (2013). PP values>0.95 obtained in the Bayesian analysis and ML bootstrap values >70 are indicated above the branches. Support values are ordered as PP/ML BS. The monophyletic groups discussed in Otálora et al. (2013) are indicated by letters (**A**–**K**)

tree using the -f g option in RAxML-HPC2 (Stamatakis 2006). Log-likelihoods of site-pattern trees were then used to calculate the p-values for the SH-tests in CONSEL (Shimodaira and Hasegawa 2001).

Species characterization The morphological and ecological characterization of the species was based on own macro- and microscopic observations and complemented with information from Degelius (1954, 1974), Dodge (1964), Sierk (1964), Jørgensen (1973a, b, 1975, 1994, 1997, 2007), Awasthi and Akhtar (1977, 1979), Jørgensen and James (1983), Swinscow and Krog (1988), Verdon et al. (1992), Lindström (1993, 2007), Jørgensen and Goward (1994), Galloway and Jørgensen (1995), Jørgensen and Nash (2004), Aragón et al. (2005), Cunha (2007), Galloway (2007), Jørgensen and Kashiwadani (2008), Gilbert et al. (2009), Gilbert and Jørgensen (2009), Jørgensen and Olley (2010), Carvalho (2012), Kitaura and Marcelli (2012) and Lopez de Silanes et al. (2012).

Results and discussion

The tree topologies obtained by the maximum likelihood and a Bayesian constrained analyses did not show any supported conflict and therefore only the 50 % majority rule consensus tree from the Bayesian analysis is shown (Fig. 2). Nodes significantly supported in both the Bayesian and ML analyses are in bold. Both constrained analyses resulted in trees that are not significantly worse than the best unconstrained trees from Otálora et al. (2013). The harmonic mean ln-likelihood from the Bayes analysis was 23780.96, and the Bayes factor was 1.92. (BF <10). The ML SH-test resulted in a *P*-value=0.998. We argue that the insignificant difference between the constrained trees and the best, in both tests, suggests that the alternative hypothesis (Fig. 2) can be accepted as the working hypothesis for the phylogeny of the Collemataceae.

Our revised analysis suggests that the Collemataceae form 10 strongly supported major clades. *Collema* and *Leptogium* in the current sense are clearly not monophyletic. As shown and discussed by Otálora et al. (2013), all the ten major clades recognized here can be characterized using a combination of traits as habitat preference, thallus habit (size), ascospore characteristics, thallus anatomical structure, and cortex.

In order to reconcile molecular and morphological data into a formal classification, we here suggest treating these 10 clades as genera (Fig. 2). *Collema* and *Leptogium* are here recircumscribed and these names adopted for the species of the clades A (which contains *Collema nigrescens*, the type of *Collema*) and B+C (which contains *Leptogium azureum*, the conserved type of *Leptogium*, see Jørgensen et al. 2013), respectively. The names *Enchylium* (Ach.) Gray, *Rostania* Trevis., *Blennothallia* Trevis., *Scytinium* (Ach.) Gray, *Lathagrium* (Ach.) Gray and *Pseudoleptogium* Müll. Arg. are resurrected and adopted for species belonged to clades E, F, H, I, J and K, respectively, and the new generic names *Paracollema* and *Callome* are introduced for the species of the clade D and G (Fig. 2). Table 1 summarizes the diagnostic characters of the ten genera.

Taxonomy

Collemataceae Zenker

In Goebel & Kunze, Pharmaceutische Waarenkunde 1: 124 (1827)

Type genus: Collema F. H. Wigg, holotype

Thallus gelatinous, foliose, crustose or squamulose, homoiomerous or occasionally paraplectenchymatous throughout, eucorticate, pseudocorticate, or non-corticate, sometimes with rhizoid hyphae or hapters on the lower surface or occasionally uniformly tomentose. *Ascomata* apothecia, sessile or sometimes stipitate; thalline exciple usually persistent; true exciple cupular, paraplectenchymatous to euthyplectenchymatous; hymenium colourless. *Asci* clavate to subcylindrical with a distinct tube-like apical amyloid structure (see illustration in Spribille and Muggia 2013, Fig. 3M), normally containing 8 or rarely 4 spores. *Spores* muriform or transversally septate, colourless. *Conidiomata* pycnidia, globose to subglobose (*Lobaria*-type), marginal or laminal, immersed or slightly prominent, frequent or rare. *Conidia* simple, bacilliform, colourless. *Photobiont Nostoc*. *Secondary metabolites* lacking substances typical of lichens. *Distribution* cosmopolitan.

Key to genera

1a. Thallus with cortex or pseudocortex at least at one surface (Fig. 3A, C)…..…2
1b. Thallus without cortex (Fig. 3B)……..…… 7
2a. Thallus with proper eucortex (Fig. 3A)……..…….. 3
2b. Thallus with pseudocortex (Fig. 3C)....-***Scytinium p .p***.
3a. Thallus tomentose on at least one side (Fig. 4A–B)… ***Leptogium p .p***.
3b. Thallus glabrous…….…..... 4
4a. Thallus foliose with less than 3 mm wide lobes, sometimes small-squamulose, shrubby or crustose (Fig. 4C–E)..... 5
4b. Thallus distinctly foliose with more than 3 mm wide lobes .....……..……6
5a. Thallus placoid-squamulose areolate, forming circular patches, saxicolous (Fig. 4F) .....…. ***Pseudoleptogium***
5b. Thallus foliose, shrubby or crustose, not forming circular patches, terricolous, bryophilous corticolous, or rarely saxicolous. ..... ***Scytinium p .p***.
6a. Lobes usually larger than 5 mm wide (large species Fig. 4G) if less with anastomosing lobes and swelling considerably when wet (Fig. 4H–I), mainly corticolous, in wet tropics and wet temperate regions…..…..... ***Leptogium p .p***.
6b. Lobes usually narrower than 5 mm wide, not anastomosing, not swelling much when wet, often

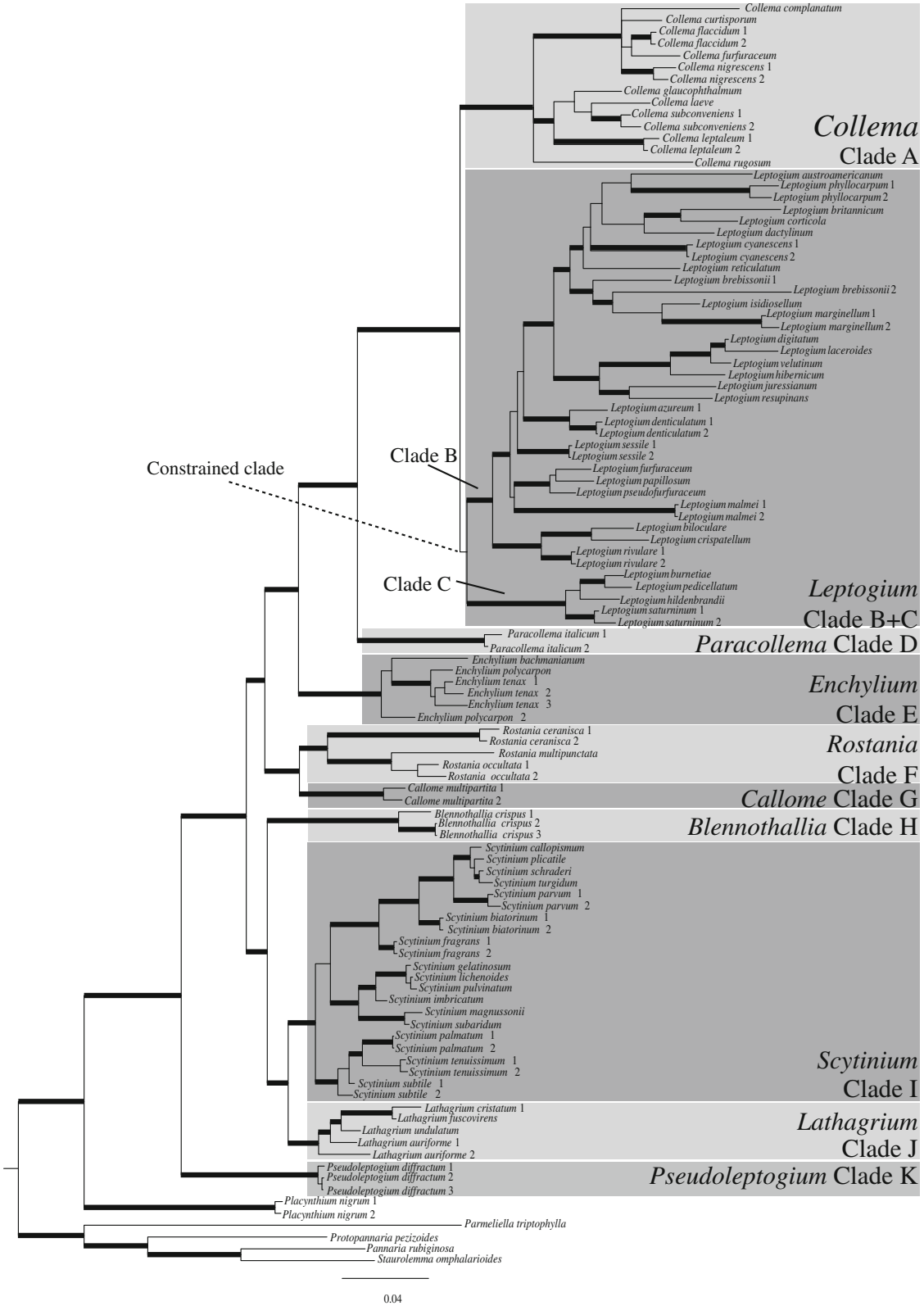

Fig. 2 The 50 % majority rule consensus tree (phylogram) from the Bayesian analysis of the combined data matrix (nuLSU, mSSU, MCM7 and Beta-tubulin) resulting from the constrained analysis (i.e. node B+C constrained as monophyletic), which was not significantly worse than the best trees of Otálora et al. (2013). Branches in boldface indicate a support of PP >0.95 and ML BS >70 %. Names follow the revised classification suggested here

Table 1 Diagnostic characters of the Collemataceae genera

Genus	Thallus size	Lobes size	Thallus anatomy	Spore	Habitat
Blennothallia	2.0–5.0 (7.0) cm diam.	0.5–4.0 mm diam.	Cortex absent, medulla paraplectenchymatous, *Nostoc* in clusters.	15–20×7–9 µm or 26–40×10–18 µm. Broadly oblong, transversally septate to sub-muriform.	Terricolous, saxicolous rarely corticolous.
Callome	1.0–3.0 (5.0) cm diam.	0.5–1.5 mm diam.	Cortex absent, medulla no paraplectenchymatous, *Nostoc* in chains.	10–45×4.5–6.5 µm. Linear oblong, transversally septate.	Saxicolous.
Collema	2.0–8.0 (15.0) cm diam.	5.0–12.0 (15.0) mm diam.	Cortex absent, medulla no paraplectenchymatous, *Nostoc* in chains.	25–35×6–7 µm or 40–90×3–6 µm. Narrowly ellipsoid to fusiform, transversally septate.	Corticolous occasionally on sheltered dam rocks.
Enchylium	1.0–7.0 cm diam.	1.0–2.0 mm or 2.0–5.0 mm diam.	Cortex absent, medulla no paraplectenchymatous, *Nostoc* in chains.	15–32×4–13 µm µm. Ellipsoid to fusiform, transversally septate to submuriform.	Terricolous, saxicolous few species corticolous.
Lathagrium	5.0–10.0 (20.0) cm diam.	1.0–3.0 mm or 2.0–5.0 mm diam.	Cortex absent, medulla no paraplectenchymatous, *Nostoc* in chains.	15–35×6–13 µm µm. Ellipsoid, submuriform.	Saxicolous.
Leptogium	4.0–10.0 (15.0) cm diam.	7.0–10.0 (20.0) mm diam.	Cortex present, medulla no paraplectenchymatous, *Nostoc* in chains	15–35×10–14 µm. Ellipsoid muriform.	Corticolous occasionally on sheltered dam rocks.
Paracollema	0.5–1.0 cm diam.	1.0–3.0 mm diam.	Cortex absent, medulla no paraplectenchymatous, *Nostoc* in chains.	10–13×3–4.5 µm. Ellipsoid suboblong, transversally septate.	Corticolous.
Pseudoleptogium	0.5–2.0 cm diam.	0.4–1.0 mm diam.	Cortex present, medulla paraplectenchymatous, *Nostoc* in clusters.	22–25×8–10 µm. Ellipsoid muriform.	Saxicolous.
Rostania	0.3–2.5 cm diam.	0.5–2.0 mm diam.	Cortex absent, medulla no paraplectenchymatous, *Nostoc* in chains.	13–20×8–20 µm. Cubic-like muriform.	Terricolous, corticolous.
Scytinium	0.2–5.0 cm diam.	1.0–5.0 mm diam.	Cortex absent, present or pseudocortex, medulla paraplectenchymatous or not, *Nostoc* in chains or in clusters.	12–35×6–17 µm. Ellipsoid muriform.	Corticolous, terricolous or saxicolous.

growing on mosses, in temperate mainly sub-dry regions (Fig. 4J–K)..... ***Scytinium p.p.***

7a. Thallus with partially paraplectenchymatous medulla, *Nostoc* in short chains with less than 3 cells (Fig 3D)..... ***Blennothallia***

7b. Thallus not paraplectenchymatous, *Nostoc* in long chains with more than 5 cells (Fig. 3E)..... 8

8a. Thallus foliose with more than 3 mm wide lobes, not squamulose, shrubby or crustose 9

8b. Thallus foliose with less than 3 mm wide lobes, small-squamulose, shrubby or crustose 11

9a. Spores narrowly ellipsoidal to fusiform, transversally septate (30–90×3–6 µm), mainly corticolous..... ***Collema***

9b. Spores ellipsoidal to fusiform or linear oblong, transversally septate sometimes submuriform (15–35×4–13 µm), mainly terricolous and saxicolous..... 10

10a. Thallus very swollen and pulpy when wet, lobes flat (Fig. 4M), proper exciple euthyplectenchymatous (Fig. 3F) ..... ***Enchylium p.p.***

10b. Thallus not much swollen when wet, with concave or undulated lobes (Fig. 4N–O), proper exciple euparaplectenchymatous (Fig. 3G)..... ***Lathagrium***

11a. Spores 2-celled and very small (10–13×3–4.5 µm)..... ***Paracollema***

11b. Spores multi-septate, 12–35×1–13 µm 12

12a. Spores muriform, cubic-like in shape..... ***Rostania***

12b. Spores transversally septate to submuriform, not cubic-like 13

13a. Thallus saxicolous, lobes convex (Fig. 5A), not pulpy and not much swollen when wet, spores narrow linear-oblong transversally septate (10–45×4.5–6.5 µm)..... ***Callome***

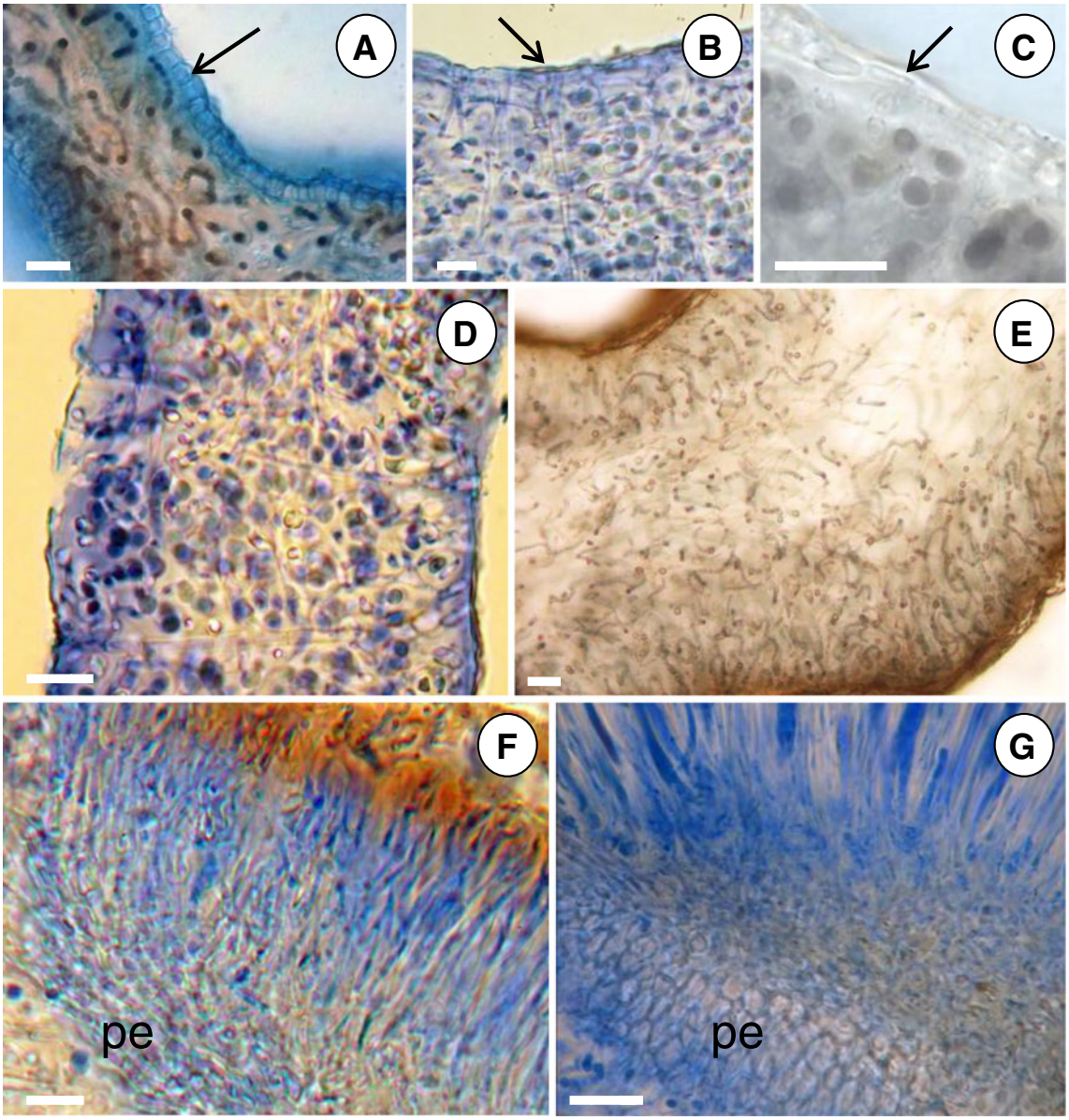

Fig. 3 Light micrographs showing sections of thalli and apothecia. **A** Thallus with proper cortex (*arrow*) (*Leptogium digitatum*). **B** thallus lacking proper cortex (*arrow*) (*Enchylium conglomeratum*). **C** Thallus with pseudocortex (arrow) (*Scytinium plicatile*). **D** Thallus partially paraplectenchymatous throughout (*Blennothallia crispa*). **E** Thallus not paraplectenchymatous throughout (*Enchylium conglomeratum*). **F** Eutyplectenchymatous proper exciple (*Enchylium conglomeratum*). **G** Paraplectenchymatous proper exciple (*Lathagrium cristatum*). Scale 5 μm

13b. Thallus corticolous or terricolous, lobes flat to concave, very swollen and pulpy when wet, spores transversally multi-septate, occasionally 2-celled or submuriform (15–32×5–13 μm)……... ***Enchylium p.p.***

***Blennothallia* Trevis.**

Caratt. Tre Nuov. Gen. Collem.: 2 (1853)

Type species: *Blennothallia cheilea* (Ach.) Trevis. (*nom. superfl.* ≡ *Collema marginale* Hoffm., Deutsch. Flora Botan. Tasch. Cryp. 2:101 (1796)), lectotype designated here = *Lichen crispus* Huds., Fl. Angl.: 447 (1762) ≡ *Blennothallia crispa* (Huds.) Otálora, P.M. Jørg. & Wedin.

Icon: Fig. 3D (thallus anatomy), Fig. 5B (habitus)

Thallus foliose, small to medium size [2–5 (−7) cm diam.]; homoiomerous but paraplectenchymatous throughout; deeply and broadly lobate, rounded, radiating to imbricating lobes 0.5–4 mm broad, dark olive green to black; lobe surface smooth; cortex absent; isidia present; tomentum absent. *Apothecia* uncommon, scattered or crowded; appressed to sessile; disc flat, red brownish; thalline margin with thin granulose to lobulated, proper exciple paraplectenchymatous. *Asci* 80–130×20–25 μm. *Spores* normally 8 per ascus, rarely less, short 15–20×7–9 μm to medium sized 26–40×10–

18 μm, broadly oblong to sub-ellipsoid, mainly transversally septate or rarely submuriform. *Pycnidia* frequent. *Habitat* terricolous and saxicolous.

Comments: *Blennothallia* includes species with a world-wide distribution but predominantly occurring in temperate regions. This genus is characterized by the distinct, partially paraplectenchymatous thallus anatomy (Fig. 3d), and corresponds to the *Collema* Crispum-group distinguished by Degelius (1954). The position of the species of this group within *Collema* was questioned, and some authors pointed out that it is the most deviant species group in *Collema* (Trevisan 1853; Degelius 1954). The phylogeny shows that *Blennothallia* is more closely related to *Scytinium* in our revised circumscription than to *Collema* (Fig. 2). It forms a well-supported lineage together with *Scytinium* and *Lethagrium*.

Nomenclatural comments: Trevisan (1853) proposed a new genus based on thallus and spore characteristics, and mentioned two species: *Blennothallia cheilea* (Ach.) Trevis. and *Blennothallia haemalea* (Sommerf.) Trevis. He expressed doubts about the second species since he did not see any material, and *Blennothallia haemalea* does not match the protologue. It is currently classified in *Euopsis* (Lichinaceae; Jørgensen 2007). We lectotypify the genus on *Blennothallia cheilea* (Ach.) Trevis., on which the protologue is based. *Lichen cheilus* Ach. (1798:134), however, is illegitimate as the already published *Collema marginale* Hoffm. is cited as synonym. Zahlbruckner (1924) misinterpreted this as *Lichen marginalis* Huds. ("*Collema*" *cristatum*). This unfortunate error (which was corrected already by Degelius (1954) is repeated in the Index Fungorum database. The oldest validly published name for this lichen is *Lichen crispus* Huds.

The species: For keys to identify species see Degelius (1954, 1974). The four species of *Blennothallia* formerly included in *Collema* require new combinations.

Blennothallia crispa (Huds.) Otálora, P.M. Jørg. & Wedin, **comb. nov**. (MB 805667) Basionym: *Lichen crispus* Huds., Fl. Angl.: 447 (1762).

Blennothallia fecunda (Degel.) Otálora, P.M. Jørg. & Wedin, **comb. nov**. (MB 805668) Basionym: *Collema fecundum* Degel., Bot. Notiser 132: 569 (1979).

Blennothallia furfureola (Müll. Arg.) Otálora, P.M. Jørg. & Wedin, **comb. nov**. (MB 805669) Basionym: *Collema furfureolum* Müll. Arg., Flora 72: 142 (1889).

Blennothallia novozelandica (Degel.) Otálora, P.M. Jørg. & Wedin, **comb. nov**. (MB 805670) Basionym: *Collema novozelandicum* Degel., Symb. Bot. Upsal. 20: 81 (1974).

Callome **Otálora & Wedin gen. nov**. (MB 805671)

Type species: *Callome multipartita* (Sm.) Otálora, P.M. Jørg. & Wedin, holotype

Fig. 4 Thalli of representative members of Collemataceae. **A** *Leptogium saturninum*. **B** *L. andinum*. **C** *Scytinium dactylinum*. **D** *S. pulvinatum*. **E** *S. tenuissimum*. **F** *Pseudoleptogium diffractum*. **G** *Leptogium cyanescens* (photo E.Timdal). **H** *L. brebissonii*. **I** *L. phyllocarpum* (photo M. Prieto). **J** *Scytinium lichenoides*. **K** *S. plicatile*. **L** *Collema nigrescens*. **M** *Enchylium tenax*. **N** *Lathagrium cristatum*. **O** *L. undulatum* (photo E.Timdal)

Etymology: *Callome*, an anagram of the original name *Collema*

Icon: Fig. 5A (habitus)

Thallus foliose, medium size (up to 5 cm usually 1–3 cm diam.), homoiomerous, dark olive green to black; lobes irregularly, deeply and repeatedly branched, usually 0.5–1.5 mm wide, convex; lobe surface smooth, not swollen; cortex absent; isidia absent; tomentum absent. *Apothecia* often present, sparse to rather numerous, laminal, sessile; disc flat, blackish brown; thalline exciple entire or lobulate, smooth to crenulate; proper exciple euparaplectenchymatous. *Asci* 70–100×15–20 μm. *Spores* 8 per ascus 10–45×4.5–6.5 μm, linear oblong, straight or curved, transversally septate. *Pycnidia* frequent. *Habitat* saxicolous.

Comments: This monospecific genus includes *Callome multipartita* and corresponds to the *Collema* Multipartitum-group distinguished by Degelius (1954). This genus is restricted to Europe, Northern Africa and North America. *Callome* is sister to *Rostania* but no unique morphological, anatomical and ecological similarities are shared by these two genera. The recognition of this genus as separate from *Rostania* is based on the thallus habitus, ecology, ascospore shape and septation. Morphologically *Callome* is similar to species of *Lathagrium*, which have similar thallus ramification but concave (not convex) lobes; the spore shape is also different.

The species:

Callome multipartita (Sm.) Otálora, P.M. Jørg. & Wedin, **comb. nov**. (MB 805672) Basionym: *Collema multipartitum* Sm., in Smith & Sowerby, Engl. Bot. 36: tab. 2582 (1814).

Collema **F. H. Wigg.**

Prim. F. Holsat.: 89 (1780) (*nom. cons.*)

Type species: *Collema lactuca* (Weber) F. H Wigg. (*nom. superfl.* ≡ *Lichen nigrescens* Huds., Flora Anglica 1:450 (1762)) ≡ *Collema nigrescens* (Huds.) DC., in Lamarck & De Candolle, Fl. Franc., ed 3, 2: 384 (1805), lectotype designated by Fink (1910).

≡ *Kolman* Adans, Fam. Pl. 2: 7 (1763), *nom. superfl.*, Art. 52.1., type species: *Lichen nigrescens* Huds., holotype.

≡ *Synechoblastus* Trevis., Caratt. Tre Nuov. Gen. Collem.: 3 (1853), *nom. superfl.*, Art. 52.1, type species: *Synechoblastus nigrescens* (Huds.) Trevis., lectotype designated here.


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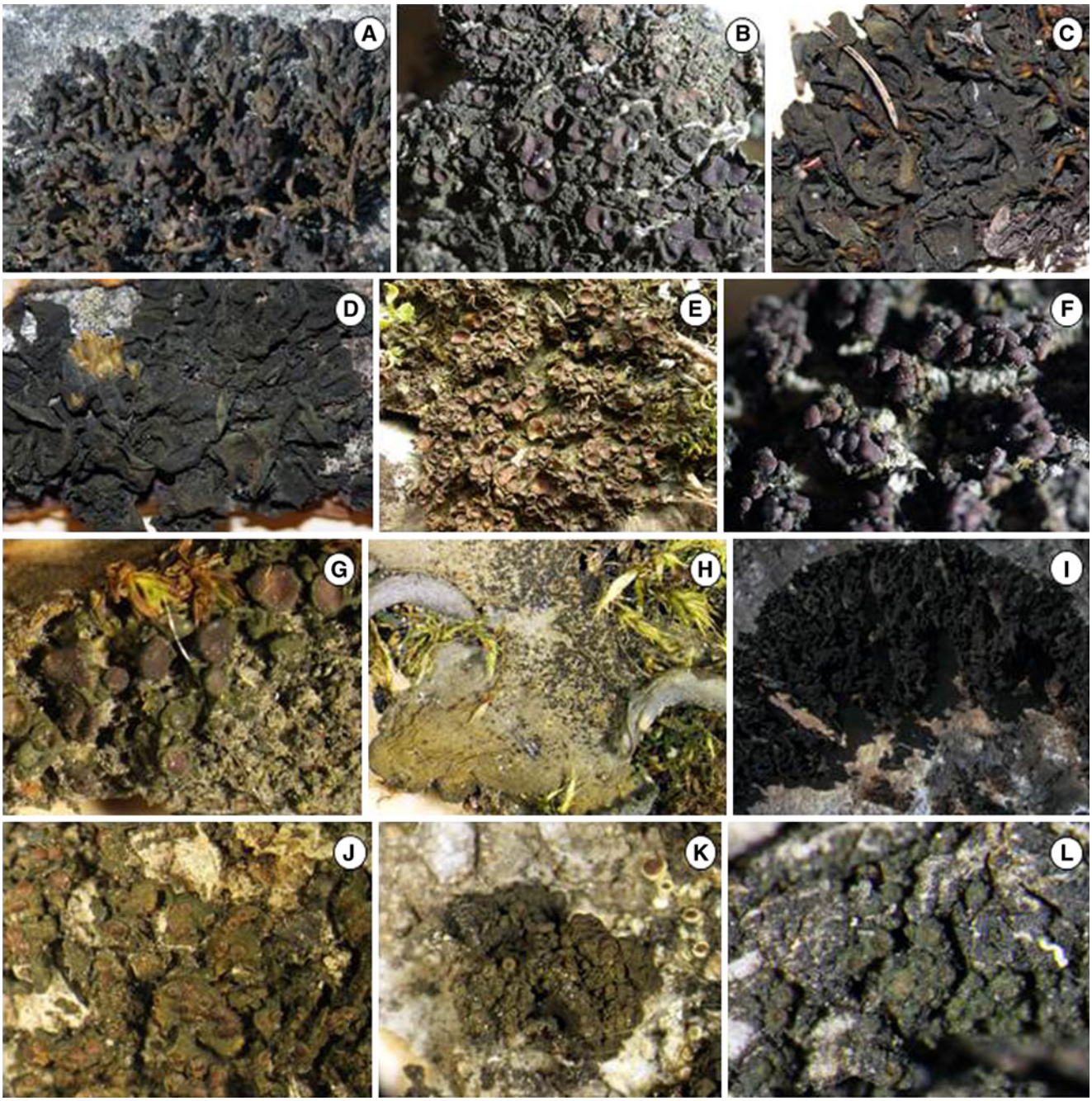

Fig. 5 Thalli of representative members of Collemataceae. **A** *Callome multipartita*. **B** *Blennothallia crispa*. **C** *Collema flaccidum*. **D** *C. furfuraceum*. **E** *Enchylium bachmanianum* (photo E.Timdal). **F** *E. conglomeratum*. **G** *E. ligerinum*. **H** *Lathagrium auriforme*. **I** *L. cristatum*. **J** *Paracollema italicum*. **K** *Rostania multipunctata*. **L** *R. occultata*

≡ *Collematomyces* Cif. & Tomas., Atti Ist. Bot. Univ. Lab. Crittog. Pavia, Ser. 5 10: 70 (1953), *nom. superfl.*, Art. 52.1., type species: *Collematomyces nigrescentis* E.A. Thomas ex Cif. & Tomas. (1953), holotype, = *Lichen nigrescens* Huds.

= *Eucollema* (Cromb.) Horw., Hand-list Lich. Great Brit.: 6 (1912), ≡ *Collema* section *Eucollema* Cromb. Monogr. Br. Lich. I: 41 (1894), *nom. illeg.*, Art. 38.1, type species: *Collema flaccidum* (Ach.)Ach., lectotype designated here.

= *Collemis* Clem., in Clements & Shear, Gen. Fung., Edn 2 (Minneapolis): 122, 316 (1931), type species: *Collemis rupestris* (Sw.) Clem., holotype, ≡ *Collema flaccidum* (Ach.) Ach.

Icon: Figs. 4L and 5C–D (habitus).

Thallus foliose, medium to large (up to 15 cm, usually 2–8 cm in diam.), homoiomerous, blackish brown; lobes entire, rounded, up to 15 (5–12) mm wide, flat to partially ascending; lobe surface smooth to markedly ridged; cortex absent; isidia

present or absent; tomentum absent. *Apothecia* often present, laminal, sessile; disc flat to convex, pale to red-brown; thalline exciple entire, sometimes isidiate; proper exciple paraplectenchymatous or euthyplectenchymatous. *Asci* 50–90×3–20 μm. *Spores* 8 per ascus, medium sized 25–35×6–7 μm or large 40–90×3–6 μm, narrowly ellipsoidal to fusiform or linear-oblong, with several transversal septa. *Pycnidia* common. *Habitat* primarily epiphytic or occasionally growing on sheltered damp rocks.

Comments: The genus *Collema* (c. 40 species) comprises the species formerly included in four morphologically similar infra-generic *Collema* units (the Coilocarpum, Japonicum, Nigrescens and Leptaleum groups) defined by Degelius (1974). The Nigrescens group is monophyletic; with four members of this unit falling in a well-supported monophyletic sub-clade together with one member of the Japonicum group (*C. flaccidum*). The relationship between other members of the Japonicum group and the Leptaleum and Coilocarpum groups is not well resolved. The Coilocarpum and Japonicum groups are very similar except from some slight differences in the proper exciple. The Japonicum and Nigrescens groups differ in the lobe surface features, which are markedly ridged in the Nigrescens and smooth in the Japonicum-group. The ascospores in the Leptaleum group are distinctly oblong to bacilar while in the other groups the spores are ellipsoidal or fusiform. *Collema* in our new circumscription comprises non-corticate, foliose large epiphytic species. The genus has a very wide distribution, with species present in most parts of the world and some of them restricted to tropical areas. Although *Collema* and *Leptogium* together form a well-supported monophyletic lineage, there are no obvious morphological connections between these two genera that have several important anatomical differences. Species in *Collema s. str.* are characterized by the absence of a cortex and by having spores with only transversal septa. This distinguishes them from *Leptogium*, which have a thallus with a well-developed eucortex in both the lower and upper surfaces, and muriform spores (with the exception of *Leptogium biloculare*).

Nomenclatural comments:

Collema F.H. Wiggers is conserved and accordingly not affected by the homonymic *Collema* P. Browne (1756), an overlooked older name.

Eucollema (Cromb.) Horw. This name is commonly cited with the authors *Eucollema* (Tuck.) Horw., but it is clear from Horwood that he based the name on Crombie's (1894) *Collema* sect. *Eucollema*, and not on Tuckerman's section (1872, 1882). As Horwood provided no description, this name is invalid.

Gabura Adans. is one of the names that *Collema* F. H. Wigg. is currently conserved against. However, as Otálora and Wedin (2013) has shown, the type species of *Gabura* (*Lichen fasciculare* L., ≡ *Collema fascicularis* (L.) F.H. Wigg.) belongs to Arctomiaceae. *Gabura* is now a threat to the generic name *Arctomia* Th. Fr., if not regarded as a separate genus.

The species: For keys to identify species see Degelius (1954, 1974), Swinscow and Krog (1988), Verdon et al. (1992), Galloway (2007), Jørgensen (2007), Gilbert et al. (2009) and Carvalho (2012).

Collema includes the following species. *C. actinoptychum* Nyl., *C. albopunctatum* Degel., *C. coilocarpum* (Müll. Arg.) Zahlbr., *C. complanatum* Hue, *C. coniophilum* Goward, *C. curtisporum* Degel., *C. delaikoroense* Degel., *C. flaccidum* (Ach.) Ach., *C. furfuraceum* (Arn.) DR., *C. glaucophthalmum* Nyl., *C. glebulentum* (Cromb.) Degel., *C. globuliferum* Degel., *C. hookeri* Degel., *C. hueanum* Degel., *C. insulare* Degel., *C. japonicum* (Müll. Arg.) Hue, *C. laeve* Hook. f. & Taylor, *C. leptaleum* Tuck., C. *leucocarpum* Hook. f. & Taylor, *C. nepalense* Degel., *C. nigrescens* (Huds.) DC., *C. peregrinum* Degel., *C. pulcellum* Ach., *C. quadriloculare* F. Wils., *C. rugosum* Kremp., *C. ryssoleum* (Tuck.) Schneid., *C. scabrum* Degel., *C. shiroumanum* Räs., *C. subconveniens* Nyl., *C. subflaccidum* Degel., *C. subnigrescens* Degel., *C. substipitatum* Zahlbr., and *C. thamnodes* Riddlle. Several of these names require further studies, however.

Enchylium (Ach.) Gray

Nat. Arr. Brit. Pl. (London) 1: 396 (1821) Basionym: *Collema* section *Enchylium* Ach., Lich. Univ.: 629 (1810).

Type species: *Enchylium tenax* (Sw.) Gray, lectotype designated here ≡ *Lichen tenax* Sw., Nova Acta Acad. Upsal. 4: 249 (1784).

= *Dicollema* Clem., Gen. Fung. (Minneapolis) 74: 174 (1909), type species: *Dicollema pycnocarpum* (Nyl.) Clem., holotype = *Collema conglomeratum* Hoffm.

= *Collemodes* Fink, Mycologia 10: 236 (1918), type species: *Collemodes bachmanianum* Fink, holotype.

Icon: Fig. 3B, E (thallus anatomy), 4M and 5E–G (habitus).

Thallus foliose, varying in size from 1 cm up to 7 cm in diam.; homoiomerous, dark olive-green to black; lobes radiating or elongated, flat to ascending, different sizes from 1 mm to 5 mm wide; lobe surface smooth to ridged or rugulose, swollen and plicate; cortex absent; isidia present or absent; tomentum absent. *Apothecia* often present, laminal or marginal, sessile or immerse; disc flat to convex, red brown; thalline exciple smooth, granulose or isidiate, sometimes persistent; proper exciple euthyplechtenchymatous. *Asci* 40–100×13–20 μm. *Spores* 8 per ascus, mainly transversally septate or occasionally submuriform or 2-celled, ellipsoid to fusiform, 15–32×4–13 μm. *Pycnidia* common, laminal or marginal. *Habitat* terricolous and saxicolous.

Comments: This genus corresponds to the *Collema* Tenax-group. Degelius (1974) included in the Tenax group saxicolous or terricolous species with a distinct habit and anatomy of the proper exciple. There are two exceptions from the saxicolous/terricolous lifestyle, *Collema conglomeratum* and

C. ligerinum, but unfortunately we did not manage to sequence these species. *Collema* and *Enchylium*, both lacking a cortex, are distinguished by ascospore sizes, and by their thallus habit and ecology preferences. The ascospores in *Collema* are larger and narrower. *Collema* species are growing in shady situations, while the species of *Enchylium* are photophilous, mainly pioneers growing on soil or rocks, preferably in open situations.

Nomenclatural comments: Acharius (1810) used the name in a wide sense for a number of unrelated species. When Gray took it up on generic level, he listed mostly small-squamulose species. Massalongo (1853), however, used it in a different sense (="Synalissae" (Th.Fr.) Trevis.). Neither of them formally typified the name, and it has not been done later, apparently. We have chosen one of the original Acharian species as the type, *Collema tenax*.

The species: For keys to identify species see: Degelius (1954, 1974), Jørgensen (2007) and Gilbert et al. (2009). Nine species of *Enchylium* formerly included in *Collema* require new combinations:

Enchylium bachmanianum (Fink) Otálora, P.M. Jørg. & Wedin, **comb. nov**. (MB 805673) Basionym: *Collemodes bachmanianum* Fink, Mycologia 10: 236 (1918) ≡ *Collema bachmanianum* (Fink) Degel., Symb. Bot. Upsal. 13: 192 (1954).

Enchylium coccophorum (Tuck.) Otálora, P.M. Jørg. & Wedin, **comb. nov**. (MB 805674) Basionym: *Collema coccophorum* Tuck., Proc. Amer. Acad. Arts. Sci. 5: 385 (1862).

Enchylium conglomeratum (Hoffm.) Otálora, P.M. Jørg. & Wedin, **comb. nov**. (MB 805675) Basionym: *Collema conglomeratum* Hoffm., Deutschl. Fl.: 102 (1796).

Enchylium confertum (Arnold) Otálora, P.M. Jørg. & Wedin, **comb. nov**. (MB 805676) Basionym: *Collema confertum* Arnold, Fl. Jena 42: 145 (1859).

Enchylium flagellatum (Degel.) Otálora, P.M. Jørg. & Wedin, **comb. nov**. (MB 805677) Basionym: *Collema flagellatum* Degel., Nordic J. Bot. 6: 345 (1986).

Enchylium limosum (Ach.) Otálora, P.M. Jørg. & Wedin, **comb. nov**. (MB 805678) Basionym: *Lichen limosus* Ach., Lich. Suec. Prod.: 126 (1799) ≡ *Collema limosum* (Ach.) Ach., Lich. Univ.: 629 (1810).

Enchylium ligerinum (Hy) Otálora, P.M. Jørg. & Wedin, **comb. nov**. (MB 805679) Basionym: *Collema pulposum* var. *ligerinum* Hy, Mém. Soc. Nat. Agricult. Sc. et Arts d'Angers: 24 (1893) ≡ *Collema ligerinum* (Hy) Harm., Lich. Fr. Fas. 1: 85 (1905)

Enchylium nipponicum (Degel.) Otálora, P.M. Jørg. & Wedin, **comb. nov**. (MB 805680) Basionym: *Collema nipponicum* Degel., Symb. Bot. Upsal. 20: 53 (1974).

Enchylium polycarpon (Hoffm.) Otálora, P.M. Jørg. & Wedin, **comb. nov**. (MB 805681) Basionym: *Collema polycarpon* Hoffm., Deutschl. Fl. 2: 102 (1796).

Lathagrium (Ach.) Gray.

Nat. Arr. Brit. Pl. 1: 399 (1821). Basionym: *Collema* section *Lathagrium* Ach., Lich. Univ.: 646 (1810).

Type species: *Lathagrium furvum* (Ach.) Gray 1821, lectotype designated here ≡ *Lichen fuscovirens* With., Bot. Arr. Veg. Gr. Brit. 1: 717 (1776) ≡ *Lathagrium fuscovirens* (With.) Otálora, P.M. Jørg. & Wedin.

Icon: Fig. 4N–O and 5H–I (habitus)

Thallus: foliose, medium to large size (up to 20 cm, usually 5–10 cm diam.), homoiomerous, dark olive green, dark brown to black; lobes extended, branched, narrow or wide (1–3 mm or 5–15 mm), flat, concave or undulated; lobe surface smooth to markedly ridged; cortex absent; isidia present or absent; tomentum absent. *Apothecia*: frequent, mainly marginal, sessile; disc concave to flat, red brownish, thalline exciple distinct, smooth, granular to isidiate, proper exciple euparaplectenchymatous. *Asci* 60–110×13–20 µm. *Spores* 8 per ascus medium sized 15–35×6–13 µm, mainly submuriform ellipsoid, or rarely fusiform or linear oblong with only transversal septa. *Pycnidia*: frequent. *Habitat*: mainly saxicolous (calciferous rocks).

Comments: This genus comprises two morphologically similar *Collema* groups (Cristatum and Durietzii groups) defined by Degelius (1974). Although no member of the Durietzii-group was sampled in the phylogenetic study, we consider that the species of this group fits better in *Lathagrium* than in *Collema* due mainly to the habitus and habitat characteristics. *Lathagrium* differs from *Collema* in spore septation and size, and by being exclusively saxicolous/terricolous. *Collema* is mainly a corticolous genus. *Lathagrium* differ from saxicolous/terricolous species of *Enchylium* in characteristics of the lobes and the proper exciple. While *Lathagrium* have swollen and plicate lobes, the *Enchylium* species have concave and undulate lobes, which are never plicate. *Lathagrium* form the well-supported sister clade to *Scytinium* (Fig. 3). Nine species of *Lathagrium* formerly included in *Collema* require new combinations.

Nomenclatural comments: Acharius (1810) included several unrelated species in his section, as did Gray (1821) when he accepted it as a genus. We have selected *L. fuscovirens* as the lectotype (= *Collema furvum*), which enables us to use this name for this distinctive group. It should be noted that Massalongo (1853) later used the name *Lethagrium* (sic) in a different sense, but without typifying the name (see Degelius 1954). His name is an ortographic variant only of Acharius', to whom he clearly refers. The name was taken up in Massalongo's sense by few botanists only, and ceased to be in use by the end of the 19th century.

The species: For keys to identify species see: Degelius (1954, 1974); Jørgensen (2007) and Gilbert et al. (2009). Ten species of *Lathagrium* formerly included in *Collema* require new combinations:

Lathagrium auriforme (With.) Otálora, P.M. Jørg. & Wedin, **comb. nov.** (MB 805682) Basionym: *Riccia auriformis* With., Bot. Arr. Veg. Gr. Brit. 1: 704 (1776) ≡ *Collema auriforme* (With.) Coppins & J.R. Laundon, in Laundon, Lichenologist 16: 228 (1984).

Lathagrium undulatum (Flot.) Otálora, P.M. Jørg. & Wedin, **comb. nov.** (MB 805683) Basionym: *Collema undulatum* Flot., Linnaea 23: 161 (1850).

Lathagrium cristatum (L.) Otálora, P.M. Jørg. & Wedin, **comb. nov.** (MB 805684) Basionym: *Lichen cristatus* L., Sp. Pl. 2: 1143 (1753) ≡ *Collema cristatum* (L.) F. H. Wigg., Prim. Fl. Holsat.: 89 (1780).

Lathagrium neglectum (Degel.) Otálora, P.M. Jørg. & Wedin, **comb. nov.** (MB 805685) Basionym: *Collema neglectum* Degel., Svensk. Bot. Tidskr. 56: 145 (1962).

Lathagrium latzelii (Zahlbr.) Otálora, P.M. Jørg. & Wedin, **comb. nov.** (MB 805686) Basionym: *Collema latzelii* Zahlbr., Öst. Bot. Z. 59: 493 (1909).

Lathagrium dichotomum (With.) Otálora, P.M. Jørg. & Wedin, **comb. nov.** (MB 805687) Basionym: *Tremella dichotoma* With., Bot. Arr. Veg. Gr. Brit. 2: 733 (1776) ≡ *Collema dichotomum* (With.) Coppins & J.R. Laundon, in Laundon, Lichenologist 16: 229 (1984).

Lathagrium durietzii (Degel.) Otálora, P.M. Jørg. & Wedin, **comb. nov.** (MB 805688) Basionym: *Collema durietzii* Degel., Symb. Bot. Upsal. 20: 98 (1974).

Lathagrium fuscovirens (With.) Otálora, P.M. Jørg. & Wedin, **comb. nov.** (MB 805689) Basionym: *Lichen fuscovirens* With., Bot. Arr. Veg. Gr. Brit. 1: 717 (1776).

Lathagrium poeltii (Degel.) Otálora, P.M. Jørg. & Wedin, **comb. nov.** (MB 805690) Basionym: *Collema poeltii* Degel., Symb. Bot. Upsal. 20: 96 (1974).

Lathagrium subundulatum (Degel.) Otálora, P.M. Jørg. & Wedin, **comb. nov.** (MB 805691) Basionym: *Collema subundulatum* Degel., Nord. J. Bot. 9: 101 (1989).

Leptogium **(Ach.) Gray**

Nat. Arr. Brit. Pl. 1: 400 (1821).

Type species: *Leptogium azureum* (Sw.) Mont., in Webb & Berthelot, Hist. Nat. Iles Canar. (Paris) 3: 129 (1840), proposed lectotype designated by Jørgensen et al. (2013) ≡ *Lichen azureus* Sw., Flor. Ind. Occid. 3: 1895 (1806).

= *Collema* sect. *Mallotium* Ach., Lich. Univ.: 644, type species: *Mallotium saturninum* (Dicks.) Gray, lectotype designated here ≡ *Mallotium* (Ach.) Gray, Nat. Arr. Brit. Pl. 1: 399 (1821).

= *Leptogiopsis* Trevis., Rev. Ist. Lomb., Milano, ser. 2 13: 73 (1880), type species: *Leptogiopsis rivularis* (Ach.) Trevis., holotype.

= *Colleptogium* Choisy, Bull. Mens. Soc. Linn. Lyon 31: 322 (1962), *nom. superfl.*, Art. 52.1, type species: *Leptogium saturninum* (Dicks.) Nyl.

Icon: Fig. 3A (thallus anatomy) and 4A–B, G–I (habitus).

Thallus foliose, medium to large (up to 15 cm or more but usually 4–10 cm in diam.), homoiomerous, lead grey to bluish, brownish or greenish; lobes irregular, orbicular or elongate up to 20 (7–10) mm wide; lobe surface smooth to markedly ridged, wrinkled and swollen; cortex present; isidia present or absent; tomentum present or absent. *Apothecia* often present, laminal to marginal, sessile or stipitate; disc concave to plane, red brown; thalline exciple distinct, sometimes isidiate or lobulated; proper exciple pseudoparaplectenchymatous. *Asci* 60–140×9–20 μm. *Spores* 8 per ascus, medium sized 15–35×7–14 μm, ellipsoidal or fusiform, mainly muriform or rarely only transversally septate. *Pycnidia* rarely observed. *Habitat* mainly epiphytic, with some species also growing on rocks but always in moist conditions.

Comments: *Leptogium* in our circumscription is the largest genus within the Collemataceae, and it comprises large foliose, eucorticate, mainly epiphytic species with a wide distribution, but also species restricted to tropical regions where the diversity of the genus is greater. It includes species classified in *Leptogium* sections *Leptogium* Zahlbr., *Mallotium* (Ach.) Vain., and *Leptogiopsis* (Müll. Arg.) Vain. *Leptogium* differs from the other eucorticate genus (*Scytinium*) in lobe and thallus size, habitat and distribution. In *Leptogium*, lobe and thallus size is larger compared to in *Scytinium*. The *Leptogium* species are mainly corticolous (rarely saxicolous or terricolous) and occur preferably in the wet tropics and humid temperate regions, while *Scytinium* species are bryophilous or saxicolous/terricolous (rarely corticolous) and occur predominantly in temperate regions. The phylogenetic relationships within *Leptogium* are not well supported (Fig. 2), and morphologically similar species appear in different sub-clades. Further studies are needed to better understand these relationships.

Nomenclatural comments: Gray (1821) elevated this name to generic rank and the name was typified by Clements and Shear (1931) on *L. lichenoides*. This choice is most unfortunate as seen from our knowledge today. We have thus proposed a conserved type (*L. azureum*), which will cause less change in the species nomenclature (Jørgensen et al. 2013).

The species: For keys to identify species see: Sierk (1964), Jørgensen (1973a, b, 1975, 1997, 2007), Awasthi and Akhtar (1977, 1979), Jørgensen and James (1983), Swinscow and Krog (1988), Verdon et al. (1992), Lindström (1993, 2007), Galloway and Jørgensen (1995), Jørgensen and Nash (2004), Aragón et al. (2005), Cunha (2007), Galloway (2007), Jørgensen and Kashiwadani (2008), Gilbert and Jørgensen (2009), and Lopez de Silanes et al. (2012).

Leptogium includes the following species: *L. aciculare* P.M. Jørg., *L. acutisporum* P.M. Jørg., *L. adpressum* Nyl., *L. americanum* Degel., *L. andinum* P.M. Jørg., *L. arcticum* P.M. Jørg., *L. arisanense* Asahina, *L. arsenei* Sierk, *L. asiaticum* P.M. Jørg., *L. askotense* Awasthi, *L. aucklandicum* Zahlbr., *L. australe* (Hook. f. & Taylor) Müll. Arg., *L.*

austroamericanum (Malme) C.W. Dodge, *L. azureum* (Sw.) Mont., *L. biloculare* Wilson, *L. brebissonii* Mont., *L. brecknockii* Hue, *L. britannicum* P.M. Jørg. & P. James, *L. burgessii* (L.) Mont., *L. burnetiae* Dodge, *L. capense* P.M. Jørg. & A.K. Wallace, *L. caperatum* P.M. Jørg. & A.K. Wallace, *L. chloromelum* (Sw.) Nyl., *L. cochleatum* (Dicks.) P.M. Jørg. & P. James, *L. coralloideum* (Meyen & Flot.) Vain., *L. corticola* (Taylor) Tuck., *L. crispatellum* Nyl., *L. cyanescens* (Rabenh.) Körb., *L. cyanizum* (Nyl.) Nyl., *L. daedaleum* (Flot.) Nyl., *L. davidii* M. Lindstr., *L. decipiens* P.M. Jørg., *L. degelii* M. Lindstr., *L. delavayi* Hue, *L. denticulatum* Nyl., *L. devertens* (Nyl.) Zahlbr., *L. diaphanum* (Sw.) Mont., *L. digitatum* (A. Massal.) Zahlbr., *L. epiphyllum* M. Lindstr., *L. eriodermoides* Arvidss. & P.M. Jørg., *L. ethiopicum* Dodge, *L. faciifictum* Verdon, *L. floridanum* Sierk, *L. foveolatum* Nyl., *L. furfuraceum* (Harm.) Sierk, *L. fusisporum* (Tuck.) Dodge, *L. granuligerum* Hue, *L. hibernicum* P.M. Jørg., *L. hildenbrandii* (Garov.) Nyl., *L. hirsutum* Sierk, *L. hypotrachynum* Müll. Arg., *L. indicum* D.D. Awasthi & Akhatar, *L. inflexum* Nyl., *L. inversum* P.M. Jørg. & A.K. Wallace, *L. isidiosellum* (Riddle) Sierk, *L. loriforme* P.M. Jørg. & Kashiw., *L. javanicum* Mont., *L. juressianum* Tav., *L. kalbii* Marcelli & I.P.R. Cunha, *L. laceroides* de Lesd., *L. mairei* (M. Choisy & Werner) Werner, *L. malmei* P.M. Jørg., *L. marginatum* M. Lindstr., *L. marginellum* (Sw.) Gray, *L. menziesii* Mont., *L. microstictum* Vain., *L. milligranum* Sierk, *L. moluccanum* (Pers.) Vain., *L. montis-wilhelmii* Diederich & Sipman, *L. papillosum* (de Lesd.) Dodge, *L. patagonicum* Zahlbr., *L. patwardhanii* A. Dube & Makhija, *L. pecten* F. Wilson, *L. pedicellatum* P.M. Jørg., *L. phyllocarpum* (Pers.) Mont., *L. pseudofurfuraceum* P.M. Jørg. & A.K. Wallace, *L. pseudopapillosum* P.M. Jørg., *L. punctulatum* Nyl., *L. resupinans* Nyl., *L. reticulatum* Mont., *L. rivulare* (Ach.) Mont., *L. rugosum* Sierk, *L. saturninum* (Dicks.) Nyl., *L. scrobiculatum* P.M. Jørg., *L. sessile* Vain., *L. sphaerosporum* P.M. Jørg. & Olley, *L. subjuressianum* Marcelli & Kitaura, *L. sulcatum* M. Lindstr., *L. transversum* M. Lindstr., *L. subazureum* A. Dube & Makhija, *L. trichophoroides* P.M. Jørg. & A.K. Wallace, *L. trichophorum* Müll. Arg., *L. ulvaceum* (Pers.) Vain, *L. valdivianum* M. Lindstr., *L. velutinum* P.M. Jørg., *L. verrucosum* A. Dube & Makhija, *L. vesiculosum* (Sw.) Malme., *L. victorianum* F. Wilson and *L. wilsonii* Zahlbr. Several of these names refer to taxonomic problems on species level, which require further studies.

***Paracollema* Otálora & Wedin gen. nov.** (MB 825692)

Type species: *Paracollema italicum* (B. de Lesd.) Otálora, P.M. Jørg. & Wedin, holotype.

Etymology: *Paracollema*, a derivation of *Collema*.

Icon: Fig. 5J (habitus)

Thallus foliose, small (up to 1 cm diam.), homoiomerous, dark olive green to brownish; lobes small, entire and rounded, up to 3 (1.0–2.5) mm wide; lobe surface smooth or slightly wrinkled; cortex absent; isidia present or absent; tomentum absent. *Apothecia* often present and numerous, laminal, sessile; disc plane to convex, dark red; thalline exciple thin and entire; proper exciple euthyplectenchymatous. *Asci* very small 30–45×8–9 μm. *Spores* 8 per ascus, very small 10–13×3–4.5 μm, narrowly ellipsoid or suboblong, 2-celled. *Pycnidia* often present. *Habitat* epiphytic.

Comments: This genus is distinguished from other Collemataceae by the very small asci and spores. Based on these characteristics Degelius (1974) defined the *Collema* Italicum-group, where he included only two species. These species are reported from Southern Europe and Northern Africa.

The species: For keys to identify species see: Degelius (1954, 1974). Two species of *Paracollema* formerly included in *Collema* require new combinations:

Paracollema almbornii (Degel.) Otálora, P.M. Jørg. & Wedin, **comb. nov.** (MB 805693) Basionym: *Collema almbornii* Degel., Symb. Bot. Upsal. 20: 61 (1974).

Paracollema italicum (de Lesd.) Otálora, P.M. Jørg. & Wedin, **comb. nov.** (MB 805694) Basionym: *Collema italicum* de Lesd., in Gyelnik, Bull. Soc. Bot. Fr. 84: 282 (1937).

***Pseudoleptogium* Müll. Arg.**

Flora, Jena 68 (28): 516 (1885).

Type species: *Pseudoleptogium diffractum* (Körb.) Müll. Arg., holotype.

Icon: Fig. 4F (habitus)

Thallus: placoid-squamulose, minutely to small size (0.5–1.0 cm diam.), forming circular patches; homoiomerous paraplectenchymatous throughout, brown-olive to black; with two distinct squamules type; marginal squamules adpressed, flat or convex, finger-like elongated (0.4–1.0 mm long and 0.2–0.5 mm wide); middle squamules reduced, like convex areoles (0.1–0.3 mm in diam.), often eroding leaving areas of radiating marginal squamules; squamules surface wrinkled and glossy at ends; cortex present; isidia absent; tomentum absent. *Apothecia*: very rare, laminal, disc convex, olivaceous brown disc. *Spores*: 8 per ascus 22–25×8–10 μm, ellipsoid, muriform. *Pycnidia*: unknown. *Habitat*: saxicolous on calcareous rocks.

Comments: Müller (1885) described *Pseudoleptogium* based on the differences in thallus structure, which he considered important enough to exclude this species from *Scytinium*. It may resemble some squamulose species of *Scytinium* from which it differ in the presence of two well-differentiated squamule types. The finger-like radiating marginal squamules make this genus superficially similar to some *Placynthium* species, but these associate with cyanobacteria of *Dichothrix* or *Scytonema*. *Pseudoleptogium* is a monospecific genus.

***Rostania* Trevis.**

Rev. Ist. Lomb., Milano, ser. 2 13: 75 (1880).

Type species: *Rostania quadrata* (Lahm ex Körb.) Trevis., holotype = *Collema occultatum* Bag., Comm. Soc. Critt. It.

1:1 (1861) ≡ *Rostania occultata* (Blag.) Otálora, P.M. Jørg. & Wedin.

≡ *Chiastosporum* Dughi., C. R. Hebd. Séanc. Acad. Sci., Paris 243: 1912 (1956). *Nom. superfl.*, type species: *Collema quadratum* Lahm ex Körb., Parerga Lichenol. (Breslau): 411 (1865), holotype ≡ *Rostania occultata* (Bagl.) Otálora, P.M. Jørg. & Wedin.

Icon: Fig. 5K–L (habitus).

Thallus subcrustaceous to subfoliose, rather small (0.3–2.5 cm diam.) homoiomerous, dark olive green or brownish, poorly developed, up to 2 mm broad but normally 1 mm wide, lobe surface smooth to ridged; cortex absent; isidia present or absent; tomentum absent. *Apothecia*: generally numerous, laminal, sessile, subglobose to flattened; disc red to red-brown; thalline exciple distinct and smooth; proper exciple euthyplechtenchymatous to euparaplectenchymatous. *Asci* 52–130×13–30 μm. *Spores* 8 or 4 per asci, small sized 12–30×8–20 μm, cubic-like in shape, muriform. *Pycnidia* rarely observed. *Habitat* primarily epiphytic, one terricolous species.

Comments: *Rostania* differs from other genera treated here by having minute thalli and cubic muriform spores. *Rostania* correspond to the *Collema* Occultatum-group (Degelius 1954). Trevisan (1880) recognized this species group as the genus *Rostania* Trevis. *Rostania* is mainly distributed in the temperate regions of the Northern Hemisphere (Europe and North America) with some representatives in subtropical Asia and Africa.

The species: For keys to identify species see: Degelius (1954, 1974). Six species of *Rostania* formerly included in *Collema* require new combinations:

Rostania callibotrys (Tuck.) Otálora, P.M. Jørg. & Wedin, **comb. nov.** (MB 805695) Basionym: *Collema callibotrys* Tuck., Proc. Amer. Acad. Arts. Sc. 5: 386 (1862).

Rostania ceranisca (Nyl.) Otálora, P.M. Jørg. & Wedin, **comb. nov.** (MB 805696) Basionym: *Collema ceraniscum* Nyl., Flora 48: 353 (1865).

Rostania coccophylla (Nyl.) Otálora, P.M. Jørg. & Wedin, **comb. nov.** (MB 805697) Basionym: *Collema coccophyllum* Nyl., Synops. Linch. 1: 112 (1858).

Rostania occultata (Bagl.) Otálora, P.M. Jørg. & Wedin, **comb. nov.** (MB 805698) Basionym: *Collema occultatum* Bagl., Comm. Soc. Crittog. Ital. 1: 23 (1861) ≡ *Collema quadratum* Lahm ex Körb., Parerga Lichenol. (Breslau): 411 (1865) ≡ *Rostania quadrata* (Lahm ex Körb.) Trevis. Rev. Ist. Lomb., Milano, ser. 2 13: 75 (1880).

Rostania multipunctata (Degel.) Otálora, P.M. Jørg. & Wedin, **comb. nov.** (MB 805699) Basionym: *Collema multipunctatum* Degel., Symb. Bot. Upsal. 13: 260 (1954).

Rostania laevispora (Swinscow & Krog) Otálora, P.M. Jørg. & Wedin, **comb. nov.** (MB 8056700) Basionym: *Collema laevisporum* Swinscow & Krog, Lichenologist 18: 69 (1986).

Scytinium (Ach.) Gray

Nat. Arr. Brit. Pl. 1: 398 (1821) Basionym: *Collema* section *Scytinium* Ach., Lich. Univ.: 642 (1810).

Type species: *Scytinium palmatum* (Huds.) Gray, proposed lectotype by Jørgensen et al. (2013) ≡ *Lichen palmatus* Huds., Fl. Angl., ed 2: 536 (1778).

= *Collemodium* Nyl. ex Lamy, Bull. Soc. Bot. Fr. 25: 341 (1878), type species: *Collemodium turgidum* (Ach.) Nyl. ex Lamy, Bull. Soc. Bot. Fr. 25: 342 (1878), lectotype designated here.

= *Homodium* Nyl. ex Olivier, Expos. Lich. Ouest Fran. 2: 359 (1903), type species: *Homodium subtile* (Schrad.) Olivier., Expos. Lich. Ouest Fran. 2: 362 (1903), lectotype designated here.

Icon: Fig. 3C (thallus anatomy), Fig. 4C–E, J–K (habitus)

Thallus crustose, squamulose or foliose, minute (up to 5 mm in diam.) to medium size (1–5 cm diam.); homoiomerous paraplectenchymatous throughout or not, lead grey to bluish, brownish or greenish; lobes spreading to cylindrical and oblong or elongated, in minute species lobe size is up to 1 mm, in medium size species lobe size is up to 5 mm wide; lobe surface smooth, to partially wrinkled, rarely swollen; cortex present or absent, or with pseudocortex; isidia present or absent; tomentum absent. *Apothecia* common, laminal or marginal, sessile; disc concave to flat, red brown; thalline exciple smooth to granulose, isidiate to lobulate, often persistent; proper exciple paraplectenchymatous. *Asci* 85–150×15–25 μm. *Spores* 8 per ascus, rather small 15–35×6–17 μm, ellipsoid and muriform. *Pycnidia* infrequent. *Habitat* corticolous, musicolous, terricolous or saxicolous.

Comments: This genus is very heterogeneous regarding morphology and ecology, but the species share the same type of ascospores (shape, septation), they have a small to medium size thallus, and most have a cortex or pseudocortex. It includes species formerly placed in three *Leptogium* sections (sect. *Homodium*, *Collemodium* and *Leptogium*) recognized by Zahlbruckner (1924) and three groups formerly included in *Collema* (the Fragrans, Callopismum and Leptogioides groups). The eucorticate species are similar to species of *Leptogium*, from which they differ in lobe, thallus and apothecium size. Unfortunately we have not found any anatomical distinction between the eucorticate *Scytinium* species and *Leptogium*, apart from general size. *Scytinium* species with pseudocortex may resemble *Blennothallia* but differ in spore shape and septation and also the cortex absence in *Blennothallia*. Most of the members of *Scytinium* occur in temperate regions of the northern hemisphere, and are very rare in tropical regions.

Nomenclatural comments: This generic name is based on *Collema* section *Scytinium* Ach. (1810), in which Acharius included three species. When Gray (1821) took it up on genus level, he included only the one species he knew from the British Isles, *S. palmatum*. This can hardly be seen as a

lectotypification, and we thus here designate *S. palmatum* as lectotype, to accommodate the minute foliose to small-squamulose species formely included in the genus *Leptogium*, in *Scytinium*. Gray also changed the spelling to *Scytenium*, something that must be seen as an orthographic variant to be corrected.

Collemodium Nyl. ex Lamy. Lamy included three species of which we designate *C. turgidum* as lectotype. The other species belong in our revised sense, to *Lathagrium* (*Collemodium cataclystum* = *Collema dichotomum*) and to the distantly related Massalongiaceae (*C. albocillatum*).

Homodium Nyl. ex Olivier is a commonly used name for parts of *Scytinium*. This name was validly published by Olivier but never typified. We designate one of the three original species that fit the description well, as lectotype.

The species: For keys to identify species see: Sierk (1964), Awasthi and Akhtar (1979), Jørgensen (1994, 2007), Jørgensen and Nash (2004), Aragón et al. (2005), Gilbert and Jørgensen (2009) and Lopez de Silanes et al. (2012). 44 species of *Scytinium* formerly included in *Collema* and *Leptogium* require new combinations, and one name is resurrected.

Scytinium apalachense (Tuck.) Otálora, P.M. Jørg. & Wedin, **comb. nov**. (MB 805703) Basionym: *Collema apalachense* Tuck., Amer. J. Sci. Arts Ser. 2 28: 200 (1859) ≡ *Leptogium apalachense* (Tuck.) Nyl., Memo. Soc. Sci. Nat. Cherb. 5: 334 (1857).

Scytinium aquale (Arnold) Otálora, P.M. Jørg. & Wedin, **comb. nov**. (MB 805704) Basionym: *Leptogium pusillum* var. *aquale* Arnold, Verh. Zool. Bot. Ges. Wien 23: 489 (1874) [1873] ≡ *Leptogium aquale* (Arnold) P.M. Jørg., Lichenologist 26: 1 (1994).

Scytinium aragonii (Otálora) Otálora, P.M. Jørg. & Wedin, **comb. nov**. (MB 805705) Basionym: *Leptogium aragonii* Otálora, in Otálora et al., Taxon 57: 915 (2008).

Scytinium biatorinum (Nyl.) Otálora, P.M. Jørg. & Wedin, **comb. nov**. (MB 805706) Basionym: *Collema biatorinum* Nyl., Act. Soc. Linn. Bord. Trois. 21: 268 (1856) ≡ *Leptogium biatorinum* Oliver, Expos. Lich. Ouest Fr. 2: 359 (1903).

Scytinium bosoense (H. Harada) Otálora, P.M. Jørg. & Wedin, **comb. nov**. (MB 805707) Basionym: *Leptogium bosoense* H. Harada, Lichenology 10: 29 (2011).

Scytinium californicum (Tuck.) Otálora, P.M. Jørg. & Wedin, **comb. nov**. (MB 805709) Basionym: *Leptogium californicum* Tuck., Syn. N. Amer. Lich. 1: 159 (1882).

Scytinium callopismum (A. Massal.) Otálora, P.M. Jørg. & Wedin, **comb. nov**. (MB 805710) Basionym: *Collema callopismum* A. Massal., Miscell. Lich.: 23 (1856).

Scytinium cellulosum (P.M. Jørg. & Tønsberg) Otálora, P.M. Jørg. & Wedin, **comb. nov**. (MB 805711) Basionym: *Leptogium cellulosum* P.M. Jørg. & Tønsberg, Bryologist 102: 412 (1999).

Scytinium chibaense (H. Harada) Otálora, P.M. Jørg. & Wedin, **comb. nov**. (MB 805712) Basionym: *Leptogium chibaense* H. Harada, Lichenology 9: 19 (2010).

Scytinium contortum (Sierk) Otálora, P.M. Jørg. & Wedin, **comb. nov**. (MB 805713) Basionym: *Leptogium contortum* Sierk, Bryologist 67: 272 (1964).

Scytinium dactylinum (Tuck.) Otálora, P.M. Jørg. & Wedin, **comb. nov**. (MB 805714) Basionym: *Leptogium dactylinum* Tuck., in Nylander, Syn. Meth. Lich. 1: 123 (1858).

Scytinium erectum (Sierk) Otálora, P.M. Jørg. & Wedin, **comb. nov**. (MB 805715) Basionym: *Leptogium erectum* Sierk, Bryologist 67: 261 (1964).

Scytinium euthallinum (Zahlbr.) Otálora, P.M. Jørg. & Wedin, **comb. nov**. (MB 805716) Basionym: *Collema leptogioides* var. *euthallinum* Zahlbr., Öst.. Bot. Z. 59: 494 (1909) ≡ *Collema euthallinum* (Zahlbr.) Degel., Symb. Bot. Upsal. 13: 268 (1954).

Scytinium ferax (Durieu & Mont) Otálora, P.M. Jørg. & Wedin, **comb. nov**. (MB 805716) Basionym: *Collema ferax* Durieu & Mont., Fl. Algér. 1–6: 206 (1847).

Scytinium fragile (Taylor) Otálora, P.M. Jørg. & Wedin, **comb. nov**. (MB 805718) Basionym: *Collema fragile* Taylor, in Mackay, Fl. Hibern. 2: 109 (1836).

Scytinium fragrans (Sm.) Otálora, P.M. Jørg. & Wedin, **comb. nov**. (MB805719) Basionym: *Lichen fragrans* Sm., in Smith & Sowerby, Engl. Bot. 27: tab. 1912 (1808) ≡ *Collema fragrans* (Sm.) Ach., Syn. Meth. Lich.: 311 (1814).

Scytinium gelatinosum (With.) Otálora, P.M. Jørg. & Wedin, **comb. nov**. (MB 805720) Basionym: *Lichen gelatinosus* With., Bot. Arr. Veg. Gr. Brit. 1: 710 (1776) ≡ *Leptogium gelatinosum* (With.) J. R. Laudon, Lichenologist 16: 219 (1984).

Scytinium imbricatum (P.M. Jørg.) Otálora, P.M. Jørg. & Wedin, **comb. nov**. (MB 805721) Basionym: *Leptogium imbricatum* P.M. Jørg., Lichenologist 26: 7 (1994).

Scytinium intermedium (Arnold) Otálora, P.M. Jørg. & Wedin, **comb. nov**. (MB 805723) Basionym: *Leptogium minutissimum* var. *intermedium* Arnold, Bull. Soc. Amis Sci. Nat. Rouen 2: 363 (1866).

Scytinium juniperinum (Tuck.) Otálora, P.M. Jørg. & Wedin, **comb. nov**. (MB 805724) Basionym: *Leptogium juniperinum* Tuck., in Nylander, Syn. Meth. Lich. 1: 125 (1858).

Scytinium leptogioides (Anzi) Otálora, P.M. Jørg. & Wedin, **comb. nov**. (MB 805725) Basionym: *Collema leptogioides* Anzi, Comment. Soc. Critt. It. 1: 132 (1862).

Scytinium lichenoides (L.) Otálora, P.M. Jørg. & Wedin, **comb. nov**. (MB 805727) Basionym: *Tremella lichenoides* L., Sp. Pl. 2: 1157 (1753) ≡ *Leptogium lichenoides* (L.) Zahlbr., Cat. Lich. Univers. 3: 136 (1924).

Scytinium magnussonii (Degel. & P.M. Jørg.) Otálora, P.M. Jørg. & Wedin, **comb. nov**. (MB 805728) Basionym:

Leptogium magnussonii Degel. & P.M. Jørg., Lichenologist 26: 14 (1994).

Scytinium massiliense (Nyl.) Otálora, P.M. Jørg. & Wedin, **comb**. **nov**. (MB 805729) Basionym: *Leptogium massiliense* Nyl., Flora 62: 354 (1879).

Scytinium palustre (P.M. Jørg.) Otálora, P.M. Jørg. & Wedin, **comb**. **nov**. (MB 805730) Basionym: *Leptogium palustre* P.M. Jørg., Lichenologist 26: 213 (1994).

Scytinium parculum (Nyl.) Otálora, P.M. Jørg. & Wedin, **comb**. **nov**. (MB 805731) Basionym: *Leptogium parculum* Nyl., Flora 68: 601 (1885).

Scytinium parvum (Degel.) Otálora, P.M. Jørg. & Wedin, **comb**. **nov**. (MB 805732) Basionym: *Collema parvum* Degel., Symb. Bot. Upsal. 13: 273 (1954).

Scytinium platynum (Tuck.) Otálora, P.M. Jørg. & Wedin, **comb**. **nov**. (MB 805733) Basionym: *Leptogium californicum* var. *platynum* Tuck., Syn. N. Amer. Lich. 1: 159 (1872) ≡ *Leptogium platynum* (Tuck.) Herre, Proc. Wash. Acad. Sci. 12: 144 (1910).

Scytinium subfragrans (Degel.) Otálora, P.M. Jørg. & Wedin, **comb**. **nov**. (MB 805734) Basionym: *Collema subfragrans* Degel., Symb. Bot. Upsal. 20: 86 (1974).

Scytinium kauaiense (H. Magn.) Otálora, P.M. Jørg. & Wedin, **comb**. **nov**. (MB 805735) Basionym: *Collema kauaiense* H. Magn., in Magnusson & Zahlbruckner, Ark. Bot. 31A: 63 (1943).

Scytinium plicatile (Ach.) Otálora, P.M. Jørg. & Wedin, **comb**. **nov**. (MB 805736) Basionym: *Lichen plicatilis* Ach., K. Vetensk-Acad. Nya Handl.: 11 (1795) ≡ *Leptogium plicatile* (Ach.) Leight., Lich. Fl. Great Brit. 3: 30 (1879).

Scytinium polycarpum (P.M. Jørg. & Goward) Otálora, P.M. Jørg. & Wedin, **comb**. **nov**. (MB 805738) Basionym: *Leptogium polycarpum* P.M. Jørg. & Goward, Acta Bot. Fenn. 150: 75 (1994).

Scytinium rivale (Tuck.) Otálora, P.M. Jørg. & Wedin, **comb**. **nov**. (MB 805739) Basionym: *Leptogium rivale* Tuck., Proc. Amer. Acad. Arts & Sci. 12: 170 (1877).

Scytinium rogersii (Verdon) Otálora, P.M. Jørg. & Wedin, **comb**. **nov**. (MB 805741) Basionym: *Leptogium rogersii* Verdon, Mycotaxon 37: 424 (1990).

Scytinium schraderi (Bernh.) Otálora, P.M. Jørg. & Wedin, **comb**. **nov**. (MB 805742) Basionym: *Lichen schraderi* Bernh., J. Bot. 1: 22 (1799) ≡ *Leptogium schraderi* (Bernh.) Nyl., Act. Soc. Linn. Bord., Trois. sér. 21: 272 (1856).

Scytinium siskiyouensis (D.F. Stone & Ruchty) Otálora, P.M. Jørg. & Wedin, **comb**. **nov**. (MB 805744) Basionym: *Leptogium siskiyouensis* D.F. Stone & Ruchty, N. Amer. Fung. 3: 2 (2008).

Scytinium subaridum (P.M. Jørg. & Goward) Otálora, P.M. Jørg. & Wedin, **comb**. **nov**. (MB 805745) Basionym: *Leptogium subaridum* P.M. Jørg. & Goward, Acta Bot. Fenn. 150: 76 (1994).

Scytinium subtile (Schrad.) Otálora, P.M. Jørg. & Wedin, **comb**. **nov**. (MB 805746) Basionym: *Lichen subtilis* Schrad., Spicil. Fl. Germ. 1: 95 (1794) ≡ *Leptogium subtile* (Schrad.) Torss., Enum. Lich. Byssac. Scandin.: 54 (1843).

Scytinium subtorulosum (Stizenb.) Otálora, P.M. Jørg. & Wedin, **comb**. **nov**. (MB 805748) Basionym: *Collema subtorulosum* Stizenb., Ber. Tät. St Gall. Naturw. Ges.: 265 (1882) ≡ *Leptogium subtorulosum* (Stizenb.) Degel., Symb. Bot. Upsal. 13: 465 (1954).

Scytinium tenuissimum (Dicks.) Otálora, P.M. Jørg. & Wedin, **comb**. **nov**. (MB 805749) Basionym: *Lichen tenuissimus* Dicks., Fasc. Pl. Crypt. Brit. 1: 12 (1785) ≡ *Leptogium tenuissimum* (Dicks.) Körb., Syst. Lich. Germ.: 419 (1855).

Scytinium teretiusculum (Wallr.) Otálora, P.M. Jørg. & Wedin, **comb**. **nov**. (MB 805750) Basionym: Lichen teretiusculus Wallr., Fl. Crypt. Germ. 1: 551 (1831) ≡ *Leptogium teretiusculum* (Wallr.) Arnold, Ber. Bayer. Bot. Ges. 2 Anhang: 26 (1892).

Scytinium tetrasporum (Th. Fr.) Otálora, P.M. Jørg. & Wedin, **comb**. **nov**. (MB 805751) Basionym: *Leptogium tetrasporum* Th. Fr., Öfvers. Förh. Kongl. Sven. Vetens.-Akad. 21: 276 (1864).

Scytinium turgidum (Ach.) Otálora, P.M. Jørg. & Wedin, **comb**. **nov**. (MB 805752) Basionym: *Collema turgidum* Ach., Lich. Univ.: 634 (1810) ≡ *Leptogium turgidum* (Ach.) Cromb., Lich. Fl. Great Brit.: 28 (1871).

Scytinium paramensis (P.M. Jørg. & Palice) Otálora, P.M. Jørg. & Wedin, comb. nov. (MB 805702) Basionym: *Collema paramense* P.M. Jørg. & Palice, Bibl. Lichenol. 108: 135 924 (2012)

The species taxonomy of several of these names needs further studies.

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References

Acharius E (1810) Lichenographia universalis. Danckwerts, Göttingen

Aragón G, Otálora MAG, Martínez I (2005) New data on the genus *Leptogium* (lichenized Ascomycetes) in the Iberian Peninsula. Nova Hedw 80:199–226

Awasthi DD, Akhtar P (1977) The genus *Leptogium* (sect. *Mallotium*) in India. Norw J Bot 24:59–71

Awasthi DD, Akhtar P (1979) The lichen genus *Leptogium* (Sects. *Leptogium*, *Leptogiopsis* and *Homodium*) in India. Geophytology 8:189–204

Browne P (1756) The civil and natural history of Jamaica. Osborne and Shipton, London.

Carvalho P (2012) *Collema*. Flora Liquenológica Ibérica. Vol 10. Sociedad Española de Liquenología, SEL, Pontevedra

Clements FE, Shear CL (1931) The genera of Fungi. MW. Wilson, New York.

Crombie JM (1894) A monograph of lichens found in Britain. Part 1. British Museum, London

Cunha IPR (2007) Fungos liquenizados do gênero *Leptogium* (Ascomycetes) no litoral sul do Estado de São Paulo. Botucatu SP, Janeiro

Degelius G (1954) The lichen genus *Collema* in Europe: morphology, taxonomy. Ecology Symb Bot Upsal 13:1–499

Degelius G (1974) The lichen genus *Collema* with special reference to the extra–European species. Symb Bot Upsal 20:1–215

Dodge CW (1964) Some Lichens of Tropical Africa. IV. Dermatocarpaceae to Pertusariaceae. Beihefte zur Nova Hedwigia, Heft 12. Verlag J. Cramer, Weinheim

Fink B (1910) The lichens of Minnesota. Contr US Nat Herb 14:1–269

Fink B (1918) A new genus and species of the Collemaceae. Mycologia 10:235–238

Flotow J (1850) Ueber Collemaceen. Linnaea 23:147–301

Galloway DJ (2007) Flora of New Zealand Lichens. Lichen-Forming and Lichenicolous Fungi. Vol 1. Manaaki Whenua Press, Lincoln

Galloway DJ, Jørgensen PM (1995) The lichen genus *Leptogium* (Collemataceae) in southern Chile, South America. In: Daniels FJA, Schultz M, Peine J (eds) Flechten Follmann. Contributions to lichenology in honour of Gerhard Follmann. Bot. inst. Univ. Cologne, Cologne, pp 227–247

Gilbert OL, Jørgensen PM (2009) *Leptogium* In: Smith CW, Aptroot A. Coppins BJ, Fletcher A, Gilbert OL, James PW, Wolseley PA (eds) The Lichens of Great Britain and Ireland. British Lichen Society, London pp 541–551

Gilbert OL, James PW, Purvis OW (2009) *Collema* In: Smith CW, Aptroot A. Coppins BJ, Fletcher A, Gilbert OL, James PW, Wolseley PA (eds) The Lichens of Great Britain and Ireland. British Lichen Society, London pp 345–357

Gray SF (1821) A natural arrangement of British plants according to their relations to each other. Baldwin, Cradock and Joy, London

Henssen A (1965) A review of the genera of the Collemataceae with simple spores (excluding *Physma*). Lichenologist 3:29–41

Henssen A (1981) The lecanoralean centrum. In: Reynolds DR (ed) Ascomycetes systematics. Springer Verlag, New York, pp 139–234

Jørgensen PM (1973a) Über einige *Leptogium*-Arten von Mallotium-Typ. Herzogia 2:453–468

Jørgensen PM (1973b) On some *Leptogium* species with short Mallotium hairs. Svensk Bot Tids 67:53–58

Jørgensen PM (1975) Contributions to a monograph of the Mallotium-hairy *Leptogium* species. Herzogia 3:433–460

Jørgensen PM (1994) Further notes on European taxa of the lichen genus *Leptogium*, with emphasis on the small species. Lichenologist 26:1–29

Jørgensen PM (1997) Further notes on hairy *Leptogium* species. Symb Bot Upsal 32:113–130

Jørgensen PM (2007) Collemataceae. Nordic Lichen Flora 3:14–42

Jørgensen PM, Goward T (1994) Two new *Leptogium* species from western North America. Acta Bot Fenn 150:75–78

Jørgensen PM, James PW (1983) Studies on some *Leptogium* species of western Europe. Lichenologist 15:109–125

Jørgensen PM, Kashiwadani H (2008) *Leptogium loriforme* P. M. Jørg. & Kashiw., a new hairy species from Papua New Guinea. Lichenologist 40:123–125

Jørgensen PM, Nash TH III (2004) Leptogium. In: Nash TH III, Ryan BD, Diederich P, Gries C, Bungartz F (eds) Lichen flora of the Greater Sonoran Desert region Vol. 2. Lichens Unlimited, Arizona State University, Tempe, pp 330–350

Jørgensen PM, Olley L (2010) A new hairy *Leptogium* from Nepal. Lichenologist 42:387–389

Jørgensen PM, Tønsberg T (1999) Notes on some small species of *Leptogium* from Pacific North America. Bryologist 102:412–417

Jørgensen PM, Otálora MAG, Wedin M (2013) Proposal to conserve the generic name *Leptogium* (lichenized Ascomycota) with a new type. Taxon 62(6)

Kass RE, Raftery AE (1995) Bayes factors. J Am Stat Assoc 90:773–795

Kitaura MJ, Marcelli MP (2012) The *Leptogium jurassianum* complex in southeastern Brazil. Mycotaxon 120:215–221

Lamy CE (1878) Catalogie raisonné des lichens du Mont-Dore et de la Haute Vienne. Bull Soc Bot France 25:321–536

Lindström M (1993) *Leptogium degelii*, a new species from South America. Graphis Scripta 5:5–7

Lindström M (2007) New species in the lichen genus *Leptogium* (Collemataceae) from tropical South America. Biblioth Lichenol 95:405–428

Lopez de Silanes ME, Paz-Bermudez G, Carballal R, Marques J (2012) The genus *Leptogium* (Collemataceae, Ascomycotina) in mainland Portugal. Sydowia 6:67–102

Magain N, Sérusiaux E (2012) A further new species in the lichen genus *Arctomia*: *A. borbonica* from Reunion (Mascarene archipelago). MycoKeys 4:9–21

Massalongo AB (1853) Memorie lichenografiche con un' appendice alle ricerche sull' autonomia dei licheni crostosi. HF Münster, Verona.

Miadlikowska J, Lutzoni F (2004) Phylogenetic classification of Peltigeralean fungi (Peltigerales, Ascomycota) based on ribosomal RNA small and large subunits. Am J Bot 91:449–464

Miadlikowska J, Kauff F, Hofstetter V et al (2006) New insights into classification and evolution of the Lecanoromycetes (Pezizomycotina, Ascomycota) from phylogenetic analyses of three ribosomal RNA and two protein–coding genes. Mycologia 98:1089–1102

Müller J (1882) Lichenologische Beiträge 15. Flora 65:291–306

Müller J (1885) Lichenologische Beiträge 22. Flora 68:503–518

Nylander JAA, Ronquist F, Huelsenbeck JP, Nieves-Aldrey LJ (2004) Bayesian phylogenetic analysis of combined data. Syst Biol 53:47–67

Oliver MH (1903) Exposé systématique et description des lichens de l'ouest et du nord-ouest de la France 2. Bazoches-sur-Houlme (Orne), Normadie, Bretagne, Anjou, Maine, Vendée

Otálora MAG, Wedin M (2013) *Collema fasciculare* belongs in Arctomiaceae. Lichenologist 45:295–304

Otálora MAG, Aragón G, Molina MC et al (2010) Disentangling the *Collema–Leptogium* complex through a molecular phylogenetic study of the Collemataceae (Peltigerales, lichen–forming Ascomycota). Mycologia 102:279–290

Otálora MAG, Aragón G, Martínez I, Wedin M (2013) Cardinal characters on a slippery slope—a re-evaluation of phylogeny, character evolution, and evolutionary rates in the jelly lichens (Collemataceae s. str). Mol Phylogenet Evol 68:185–198

Ronquist F, Teslenko M, van der Mark P et al (2011) MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. Syst Biol 61:539–542

Shimodaira H, Hasegawa M (2001) CONSEL: for assessing the confidence of phylogenetic tree selection. Bioinformatics 17:1246–1247

Sierk HA (1964) The genus *Leptogium* in North America and North of Mexico. Bryologist 67:245–317

Spribille T, Muggia L (2013) Expanded taxon sampling disentangles evolutionary relationships and reveals a new family in Peltigerales (Lecanoromycetidae, Ascomycota). Fungal Divers 58:171–184

Stamatakis A (2006) RAxML–VI–HPC: maximum likelihood–based phylogenetic analyses with thousands of taxa and mixed models. Bioinformatics 22:2688–2690

Swinscow TDV, Krog H (1988) Macrolichens of East Africa. British Museum (Natural History), London

Trevisan V (1853) Caratteri di tre nuovi generi di Collemacee. Padova.

Trevisan V (1880) Sulle Garovaglinee, nuovo tribu di Collemacee. Rend R Ist Lomb Scie Lett Ser 2(13):65–77

Tuckerman E (1872) Genera Lichenum: an arrangement of the North American lichens. E Nelson, Amherst

Tuckerman E (1882) A sypnosis of the North American lichens I. Lewiston, Maine

Vainio E (1890) Etude sur la Classification Naturelle et la Morphologie des Lichens du Bresil. Fauna Flora Fenn 7:1–256

Verdon D, Filson RB, Henssen A (1992) Collemataceae. Flora Aust 54: 173–192

Wedin M, Wiklund E (2004) The phylogenetic relationships of Lecanorales suborder Peltigerineae revisited. Symb Bot Upsal 34: 469–475

Wedin M, Wiklund E, Jørgensen PM, Ekman S (2009) Slippery when wet: phylogeny and character evolution in the gelatinous cyanobacterial lichens (Peltigerales, Ascomycetes). Mol Phylogenet Evol 53:862–871

Wiklund E, Wedin M (2003) The phylogenetic relationships of cyanobacterial lichens in the Lecanorales suborder Peltigerineae. Cladistics 19:419–431

Zahlbruckner A (1907) Lichenes (Flechten), In: Engler A, Prantl K (ed.) Die natürlichen Pflanzenfamilien I. W. Engelmann, Leipzig, pp 49–249.

Zahlbruckner A (1924) Catalogus Lichenum Universalis vol. 3. Borntraeger, Leipzig.

Zahlbruckner A (1926) Catalogus Lichenum Universalis vol. 4. Borntraeger, Leipzig.