Two new species of *Leptogium* (Collemataceae) with transversely septate ascospores from East Africa

Ulla Kaasalainen¹, Paul M. Kirika², Neduvoto P. Mollel³, Andreas Hemp⁴ & Jouko Rikkinen^{1,5}

¹ Finnish Museum of Natural History, University of Helsinki, P.O. Box 7, 00014 Helsinki, Finland E-mail: ulla.kaasalainen@helsinki.fi

² National Museums of Kenya, East African Herbarium, Museum Hill Road, P.O. Box 45166, Nairobi 00100, Kenya ³ National Herbarium, Tropical Pesticides Research Institute, P.O. Box 3024, Arusha, Tanzania

⁴ Department of Plant Systematics, University of Bayreuth, Universitätsstraße 30, 95440 Bayreuth, Germany

⁵ Organismal and Evolutionary Biology Research Programme, Faculty of Biological and Environmental Sciences,

University of Helsinki, P.O. Box 65, 00014 Helsinki, Finland

Abstract: Two epiphytic *Leptogium* species from East Africa, both with transversely septate ascospores, are here described as new. They produce plicate thalli and have a paraplectenchymatous proper exciple and a one cell layer thick cortex on the thalline exciple. *Leptogium bellum* has so far only been collected from Mt. Kilimanjaro, Tanzania, where it occurs from midmontane forests up to the subalpine zone. *Leptogium tiinae* occurs in relatively open habitats at lower elevations, with the type specimen collected from the Taita Hills, Kenya. Additionally, details from a *Leptogium chloromeloides* isotype and a key for *Leptogium* species with transversely septate ascospores are provided.

Keywords: Eastern Arc, Mt. Kilimanjaro, Taita Hills, paleotropics, biodiversity hotspot, afromontane, *Leptogium* section *Leptogiopsis*, Peltigerales

INTRODUCTION

Leptogium (Ach.) Gray is the most species-rich genus within Collemataceae (Peltigerales), with its highest diversity in tropical regions (Otálora et al., 2014). While most Leptogium species have muriform spores, some species produce ascospores with only transverse septa and have traditionally been placed into Leptogium section Leptogiopsis Vain. Kitaura et al. (2013) list eleven such species: Leptogium adpressum Nyl., Leptogium ankolense C.W. Dodge, Leptogium brebissonii Mont., Leptogium chloromeloides Nyl., Leptoqium fusisporum (Tuck.) C.W. Dodge, Leptogium granadillae (C.W. Dodge) Degel., Leptogium longisporum Kitaura & Marcelli, Leptogium megapotamicum Malme, Leptogium pacificum Vain., Leptogium reticulatum Nyl., and Leptogium thoroldii C.W. Dodge. Even though with similar ascospores, these species differ significantly in apothecial anatomy (Kitaura, 2012; Kitaura et al., 2013) and hence probably do not form a monophyletic group.

In their handbook of East African macrolichens, Swinscow and Krog (1988) confirm only one species of *Leptogium* with transversely septate ascospores, *L. adpressum*. Also *L. brebissonii* is mentioned, but only on the basis of sterile specimens. Some further species of this group have been reported from Africa in older literature, including *L. ankolense* from Uganda (Dodge, 1971), *L. thoroldii* from western Africa (Dodge, 1964), and *L. chloromeloides* from South Africa (Nylander, 1869).

We recently analyzed nearly 600 *Leptogium* specimens collected from Kenya and Tanzania (Kaasalainen et al., 2021). The results revealed that montane forests of the East African mountains, belonging to the Eastern Afromontane biodiversity hotspot, support a very high diversity of *Leptogium* species, most of them presently undescribed. Here we describe two such taxa, both with transversely septate ascospores.

MATERIAL AND METHODS

The material of Kaasalainen et al. (2021) were revisited and all fertile specimens with transversely septate ascospores were picked for closer inspection and compared with available older herbarium specimens. For details on the study region, sampling, and the phylogenetic analysis of the nuITS and mtSSU genetic regions of the specimens see Kaasalainen et al. (2021). The morphological and anatomical characters were assessed using a Leica S8APO stereo and an Olympus BX51 compound light microscope, the latter equipped with a Deltapix Invenio 12EIII camera.

RESULTS AND DISCUSSIONS

In our material from East Africa, specimens with transversely septate ascospores occur only in two closely related taxa, OTUH1 and OTUH2 of Clade H (Fig. 4 in Kaasalainen et al., 2021). Closer inspection of the specimens revealed differences in morphology and anatomy, confirming that the two taxa represent distinct species, further characterized by contrasting altitudinal distributions. By comparing these specimens with herbarium material and published descriptions of all known *Leptogium* species with transversely septate ascospores, it became evident that both species are new to science.

Species of *Leptogium* with transversely septate ascospores are best distinguished based on anatomical differences in the apothecia, such as the presence or absence of a paraplectenchymatous proper exciple and cortical thickness of the thalline exciple (either consisting of only one or several cell layers), structure of outgrowths on the apothecial margin, and size of the ascospores. It should be emphasized that when measuring the length of ascospores in this group, only spores from mature apothecia (generally with flattened discs) should be analysed as the ascospores of young apothecia (generally with concave discs) tend to be shorter, wider and with fewer septa.

Both *Leptogium bellum* and *L. tiinae* have a thick paraplectenchymatous proper exciple but lack a paraplectenchymatous cortex of thalline exciple and apothecial base. Previously described *Leptogium* species with similar apothecial features include *L. adpressum* (Kitaura, 2012), *L. longisporum* (Kitaura et al., 2013), and *L. thoroldii* (Dodge, 1964). The diagnostic characteristics of these species are summarized in Table 1.

An additional species with a prominent paraplectenchymatous proper exciple is *Leptogium granadillae*, originally described from Costa Rica. However, *L. granadillae* also has a paraplectenchymatous cortex of thalline exciple (Dodge, 1933; Degelius, 1962), unlike the newly described species. **Table 1.** Summary of the presently known *Leptogium* species with acicular, transversely septate ascospores, a paraplectenchymatous +40 +4011:00 (Polloo and this (and 1010

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	Type	Known distribution	Apothecial margin	Ascospores (µm)	Comments	References
Leptogium adpressum	H-NYL 41254!	Mexico*, reported to be widespread in tropical and temperate regions.	With braid- resembling wrinkles.	50-60 × 7-8	Previous reports of this species from East Africa probably represent <i>L.</i> <i>bellum</i> and/or <i>L. tiinae</i> .	Nylander, 1858; Sierk, 1964; Swinscow and Krog, 1988; Kitaura, 2012.
<i>Leptogium bellum</i> sp. nov.	H 9234932	Tanzania*	With delicate sack- like nodules.	$40-60 \times 6-12$	Leptogium OTUH2	Kaasalainen et al., 2021.
Leptogium longisporum	SP	Brazil*	Densely ridged, cerebroid contorted.	55–90 × 5		Kitaura et al., 2013.
Leptogium thoroldii	FH 00302796	Nigeria, Cameroon	Minutely and deeply scrobiculate.	50-55 × 3-4		Dodge, 1964.
<i>Leptogium tiinae</i> sp. nov.	EA JR10017a (duplicate H 9234943)	Kenya*, Tanzania	With robust cerebroid structures.	60-90 × 5-9	Leptogium OTUH1	Kaasalainen et al., 2021.
* True 100041000						

Type location

Several of the Leptogium species with transversely septate ascospores are characterized by a presence of several cell layers of paraplectenchymatous tissue in the cortex of thalline exciple and a lack of paraplectenchymatous proper exciple. According to Kitaura (2012), the apothecia of L. brebissonii from Brazil have paraplectenchymatous cortex of thalline exciple and a colloplectenchymatous proper exciple. Leptogium brebissonii was originally described from the Canary Islands (Webb and Berthelot, 1840), and only sterile specimens have been reported from East Africa (Swinscow and Krog, 1988; Kaasalainen et al., 2021). In the phylogenetic analysis of Kaasalainen et al. (2021), such specimens grouped into Clade E and are thus not closely related to L. bellum and L. tiinae. Also Leptogium ankolense from Uganda (Dodge, 1971), L. megapotamicum from Brazil (Kitaura et al., 2013), and L. pacificum from the Philippines (Kitaura, 2012) are characterized by a several cell layers thick cortex of the thalline exciple and lack of paraplectenchymatous proper exciple. The last-mentioned taxon has also been reported to have a pseudocortex on its lower surface (Kitaura, 2012), which is uncharacteristic for Leptogium s. str. (Otálora et al., 2014).

Leptogium chloromeloides, on the other hand, seem to lack both apothecial paraplectenchymatous tissues. Even though the original description lacks the details of apothecial anatomy (Nylander, 1869) and the type specimen in DBN (Medeiros, 2019) was not available for loan, an isotype in G (G00047541, Afrique du Sud; Wood, J.M. 326) was most helpfully sent for inspection. The lobes of the specimen are up to 2 cm long and 5 mm wide, relatively thick, adnate, and rounded; margins are ascending, often clearly wrinkled, thicker and darker than the central parts of the thallus. The upper surface is light grey and slightly wrinkled on the central parts, with occasional ridges, darker especially towards the margins. The lower surface is longitudinally plicate, yellowish brown or grey. Isidia and phyllidia were not seen. Some pycnidia are present on the thickened margins of the thallus. Apothecia are mainly marginal, slightly congested, up to 1.9 mm in diam., with reddish brown, flat to convex discs. Apothecial margins are slightly wrinkled or uneven and without ornamentation.

The cortex of thalline exciple is one cell layer thick and thick, paraplectenchymatous proper exciple is not present. Hymenium is 80-85 µm and subhymenium 50-55 µm thick (N=1). The few seen ascospores fit well the original description by Nylander (1869): $34-40 \times 4.5$ µm with 5-7 septa.

Additionally, two species lack the information of apothecial anatomy or have contradicting previous descriptions: Leptogium reticulatum from the Neotropics has a reticulately ridged thallus. We could not find mature apothecia in any of the available specimens (isotype H-NYL 41389, French Guiana; H-NYL 41390, Guadalupe; H-NYL 41391, Cuba). The original description also lacks information on ascospore and apothecial characters (Montagne, 1841). However, the thallus morphology of this species is quite distinct, and a sequence of L. reticulatum from Colombia did not group with our new species in the phylogenetic analysis (Kaasalainen et al., 2021). Leptogium fusisporum from the USA was originally described as having granular apothecial margins and ascospores up to 48 µm long and with 8-10 cells, but details of the apothecial anatomy were not given (Tuckerman, 1882; Dodge, 1933). According to Sierk (1964), the apothecia have entire margins, the proper exciple is paraplectenchymatous, the thalline exciple has a one layered cortex, and the as cospores are $25-40 \times 6-7 \mu m$ with 3-5 septa. Kitaura et al. (2013) mention that apothecia of L. fusisporum "lack subhymenial paraplectechyma tissue, but have a paraplectenchymatous multilayered amphithecium instead", but do not provide details of the source of this information. In any case, none of the combination of features described above are concurrent with those of L. bellum and L. tiinae.

TAXONOMY

LEPTOGIUM BELLUM Kaasalainen sp. nov. (Fig. 1)

Mycobank # MB848314

Species of *Leptogium* with a plicate thallus, delicate nodules on thallus and apothecial thalline exciple, apothecia with a paraplectenchymatous proper exciple and one-celled cortex of the thalline exciple, and $40-60 \mu m \log transversely$ septate ascospores.

Holotype: Tanzania, Mt. Kilimanjaro, upper montane secondary forest with *Erica excelsa* near the Maua Route, 3.1864°S 37.4403° E, 2820 m elevation, on a fallen branch, 11 March 2017, U. Kaasalainen UK170821a (H 9234932).

ITS barcoding marker accession (GenBank): MW340331 (holotype).

Description: Thallus up to 3 cm wide, opaque, glossy. Lobes laciniate, up to 5 mm wide, adnate or ascending. Upper surface longitudinally plicate, dirty white to gray; abundant, gray, delicate sack-like nodules clustered on lobe margins and apices, thallus ridges and the apothecial thalline exciple. Lower surface longitudinally plicate, dirty white or brownish grey. Isidia and lobules absent, but sack-like nodules on thallus and apothecia may resemble isidia. Rhizines and hairs absent, thallus attached to substrate by hapters. Apothecia common, up to 4.4 mm in diam., developing into the apices of stipe-like ascending lobes; discs of mature apothecia plane; thalline exciple gray, with abundant delicate nodules.

Anatomy: Thallus 200-450 µm thick, clearly thicker at ridges; quadratic cortical cells ca. 5 µm wide; medulla loose, columnar hyphae absent. Cyanobacteria (Nostoc) as long filaments, cells oval, $3-7 \times 3-4 \mu m$, heterocysts slightly larger. Apothecia with hymenium 110-140 µm thick; subhymenium 50-90 µm thick, orange-brownish; proper exciple paraplectenchymatous, 80-150 µm thick (12-15 cell layers) at the center, mainly pinkish grey, becoming more hyaline towards the (sub)hymenium; parahymenial tissue mainly consisting of the paraplectenchymatous proper exciple, 20-40(60) µm at the margin (on the level of hymenium surface); cortex of thalline exciple one cell layer thick. Ascospores acicular with 6-9 transverse septa, 40-60 \times 6-12 μ m (m = 52×9 , SD = 6×1.7 , N = 27). Pycnidia common and abundant, on and between the sack-like nodules, brown to dark brown; conidia rodshaped, often slightly narrower at the middle, 3.4-4.0 × 1.5-1.8 μm in size.

Etymology: The specific epithet refers to the elegant appearance of the species.

Ecology and distribution: *Leptogium bellum* is so far only known from Mt. Kilimanjaro, Tanzania, where it is quite consistently present especially in middle and upper montane forests but also in subalpine shrublands (2260–3520 m). The species grows as an epiphyte on branches of montane trees and, in more open habitats in the subalpine zone and upper montane secondary *Erica excelsa* forest, also on tree trunks.

Notes: *Leptogium bellum* is easily distinguished from other *Leptogium* species with transversely septate ascospores due to the abundant, delicate, sack-like nodules on the thallus and thalline exciple. Additionally, the two species in East Africa, *L. bellum* and *L. tiinae*, are distinguished by ascospore size and habitat. *Leptogium bellum* occurs at high elevations (>2000 m) from middle montane forests to the subalpine zone and has shorter ascospores less than 60 μ m long, while *L. tiinae* has ascospores over 60 μ m long and is found from lower elevations (<1500 m) in relatively open habitats.

Additional specimens examined: Tanzania, Mt. Kilimanjaro, middle montane Ocotea forest near the Machame route, 3.1368° S 37.2455° E, 2260 m elevation, on a fallen branch, 9 March 2017, U. Kaasalainen UK170792g (H 9234931; ITS: MW340330, mtSSU: MW335316); near the Umbwe route, 3.1385° S 37.3052° E, 2650 m elevation, on a fallen branch, 20 June 2017, U. Kaasalainen UK171478e (H 9234938; ITS: MW340336, mtSSU: MW335322); 3.1400° S 37.3031° E, 2540 m elevation, on a fallen branch, 20 June 2017, U. Kaasalainen UK171494b (H 9234939; ITS: MW340337, mtSSU: MW335323); near the Mweka route, 3.1722° S 37.3583° E, 2750 m elevation, on a fallen branch, 24 June 2017, U. Kaasalainen UK171516y (H 9234942; ITS: MW340338, mtSSU: MW335324); previously logged middle montane Ocotea forest near the Marangu route, 3.2018° S 37.5159° E, 2370 m elevation, on a fallen branch, 14 March 2017, U. Kaasalainen UK170911a (H 9234935; ITS: MW340333, mtSSU: MW335319); upper montane Podocarpus forest near the Marangu route, 3.1788° S 37.5126° E, 2800 m elevation, on a fallen branch, 13 March 2017, U. Kaasalainen UK170880n (H 9234934; ITS: MW340332, mtSSU: MW335318); near the Mweka route, 3.1659° S 37.3626° E, 2940 m elevation, on a fallen branch, 24 June 2017, U. Kaasalainen UK171525k (H 9234940; ITS: MW340339, mtSSU: MW335325); upper montane secondary forest with Erica excelsa near the Maua route, 3.1864° S 37.4403° E,



Fig. 1. *Leptogium bellum.* A–B. Type UK170821. A. General habit of moist thallus. B. Pycnidia on dry thallus. C. Habit when dry, showing the plicate thallus and delicate nodules on thallus and apothecia (UK171494b). D. Cross-section of an apothecium, showing the nodular thalline margin with one cell layer thick cortex and thick, paraplectenchymatous proper exciple (UK170911a). E. A transversely septate ascospore (UK170822e). Scales 2 mm in A and C, 200 µm in B and D, 10 µm in E.

2820 m elevation, on a fallen branch, 11 March 2017, U. Kaasalainen UK170822e (H 9234933); near the Mweka route, 3.1640° S 37.3675° E, 2990 m elevation, on a tree trunk, 25 June 2017, U. Kaasalainen UK171584c (H 9234941; ITS: MW340340, mtSSU: MW335326); subalpine Erica trimera forest near the Umbwe route, 3.1073° S 37.3184° E, 3510 m elevation, on an Erica trunk, 19 June 2017, U. Kaasalainen UK171439e (H 9234937; ITS: MW340335, mtSSU: MW335321); subalpine fire disturbed Erica shrubbery near the Machame route, 3.0854° S 37.2794° E, 3520 m elevation, on a branch in an Erica thicket, 15 June 2017, U. Kaasalainen UK171340j (H 9234936; ITS: MW340334, mtSSU: MW335320).

LEPTOGIUM TIINAE Kaasalainen & Rikkinen sp. nov. (Fig. 2)

Mycobank # MB848315

Species of *Leptogium* with a plicate thallus, robust nodules forming cerebroid structures on the apothecial thalline exciple and lobe apices, apothecia with a paraplectenchymatous proper exciple, one celled cortex of thalline exciple, and $60-90 \mu m \log transversely$ septate ascospores.

Holotype: Kenya, Taita Taveta County, Wundanyi, alongside a dusty dirt road near the Taita Research Station of the University of Helsinki, 3.3981° S 38.3655° E, 1350 m elevation, on a basal trunk of large *Ficus thonningii*, 8 January 2010, J. Rikkinen JR10017 (EA; duplicate in H – H 9234943).



Fig. 2. Leptogium tiinae (JR10017 TYPE). A–B. Dry type material photographed *in situ* in the Taita Hills, showing the large and abundant apothecia with cerebroid structures on the thalline exciple. C. Pycnidia on cerebroid structures. D. Conidia from a pycnidium. E. Habit when moist. F. Apothecial section showing the paraplectenchymatous proper exciple. Scales 100 μ m in C and F, 5 μ m in D, 2 mm in E.

ITS barcoding marker accession (GenBank): JX503805 (holotype).

Description: Thallus up to 4 cm broad, opaque, usually glossy. Lobes laciniate, up to 3 mm wide, adnate, apices ascending, with robust and rounded cerebroid structures. Upper surface densely longitudinally plicate and wrinkled, dirty white to gray. Lower side longitudinally plicate, gray mottled with dirty white or yellow. Isidia and lobules absent. Cerebroid structures on thallus and apothecial margin formed by gray, wrinkled, sack-like nodules that become bloated when wet. Rhizines and hairs absent, thallus attached to substrate by hapters. Apothecia subpedicellate, up to 4.5 mm in diam., forming on the margins and apices of thallus lobes, often abundant and eventually covering a large portion of the thallus; disc in mature apothecia usually plane; thalline exciple gray, with abundant, robust and rounded cerebroid structures ca. 0.5-1.5 mm in diam.

Anatomy: Thallus 200-400 µm thick, several times thicker at the ridges; quadratic cortical cells 4-6 µm wide; medulla loose, columnar hyphae absent. Cyanobacteria (Nostoc) as long filaments, cells oval, $4-8 \times 3-4 \mu m$, heterocysts slightly larger. Apothecia with hymenium (95)130-170 µm thick; subhymenium (60)75-130 µm thick, orange-brownish; proper exciple paraplectenchymatous, (70)80-120 µm thick (8–10 cell layers) at the center, mainly pinkish grey, becoming more hyaline towards the (sub) hymenium; parahymenial tissue consisting mainly of the paraplectenchymatous proper exciple, 20–50 μ m wide at the margin (on the level of hymenium surface); cortex of thalline exciple one cell layer thick. Ascospores acicular with 5-10(12) transverse septa, $60-90 \times$ 5-9 μ m (m = 70 × 7, SD = 9 × 0.9, N = 17). Pycnidia common and abundant, on and between the sack-like nodules, opening brown to black; conidia rod-shaped, often slightly narrower in the middle, 3.6–4.1 \times 1.3–1.7 μm in size.

Etymology: The specific epithet is dedicated to Estonian lichenologist Tiina Randlane, who visited the Taita Hills and the type locality of this species in October 2016.

Ecology and distribution: Fully developed specimens of *Leptogium tiinae* are known only from the type locality in the Taita Hills, Kenya. Additional specimens collected from a savanna habitat near Mt. Kilimanjaro, Tanzania, may represent *L. tiinae* (see Notes). All the specimens grew epiphytically on tree trunks in relatively open, sun exposed habitats at elevations below 1500 m.

Notes: The two specimens collected from Tanzania (UK160418b & d) are dark brown and notably smaller than the three well-developed thalli in the type collection of *L. tiinae*. Good quality ITS sequences were not obtained from these specimens, and their apothecia are not developed well enough to reveal all apothecial and ascospore characters. However, the mtSSU sequences confirm a close relationship between the two specimens and the type (Kaasalainen et al. 2021), and they are for now tentatively identified as *L. tiinae*.

Leptogium tiinae is easily distinguished from other Leptogium species with transversely septate ascospores based on the robust cerebroid structures that are especially abundant on the thalline exciple of the apothecia. For separation from L. bellum, see Notes under that species. Out of the previously described species with a similar apothecial anatomy, i.e., a paraplectenchymatous proper exciple and a one celled cortex of the thalline exciple, L. tiinae bears most resemblance to L. longisporum. However, the cerebroid structures on L. tiinae are more robust and rounded than those on L. longisporum. Additionally, the thallus of L. tiinae is thicker and always has abundant pycnidia, which have not been reported from L. longisporum.

Additional specimens examined: Tanzania, Kilimanjaro Region, Uchira, 3.3747° S 37.4549° E, 871 m elevation, on a trunk of a small tree on savanna, 10 December 2016, U. Kaasalainen UK16418b (H 9234944; mtSSU: MW335314), UK16418d (H 9234945; mtSSU: MW335315). A key for *Leptogium* species with transversely septate ascospores

The key is based on inspected specimens (*L. bellum, L. chloromeloides, L. reticulatum, L. tiinae*), previously published descriptions (*L. ankolense, L. brebissonii, L. fusisporum, L. granadillae, L. longisporum, L. megapotamicum, L. pacificum, L. thoroldii*), or the combination of the two (*L. adpressum*). For *L. fusisporum*, both options for character combinations are included, following the descriptions given by Tuckerman (1882), Kitaura (2012), and Kitaura et al. (2013) and the description given by Sierk (1964). See Results and Discussion for more details and references.

- 1a. Thallus lobes large and robust, rounded, and clearly reticulately ridged *Leptogium reticulatum*
- Lobes without reticulate ridges (but wrinkles and/or longitudinal ridges are often present) – 2.
- 2a. Lower cortex consisting of the basal cells of columnar hyphae connected by very thin longitudinal hyphae (pseudocortex) – *Leptogium pacificum*
- 2b. Lower cortex consisting of a single layer of ~isodiametric cells (eucortex) 3.
- Apothecia with a thick paraplectenchymatous proper exciple (e.g. Figs 1D, 2F) – 4.
- Apothecia without a thick, paraplectenchymatous proper exciple – 10.
- 4a. Cortex of thalline exciple paraplectenchymatous, several cell layers thick – *Leptogi um granadillae*
- 4b. Cortex of thalline exciple one cell layer thick (e.g. Fig. 1D) 5.
- 5a. Thallus and apothecial margin with cerebroid structures (e.g. Fig. 2B); ascospores mainly >60 μm long 6.
- 5b. Cerebroid structures absent (more delicate nodules and/or ridges may be present); ascospores <60 μm long 7.
- 6a. Abundant pycnidia present, especially among the cerebroid structures (Fig. 2C); rounded and robust (up to 1.5 mm in diam.) cerebroid structures abundant on apothecial margins; thallus very thick (>200 μm between ridges) -- Leptogium tünae
- 6b. Pycnidia absent; thallus thinner (150 μm between ridges) *Leptogium longisporum*
- Thallus and apothecial margin with abundant delicate sack-like nodules (Fig. 1A, C) Leptogium bellum

- 7b. Delicate nodules absent 8.
- 8a. Ascospores <40 μm long; apothecial margin entire – *Leptogium fusisporum* sensu Sierk (1964)
- 8b. Ascospores 50-60 µm long 9.
- 9a. Apothecial margin with braid-resembling wrinkles *Leptogium adpressum*
- 9b. Apothecial margin minutely and deeply scrobiculate *Leptogium thoroldii*
- 10a. Thallus with granular to coralloid isidia 11.
- 10b. Thallus without isidia 12.
- 11a. Thallus with coralloid isidia; apothecial margin entire, with thalline cortex gradually thickening from one cell layer at the margin to several layers of paraplectenchymatous tissue towards the base – *Leptogium ankolense*
- 11b. Thallus with granular to shortly cylindrical isidia; apothecial margin variable – *Leptogium brebissonii*
- 12a. Ascospores >60 μm long; apothecial margin verrucose with paraplectenchymatous tissue present between the verrucae – *Leptogium megapotamicum*
- 12b. Ascospores <60 µm long 13.
- 13a. Apothecial margin wrinkled to uneven; cortex of thalline exciple one cell layer thick – *Leptogium chloromeloides*
- 13b. Apothecial margin granular; cortex of thalline exciple with several cell layers of paraplectenchymatous tissue – *Leptogium fusisporum* (sensu Tuckerman 1882; Kitaura 2012; Kitaura et al. 2013)

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REFERENCES

- Degelius, G. 1962. Studies in the lichen family Collemataceae. III. On some American species. *Svensk Botanisk Tidskrift* 56: 145–155.
- Dodge, C. W. 1933. The foliose and fruticose lichens of Costa Rica. I. Annals of the Missouri Botanical Garden 20: 373–467.
- Dodge, C. W. 1964. Some Lichens of Tropical Africa: IV: Dermatocarpaceae to Pertusariaceae. *Beihefte Nova Hedwigia* 12: 1–282.
- Dodge, C. W. 1971. Some lichens of tropical Africa. V. Lecanoraceae to Physciaceae. Beihefte Nova Hedwigia 38: 1–225.
- Kaasalainen, U., V. Tuovinen, P. M. Kirika, N. P. Mollel, A. Hemp & Rikkinen J. 2021. Diversity of *Leptogium* (Collemataceae, Ascomycota) in East African Montane Ecosystems. *Microorganisms* 9: 314. https://doi.org/10.3390/microorganisms9020314.
- Kitaura, M. J. 2012. Estudo taxonômico de Leptogium (ACH.) S.F. Gray (Collemataceae, fungos liquenizados). PhD thesis, Universidade Estadual Paulista, Botucatu. 249 pp.
- Kitaura, M. J., M. P. Marcelli, B. R. Hora & Jungbluth P. 2013. A new non-isidiate *Leptogium* species with transverse septate ascospores from Southeastern Brazil. *Mycosphere* 4:986–992. https:// doi.org/10.5943/mycosphere/4/5/11.
- Medeiros, I. D. 2019. Determining the type locality and collector of Nylander's South African lichens. *Bothalia* 49: a2384. https://doi.org/10.4102/ abc.v49i1.2384.
- Montagne, J. F. C. 1841. Séconde centurie de plantes cellulaires exotiques nouvelles, Décade IX. Annales des Sciences Naturelles Botanique 16: 108–128.
- Nylander, W. 1858. Synopsis Methodica Lichenum Omnium hucusque Cognitorum, Praemissa Introductione Lingua Gallica. L. Martinet, Paris. 430 pp.
- Nylander, W. 1869. Note sur les lichenes de Port-Natal. *Bulletin de la Société linnéenne de Normandie* 3: 4–15.
- Otálora, M. A. G., P. M. Jørgensen & Wedin M. 2014. A revised generic classification of the jelly lichens, Collemataceae. Fungal Diversity 64: 275–293. https://doi.org/10.1007/s13225-013-0266-1.
- Sierk, H. A. 1964. The Genus *Leptogium* in North America North of Mexico. *Bryologist* 67: 245–317.
- Swinscow, T. D. V. & Krog H. 1988. Macrolichens of East Africa. Natural History Museum Publications, London. 390 pp.
- Tuckerman, E. 1882. A synopsis of the North American lichens. S.E. Cassino, Boston. 261 pp.
- Webb, P. B. & Berthelot S. 1840. *Histoire naturelle des Iles Canaries*. Béthune, Paris. 208 pp.