A review of the genus *Bulbothrix* Hale: the isidiate, lacinulate, sorediate and pustulate species with medullary gyrophoric, lecanoric and lobaric acids, together with a world key for the genus

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ABSTRACT. – This study is a taxonomic review of the species of *Bulbothrix* (Parmeliaceae, lichenized fungi) containing gyrophoric, lecanoric or lobaric acid in the medulla (*Bulbothrix apophysata*, *B. funicola*, *B. laevigatula*, *B. leprieurii*, *B. oliveirae*, *B. papyrina*, *B. pseudofungicola*, *B. pseudocoronata*, *B. scortela*, *B. sipmanii*, *B. subdissecta* and *B. thomasianna*) that reproduce by lichenized diaspores (isidia, lacinulae, pustules, or soredia). Some of these species (*B. bulbillosa*, *B. papyrina*, *B. pseudocoronata*, *B. pseudofungicola*, *B. scortela*, *B. subdissecta*, and *B. thomasianna*) have been separately treated on previous papers as novelties, new combinations or resurrected valid names. The current species delimitations are confirmed. New characters are detailed (for *B. laevigatula*, *B. leprieurii*, *B. oliveirae*, and *B. sipmanii*), and range extensions are given (for *B. apophysata*, *B. fungicola*, *B. laevigatula*, and *B. leprieurii*). Two names (*B. suffixa* and *Parmelia appressa*) are respectively considered as *nomen dubium* and *nomen illegitimum* and the problems relative to them are also discussed. A key covering all 59 accepted species of *Bulbothrix* is provided. A lectotype is designated for *B. fungicola*. An index for all names related to the genus, with their current statuses, is also given.


INTRODUCTION

*Bulbothrix* Hale was proposed for a group of species that had previously been referred to *Parmelia* series *Bicornutae* (Lynge) Hale & Kurok. (Hale 1974). The group was characterized by small, laciniate and usually adnate thalli, simple to branched bulbate marginal cilia, cortical atranorin, simple to branched rhizinae, smooth to coronate apothecia, hyaline unicellular ellipsoid to bicorneata ascospores 5.0–21.0 × 4.0–12.0 μm in size, and bacilliform to bifusiform conidia 5.0–10.0 × 0.5–1.0 μm in size (Hale 1976, Elix 1993). In a recent paper presenting revised generic concepts of parmelioid lichens based on molecular, morphological and chemical evidence, Crespo et al. (2010) found that *Bulbothrix* as currently defined was nested in the *Parmelina* clade and that some species grouped with *Parmelinella* Elix & Hale, making the genus *Bulbothrix* paraphyletic.

As part of my revision of *Bulbothrix* (Benatti 2010), type specimens and additional material of many species were studied. All of the members of the genus have cilia with hollow basal bulbs, which contain differentiated (round) cells and a characteristic oily substance (Hale 1975, Feuerer & Marth 1997, Benatti 2011a). The first part of my revision concerned new combinations for four species that had been placed in *Bulbothrix* but had to be excluded due to the lack of true bulbate cilia (Benatti & Marcelli 2010). The subsequent parts treated the species containing norstictic and protocetraric acids in the medulla (Benatti 2012b), those with salazinic acid that do not form isidia, soredia, lacinulae or pustulae (Benatti 2012d), those with salazinic acid that form isidia, soredia or pustulae (Benatti 2013a), those with fatty acids or no
substances in the medulla (Benatti 2013b), and those containing gyrophoric/lecanoric/lobaric acids that do not reproduce by vegetative propagules (Benatti 2013c).

This paper reviews for the first time four species with gyrophoric acid (Bulbothrix fungicola, B. leprieurii, B. oliveirae, B. sipmanii), one with lecanoric acid (B. laevigatula), and one with lobaric acid (B. apophysata), that form isidia, lacinulae, soredia or pustulae. The remaining species reviewed here (B. bulbillosa, B. papyrina, B. pseudocoronata, B. pseudofungicola, B. scortella, B. subdissecta, B. thomasiana) were all treated in other recent publications but are included for completeness due to their medullary chemistries and production of lichenized diaspores (Marcelli et al 2011, Benatti 2011a-b, 2012a-d, 2013a-c).

In order to complete my revision of the genus and clarify the concepts of species, the type specimens of all Bulbothrix names and many additional specimens from several herbaria worldwide were studied. After having revised all of the species of Bulbothrix in groups according their reproductive mode and chemistry (Benatti 2011a-b, 2012a-d, 2013a-c, Benatti & Marcelli 2010, Benatti & Elix 2012, Bungartz et al. 2013 and herein) I compiled a key to the genus, which is also presented here. This key is based on the considerable amount of new data obtained from type and additional specimens, as well as from recent publications that were not directly part of my revision (Benatti 2011a-b, 2012a-d, 2013a-c, Benatti & Elix 2012, Benatti & Marcelli 2010, Marcelli et al. 2011, Bungartz et al. 2013). It is hoped that this key, which synthesizes the available literature and my research to date, will facilitate the identification of Bulbothrix specimens and stimulate further study. Also, an index with all the names related to Bulbothrix, including the basionyms and current accepted names, is given for historical reference.

MATERIALS AND METHODS

For the taxonomic review presented below, type material and additional specimens were borrowed from the following herbaria: B, BM, DUKE, FH, G, H, LD, M, MSC, NY, PC, S, SP, TNS, U, US UPS, and W. This material originated from Asia, Africa, North America, Central America, the Caribbean and South America. Also included in the studied material were the Brazilian collections made during the last 30 years, mainly by the author and the members of the Lichenological Study Group of the Instituto de Botânica (GEL) in Brazil.

The methods and terminology follow those detailed in Benatti (2012a). The following terms that may be unfamiliar to readers are also used: “sublacinulate” follows Marcelli et al. (2008) and Spielmann and Marcelli (2009) to describe that there are not true lacinulae as intended as a secondary outgrowth similar to the main ramifications, but rather occasional poorly developed small outgrowths. Bulbs on cilia, rhizines, apothecia and other thallus parts were examined using the clarification method outlined by Benatti (2011a). Chemical constituents of the additional specimens examined were identified by thin-layer chromatography (TLC) using solvent C (Bungartz 2001), and compared with the data on labels included with the specimens. The chemical constituents of the type specimens were examined by high performance liquid chromatography (HPLC) by J.A. Elix, following the methods described in Elix et al. (2003).

Gyrophoric and lecanoric acids have similar spot test reactions for the C and KC tests, but it was found that at least in Bulbothrix, the color reactions for the two substances are noticeably distinct, especially when comparing specimens side by side. Those containing gyrophoric acid usually react C+ and KC+ rose (with a weakly white bluish brightness under UV depending on concentrations), while those containing lecanoric have a stronger red reaction without any apparent signs of UV brightness. Microcrystal tests (G.E. and G.A.W.) were also used to confirm which of these two substances was present in the specimens studied, as the crystals are very different in shape and size. Lobaric acid was detected by a C- and KC+ violet rose reaction and a typical white bluish brightness under UV light.

The key appended to the treatment below consists of data obtained from the study of type material and additional specimens from B, BM, C, CANB, DUKE, FH, FI, G, GLAM, H, HMAS, HUFSCAr, L, LD, LG, LWG, M, MEL, MSC, NY, PC, S, SP, TNS, TUR, U, US, UPS, VEM, W, WU, and from the personal herbarium of Dr. Klaus Kalb (hb. Kalb, now transferred to WIS). This material was collected in Oceania, Asia, Africa, North America, Central America, Caribbean and South America. The methods and terminology used follow those detailed in the published treatments of each group of species in the literature cited.
RESULTS

I: REVIEW OF THE SPECIES

Examination of the specimens outlined in the materials and methods section above confirmed the existence of twelve *Bulbothrix* species containing gyrophoric, lecanoric or lobaric acids that develop vegetative propagules. Below, all species not already treated elsewhere in recent contributions by me are described in detail and their diagnostic characters are discussed. In many cases new morphological data are presented and the secondary metabolites present are clarified. Based on this study *B. apophysata, B. fungicola, B. laevigatula, B. leprieurii, B. oliveira, B. papyrina, B. pseudofungicola, B. pseudocoronata, B. scortella, B. sipmanii, B. subdissecta* and *B. thomasiana* are recognized. All of these are considered to be corticolous species, since so far none has been found to be saxicolous.

SPECIES NOT TREATED IN PREVIOUS CONTRIBUTIONS


**FIGURE 1.**

**DESCRIPTION.** – Thallus sublinear, laciniate, pale dusky gray in herbarium, up to 5.3 cm diam., subcoriaceous, corticolous, upper cortex 20.0–35.0 µm thick, algal layer 20.5–30.0 µm thick, medulla 37.5–55.0 µm thick, lower cortex 10.0–15.0 µm thick. Laciniae anisotomic to irregularly dichotomously branched, 0.4–1.6 mm wide, contiguous to imbricate, adnate and appressed, with flat, truncate to subtruncate apices, margins plane, smooth and sinuous to irregular, entire, scarcely sublacinulate, axils oval. Upper surface smooth, slightly to densely irregularly cracked (especially at older parts), laminal ciliary bulbs absent. Adventitious marginal lacinulae scarce on random parts, short, 0.2 × 0.1–0.2 mm, plane, simple to irregularly branched, apices truncate, lower side concolorous with the lower marginal zone. Maculae weak and scarce, punctiform, laminal but restricted to a few parts, usually amidst the scars left by fallen isidia. Cilia black to occasionally brown, apices initially simple, furcate or trifurcate, soon becoming dichotomously or irregularly branched, 0.05–0.25 (−0.35) × ca. 0.03 mm, with semi-immersed to sessile bulbate bases ca. 0.05–0.10 mm wide, abundant throughout the margin spaced 0.05–0.10 mm from each other to contiguous at the axils, absent at the apices of the laciniae. Soredia, and pustulae absent. Isidia frequent, laminal, granular to smooth cylindrical, straight to tortuous, 0.05–0.25 × ca. 0.05 (−0.10) mm, simple to rarely slightly branched, erect, persistent to ±caducous, concolorous with the cortex or with pale brownish apices, eciliate. Medulla white. Lower surface black with brown to dark brown parts at the transition from the margins, shiny, smooth, papillate, densely rhizinate. Marginal zone pale brown to brown, occasionally slowly attenuate gradually darkening to black in the center, the paler part ca. 0.5–2.5 mm wide, shiny, smooth, papillate, becoming rhizinate towards the center. Rhizinae black, brown or whitish, initially simple or furcate becoming dichotomously or irregularly branched, bulbs typically basal but also sometimes displaced further along the length, 0.05–0.30 (−0.40) × ca. 0.03 mm, usually frequent but less common at the marginal zone, evenly distributed. Apothecia and pycnidia not found.

**CHEMISTRY.** – Atranorin, lobaric acid (TLC/HPLC). Spot tests: upper cortex: K+ yellow; medulla K−, C−, KC+ violet rose, P−, UV+ bluish white to pale blue.

When Hale and Kurokawa (1964) described this species they did not identify the KC+ substance in the medulla, although they thought it may be related to alectoronic acid. The identity of the substance as lobaric acid was later determined by Hale (1976).
Figures 1-4. 1, holotype of Bulbotrhix apophysata (US). 2, type collection of B. fungicola (S); the lectotype is composed of the three fragments from center to right; the leftmost fragment belongs to B. pseudocoronata. 3, detail of one of the fragments of B. fungicola showing isidia. 4, detail of the leftmost fragment belonging to B. pseudocoronata, showing typical laminal lacinulae and a coronate apothecia. Scale bars = 1 cm, except where noted.

NOTES ON THE TYPE SPECIMENS. – The holotype (fig. 1) of Bulbothrix apophysata is a very fragmented specimen, consisting of small, partially moldy pieces 1.0–2.5 cm in diameter, without apothecia or pycnidia. The isotype also consist of fragments 1.0–3.0 cm in diameter that are not moldy and are better preserved, although also without any apothecia or pycnidia.

COMMENTS. – The material examined corresponds well to the descriptions of Hale and Kurokawa (1964) and Hale (1976), especially regarding the width of the laciniae, the cracks and weak maculae of the upper cortex, the branching pattern of the cilia and rhizines and the size and shape of the isidia. The authors did not mention ciliate isidia, such as those described by Marcelli (1993). In fact, no isidia in the material I studied, even the most developed ones, showed any sign of the formation of cilia.

Hale and Kurokawa (1964) and Hale (1976) described a peculiarity related to the color contrast between the center and the margins on the lower surface of this species. The presence of a centrally black lower surface starkly contrasting with a broad pale brown marginal zone is a most notable feature in the specimens. This feature is variable however, with some laciniae superficially appearing to have a variable brown lower surface until close examination reveals a black area in the central portions.

Hale and Kurokawa (1964) compared Parmelia apophysata (= Bulbothrix apophysata) only to P. subdissecta (= B. subdissecta (Nyl.) Hale), which was later placed in synonymy with B. goebelii (Zenker) Hale by Hale (1976). Study of the type of B. goebelii revealed that the name actually should be applied to a non-isidiate taxon that could be considered the parental species of B. apophysata (Benatti & Elix 2012). Thus B. subdissecta, proved to be a distinct taxon that differs by its somewhat narrower laciniae (ca. 0.5–1.0 mm wide), predominantly black lower cortex with subtly attenuated brown margins, and medullary gyrophoric acid often with small amounts of lobaric acid (Benatti & Elix 2012).

The specimens cited by Marcelli (1993) as Bulbothrix apophysata have a pale brown lower cortex and mostly ciliate isidia, with small cilia bearing branched apices. This material was recently described as B. thomasiana Benatti & Marcelli (Marcelli et al. 2011). Bulbothrix thomasiana is indeed similar to B. apophysata, but differs by the presence of ciliate isidia, cilia that are often branched at the apices and by the overall pale brown lower surface which is usually hidden by concolorous or somewhat darker rhizines.

Additional specimen examined. – PERU: SAN MARTÍN: Tingo Maria, near Huallaga River near Tingo Maria, 625-1100 m, on tall vine, 30.viii.1949-19.ii.1950, H. A. Allard 22256 (US).

Mycobank #341598.


FIGURES 2, 3 AND 4.

DESCRIPTION. – Thallus sublinear laciniate, dusky gray in herbarium, fragments up to 2.7 cm diam., subcoriaceous, corticolous (often ramulicolous), upper cortex 17.5–20.0 µm thick, algal layer 15.0–25.0 µm thick, medulla 35.0–55.0 µm thick, lower cortex 15.0–20.0 µm thick. Laciniae isotomic to anisotomic dichotomously or trichotomously to occasionally irregularly branched, 0.2–0.7 (~ very rarely 1.2) mm wide, contiguous to slightly imbricate, very adnate and strongly appressed, with flat, truncate to subtruncate or occasionally acute apices, the margins plane, smooth to sinuous or subirregular, entire to slightly incised, scarcely sublacinulate, the axils oval and narrow. Upper surface smooth and continuous, becoming subrugose at older parts, laminal ciliary bulbs absent (ciliary bulbs that superficially appear to be laminal can be seen sometimes due to the initial growth of isidia and apothecia). Adventitious marginal laciniae scarce and randomly arranged, short, 0.2–0.5 × 0.1–0.2 mm, plane, simple to rarely furcate, truncate or acute, lower side concolorous with the lower marginal zone. Maculae distinct, punctiform to efigurate,
laminal, amidst the scars left by fallen isidia. Cilia black, apices absent to simple or occasionally furcate, frequently bent downwards, 0.05−0.10 (−0.15) \times ca. 0.03 mm, with semi-immersed bulbate bases ca. 0.05 (−0.10) mm wide, abundant along the margins spaced ca. 0.05 (−0.10) mm from each other to contiguous, becoming absent at the apices of the laciniae. Soredia and pustulae absent. Isidia frequent to abundant, laminal, granular to irregularly bent cylindrical, occasionally globose, straight to slightly tortuous, 0.05−0.20 \times ca. 0.05 mm, simple to rarely weakly branched, erect, persistent to caducous, concolorous with the cortex or with brownish apices, usually ciliate with tiny ciliary bulbs without apices or with very short apices. Medulla white. Lower surface black, shiny, smooth to subrugose, densely rhizinate. Marginal zone pale brown and in a narrow band ca. 0.5 mm wide, shiny, smooth, slightly papillate and slightly rhizinate. Rhizinae black, partially dark brown or rarely whitish, simple to partially furcate or rarely irregularly branched, without basal bulbs, 0.05−0.20 (−0.40) \times ca. 0.03 mm, abundant sometimes almost as a tomentum, partially agglutinated, evenly distributed. Apothecia concave to plane, adnate to sessile, 0.3−1.8 mm diam., laminal, margin smooth eventually becoming crenate and almost lobulate due to incisions, coronate, amphithecia smooth or occasionally ornamented with scarce ciliary bulbs, also rarely becoming slightly isidiate. Disc pale to dark castaneous brown, epruinose, imperforate, epithecium 10.0−15.0 \mu m high, hymenium 37.5−55.0 \mu m high, subhymenium 15.0−22.5 \mu m high. Ascospores subglobose to ellipsoid, occasionally with ±acute apices and with an almost fusiform aspect, (6.5−) 8.0 (−10.0) \times 0.5 \mu m, epispore 1.0−1.5 \mu m wide, abundant along the margins spaced ca. 0.05 (−10.0) \times 0.5 \mu m.

CHEMISTRY. – Atranorin, gyrophoric acid (TLC/HPLC). Spot tests: upper cortex: K+ yellow; medulla: K−, C+ and KC+ rose to reddish rose, P−, UV−.


NOTES ON THE TYPE SPECIMENS. – The type collection of Bulbothrix fungicola (fig. 2) consists of four fragments of tree bark, all in good condition, that are glued to a card backing. Despite their morphological and chemical similarity, one of the fragments lacks laminal isidia and actually belongs to a densely lacinulate species (fig. 4). The admixture of solely laminal lacinulae and solely isidiate fragments (fig. 3) was the probable cause of the confusion by both Lyne (1914) and Hale (1976) that B. fungicola was a species that formed both isidia and laminal lacinulae. The lacinulate fragments belong to Parmelia pseudocoronata Gycln. (= B. pseudocoronata (Gycln.) Benatti & Marcelli) (see Benatti 2012c), which was accepted as a synonym of B. fungicola by Hale (1976), even though the type material of that name is lacinulate and not isidiate.

COMMENTS. – Lyne (1914) apparently noticed the bulbate marginal cilia in this species but thought that they were a parasitic fungus (“fungo parasitico instructus”). He also misinterpreted the medullary reactions, citing them as K+ yellow and C− while they are, as Hale (1960) reported, C+ rose and KC+ reddish rose. Hale (1960) also initially believed that "parasitic fungi on the underside were a conspicuous feature" of this species, misinterpreting the cilia or rhizines in the same manner as Lyne. It was only later that he recognized the bulbate cilia were not parasitic fungi (Hale & Kurokawa 1964, Hale 1976).

Marcelli (1993) commented that in cerrado (savannah) environments thalli of Bulbothrix fungicola and B. suffixa were often found growing together or mixed, and mentioned an unusual feature of B. fungicola cited by Hale (1976), the fact that both isidia and lacinulae were present in the same species. Evidently both Lyne (1914) and Hale (1976) believed that the isidia present in B. fungicola developed into lacinulae. As has been discussed in the preceding section, the type of B. fungicola consists mostly of isidiate material, with a single admixed fragment of a lacinulate thallus that is B. pseudocoronata. This admixture is almost certainly what led to the misinterpretation of the vegetative propagules in B. fungicola by previous authors, and also may have led Hale (1976) to consider B. pseudocoronata to be a synonym of B. fungicola. Bulbothrix pseudocoronata differs from B. fungicola mainly by the formation of laminal and marginal lacinulae that at the very beginning of their development, resemble isidia, but soon afterward start
to flatten to form lacinulae. The laminal isidia produced by B. fungicola typically do not resemble the lacinulae of B. pseudocoronata. In the rare cases where confusion may occur, the lacinulae found in B. pseudocoronata are typically longer, wider, more abundant, more branched, and firmer than the isidia found on thalli of B. fungicola. Furthermore, B. pseudocoronata has no maculae on the upper surface, the rhizines are less frequent, and the rhizines have bulbate bases.

The material referred by Hale (1971) to Bulbothrix fungicola was described as having lobulate isidia, and possibly could be B. pseudocoronata. Another curiosity about this material is that it was described as having bicornute ascospores, which would make these isidiate/lobulate specimens similar to B. semilunata (Lyne) Hale rather than to B. fungicola which does not have bicornute ascospores. It is also possible that these specimens could be either B. caribensis Marcelli & Benatti (lacinulate without medullary substances) or B. lyngei Benatti & Marcelli (isidiate with small amounts of fatty acids, also no reactions) (Benatti 2011b).

Specimens of Bulbothrix fungicola have narrow laciniae, very rarely exceeding 1 mm wide. The size of the laciniae (0.5–1.5 mm wide) given by Hale (1976) is larger than what was observed in the lectotype and additional material. These were closer to the size cited by Lyne (1914; 0.5–1.0 mm wide). The sizes mentioned by Marcelli (1993) and Jungbluth (2006) best corresponded to those observed here (0.2–0.7 mm wide). Bulbothrix fungicola presents only adventitious laminal lacinulae, which are occasional, sparse and random, as poorly developed structures without any apparent function of propagation.

Hale (1976) mentioned simple rhizines for Bulbothrix fungicola, while Marcelli (1993) and Jungbluth (2006) reported dichotomously branched rhizines. In the material studied, including the type, simple rhizines dominate among a smaller number of fucrate rhizines. Bulbothrix pseudofungicola Benatti & Marcelli is similar to B. fungicola, but differs by having dichotomously branched cilia and rhizines, coronate apothecia, and usually smaller, mostly subglobose ascospores (Benatti 2012a).

The ascospore sizes for Bulbothrix fungicola given by Lyne (1914) and Hale (1976) are similar to those found here. The occasional formation of apiculate ascospores that was mentioned by Lyne (1914) was also observed here. These ascospores are sometimes slightly narrower than the ellipsoid ones, and it is difficult to ascertain if they could somehow be related to the bicornate ascospores of other species in the genus, such as B. semilunata. Only a small portion of the ascospores observed in B. fungicola have this apiculate aspect and these are mixed among asci with typical ellipsoid ascospores.

Bulbothrix subdissecta is also similar to B. fungicola but has larger eciliate isidia (about twice the size of those of B. fungicola), dichotomously branched cilia and rhizines, coronate apothecia and usually additionally contains medullary lobaric acid together with the gyrophoric acid (Benatti & Elix 2012).

Bulbothrix suffixa (Stirt.) Hale is a name of uncertain application with a complicated relationship to B. fungicola. The issues surrounding the application of B. suffixa are discussed under that name at the end of the taxonomic section herein.


≡ *Parmelia laevigatula* Nyl., Flora 68: 614. 1885. **TYPE:** FRENCH GUIANA: Cayenne, F.M.R. Leprieur 504 (H-NYL 35653!, lectotype (selected by Hale 1976); PC!, isoselectotype).

≡ *Parmelia hookeri* Taylor, London J. Bot. 6: 169. 1847 [non *P. hookeri* (Borrer) Spreng.]. **TYPE:** SAINT VINCENT: without locality, *L. Guilding s.n.* (FH-TAYLOR! lectotype (selected by Hale 1976); BM!, isoselectotype).

**FIGURES 5 AND 6.**

**DESCRIPTION.** — Thallus sublinear to partially linear sublaciniate, pale dusky gray in herbarium, up to 6.3 cm diam., subcoriaceous to coriaceous, corticolous, upper cortex 10.0–15.0 µm thick, algal layer 20.0–25.0 µm thick, medulla 50.0–70.0 µm thick, lower cortex 12.5–20.0 µm thick. Laciniae isotomic to anisotomic dichotomously or trichotomously branched, 0.4–2.1 mm wide, contiguous to slightly imbricate, adnate and adpressed, with flat, subtruncate to truncate apices, the margins plane, smooth to sinuous or subcrenate, entire, rarely sublacinulate, the axils oval. Upper cortex continuous and smooth occasionally becoming irregularly cracked on older parts, laminal ciliary bulbs absent. Adventitious lacinulae absent to few scarce on random parts at the margins, short, 0.2–1.1 × 0.1–0.3 (–0.8) mm, plane, simple to rarely furcate, apices truncate, lower side concolorous with the lower marginal zone. Maculae absent, only with some scars left by fallen isidia. Cilia black or rarely pale, apices initially simple, soon becoming furcate, trifurcate and then subdichotomously or irregularly branched, 0.05–0.30 (–0.40) × ca. 0.03 mm, with semi-immersed to sessile bulbate bases 0.05–0.15 mm wide, abundant along the margins, spaced ca. 0.05 mm from each other to contiguous at the axils, usually absent at the apices of the laciniae. Soredia frequent, laminal, often sparse to grouped, granular to smooth cylindrical, straight to slightly tortuous, 0.05–0.25 (–0.40) × ca. 0.05 mm, simple, erect to procumbent, persistent to caducous, brownish or concolorous with the upper cortex, sometimes with brownish apices, eciliate, variably (few to most) losing the apical portion. Medulla white. Lower surface black, shiny, smooth to subrugose, moderate to densely rhizinate. Marginal zone black and indistinct from the central portions to brown in a narrow band 0.5–1.5 mm wide, shiny, smooth, papillate, becoming rhizinate at the transition to the center. Rhizinae black, often brown when near the margins, initially simple or furcate soon becoming dichotomously or irregularly branched, without bulbate bases (a few seen appear to have very subtle ones), 0.05–0.30 (–0.50) × ca. 0.03 mm, frequent to abundant almost like a tomentum being scarcer next to the margins, evenly distributed. Apothecia subconvex to ±plane or concave, sessile to adnate or substipiate, 0.2–2.9 mm diam., laminal or submarginal, margin smooth to subcrenate, ecoronate, amphithecia smooth eventually becoming isidiate. Disc brown to dark brown, epruinose, imperforate, epithecium 5.0–7.5 µm high, hymenium 25.0–37.5 µm high, subhymenium 12.5–15.0 µm high. Ascospores subglobose to ellipsoid or ovoid, 6.0–8.0 (very rarely −11.5) × 4.0–5.0 (−6.0) µm, epispore ca. 0.5 (−1.0) µm. Pycnidia scarce, laminal, immersed, with black ostioles. Conidia bacilliform to weakly bifusiform, 5.0–7.5 × 0.75 µm.

**CHEMISTRY.** — Atranorin, lecanoric acid (TLC/HPLC); upper cortex K+ yellow, medulla K−, C+ bright red, KC+ bright red→pale orange, P−, UV−.

**DISTRIBUTION.** — Asia: Japan (Nylander 1890), Philippines (Vainio 1909 sub *Parmelia hookeri*) and Thailand (Wolseley et al. 2002 sub *P. hookeri*). Africa: Angola (Vainio 1901 sub *P. hookeri*). North America: Mexico (Hale 1976) and United States of America (Hale 1976, McCullough 1964, Moore 1968). Central America and Caribbean Sea: Costa Rica (Nájera et al. 2002, Tenório et al. 2004 as the synonym *P. hookeri*), Cuba, Dominican, Dominican Republic, Granada, Jamaica, Saint Lucy, Trinidad and Tobago (Hale 1976), Saint Vincent (Taylor 1847 sub *P. hookeri*). South America: Colombia, Ecuador, Peru, Venezuela (Hale 1976) and Brazil (?), Nylander 1885 [see comments below], Hale 1976; Marcelli 1987, 1991, 1993). The species is reported here for the first time from Honduras and Puerto Rico, and to the Brazilian states of Amazonas and Pará.
Figures 5-9. 5, lectotype of Bulbothrix laevigatula (H-Nyl). 6, lectotype of Parmelia hookeri (FH). 7-9, holotype of B. leprieuri (U) showing overall appearance of specimen (7), soralia eroding on a fragment (8) and detail of a soralia with soredia (9). Scale bars = 1 cm, except where noted.
NOTES ON THE TYPE SPECIMENS. – The lectotype of *Bulbothrix laevigatula* (fig. 5) is a small thallus fragment in good condition, on tree bark and glued to a card. It has only two apothecia and few intact isidia. Apparently this was part of a larger collection identified as “LePrieur 504” that was distributed to various herbaria, as duplicates were also found in H-NYL and in PC.

Regarding these duplicates, two specimens in H-NYL belong to different species, but the specimen cited by Hale (1976) and labeled by him as the lectotype is indeed *Bulbothrix laevigatula*. The other specimen in H-NYL has ciliate isidia, a pale brown lower cortex, medullary lobaric acid, and was identified as *B. thomasiana* Benatti & Marcelli (Marcelli et al. 2011). The duplicate in PC is an isidiate fragment containing lecanoranic acid and probably is *B. laevigatula*, but is in poor condition, very damaged and dusky brownish. Because Hale (1976) did not mention ciliate isidia, and described the lower surface as black, I believe that he did not carefully examine other specimens such as those cited here.

There are two specimens at FH representing type material of *Parmelia hookeri*. As discussed by Hale (1958), one of them (“collection 1”) has gyrophoric acid and branched cilia, while the other (“collection 2”) has lecanoranic acid. Hale (1976) selected “collection 2” as the lectotype (fig. 6 herein) and this specimen clearly is conspecific with *Bulbothrix laevigatula*. The lectotype comprises two fragments on bark, both glued to a backing, but in excellent condition. I removed a fragment from the substrate for observation of the characteristics of the lower cortex. The specimen referred to as “collection 1” was identified only to genus (i.e., *Parmelia* sp.) and considered to be related to *P. chileana* Nyl. by Hale (1958). Following Hale (1971) *P. chileana* is likely a synonym of *P. scortella*. Nonetheless my examination of “collection 1” revealed it to be a species of *Parmelinopsis*, likely *P. minarum* (Vain.) Elix & Hale.

The isolectotype of *Parmelia hookeri* in BM was annotated by Hale as the “lectotype”. This material is not a fragment, but an entire well developed thallus in good condition. A label from Bruno Mies noted the presence of lecanoranic acid in the material, and there is another label proposing a combination of this epithet into *Parmelina*. Evidently the latter combination was never published. The material has bulbate cilia and is *B. laevigatula*. At some point Hale must have decided to select a specimen in FH-TAYLOR as the lectotype rather than the well developed specimen in BM.

The type material and additional specimens examined of *Bulbothrix laevigatula* and *Parmelia hookeri* lack ciliate isidia, and have ecoronate apothecia. No specimen found, even those already identified with these names, showed variation in these characteristics.

COMMENTS. – Nylander (1885) described the ascospores of *Bulbothrix laevigatula* as “7.0–8.0 × 4.0–5.0 µm”, and on a label with the lectotype drew ellipsoid ascospores marking them with similar measurements (“8.0 × 5.0 µm”). The specimens seen here generally have ascospores of this size range, except for a single specimen of the Brazilian State of Amazonas, which has occasional ascospores up to 11.5 µm in length, which is unusual for the species.

The descriptions of Hale (1976) and Marcelli (1993) match well the material studied here, however those authors mentioned slightly smaller ascospores than were found here. The description by Hale (1976) did not include data on the chemistry of the species. Marcelli (1993) described thalli with a very pale yellowish lower marginal zone and black rhizines, with occasional subtle bulbate bases. One specimen cited by Marcelli that I examined has ciliate isidia and a pale lower cortex, lobaric acid, and it is in fact a small specimen of *B. thomasiana*. According to Nylander (1885) the lectotype had acicular acuminate conidia, 6.0–7.0 × 0.5–0.6 µm in size. After careful examination of the specimen no pycnidia with conidia were found.

As seen in several specimens, including the type material of *Parmelia hookeri*, it is common that some of the isidia have severed apices, thus resembling pseudocyphellae. This feature varies from few to almost all isidia on some thalli (few specimens lack this feature). This may represent a stage of development in the isidia or be due to environmental factors (Bungartz et al. 2013).

*Bulbothrix goebelii* was compared to *B. laevigatula* by Hale (1976) and Marcelli (1993). Although many authors had applied the name to *B. goebelii* to an isidiate species, Benatti and Elix (2012) recently showed that the type was a mixture and the name should be applied to a species without propagules and containing medullary lobaric acid. The concept of *B. goebelii* followed by Hale (1976) best corresponds to *B. subdissecta*. That species has a black lower surface with black rhizines, a brown lower marginal zone and contains gyrophoric acid as the main substance often associated with small quantities of lobaric acid. The concept of *B. goebelii* followed by Marcelli (1993) corresponds to *B. scortella*, another species which has a brown lower surface, brown rhizines and gyrophoric acid as the main substance (Benatti & Elix 2012). In direct comparison of the thalli, cilia and rhizine branching in *B. goebelii*, *B. scortella* and *B.
subdissecta are more prominently dichotomously branched than in B. laevigatula. Moore (1968) compared B scortella to B. laevigatula, separating it from B. laevigatula by the brown lower surface and presence of gyrophoric acid instead of lecanoric acid.

Hale (1976) considered Bulbothrix laevigatula possibly to be the isidiate counterpart of B. confoederata (W.L. Cubl.) Hale. Bulbothrix confoederata differs by the absence of isidia, usually having narrower laciniae (ca. 0.5–1.0 mm wide), and a lower surface with mixed patches of black and brown (most often brown). Bulbothrix bicornuta (Müll. Arg.) Hale is another species with lecanoric acid, it differs from B. laevigatula in lacking isidia and having apothecia with much larger, bicornute ascospores (13.0–21.0 × 3.0–4.0 µm).

Bulbothrix apophysata is also similar to B. laevigatula and differs almost exclusively by the presence of lobaric acid instead of lecanoric acid. The lower surface of B. apophysata also often has a much more indistinct transition from the pale marginal zone to darker center compared with B. laevigatula and other members of the genus. This feature was also noted by Hale (1976).

Vainio (1909) mentioned a single specimen he identified as Parmelia hookeri, citing a K+ yellow→red (salazinic or norstictic acid?) and a C− medulla. Although the material supporting this concept is currently missing, it is clearly not conspecific with B. laevigatula.


Mycobank #358463.

TYPE: GUYANA: Upper Mazaruni District, small white sand-savannah ca. 2 km S of Waramadan, ca. 600 m, 5° 47′N, 60° 46′W, epiphyte on isolated, dwarfed tree, 1.iii.1985, H.J.M. Sipman & A. Aptroot 19187 (U!, holotype).

FIGURES 7, 8 AND 9.

DESCRIPTION. – Thallus linear to sublinear laciniate, pale greenish gray in herbarium, fragments up to 3.2 cm diam., submembranaceous, corticolous, upper cortex 12.5–17.5 µm thick, algal layer 15.0–20.0 µm
thick, medulla 55.0–72.5 µm thick, lower cortex 12.5–15.0 µm thick. Laciniae anisotomic dichotomously to occasionally irregularly branched, 0.3–0.7 mm wide, contiguous, adnate and appressed, with flat, truncate to subtruncate apices or partially acute, the margins plane, smooth and sinuous to irregular, entire, scarcely sublacinulate, the axils oval or irregular. Upper cortex mostly continuous and smooth, but often with many transverse cracks on older or densely sorediate parts, laminal ciliary bulbs absent. Adventitious marginal laciniae scarce on older parts, short, flat, 0.20–0.50 × 0.05–0.30 mm, simple or irregularly branched, truncate or acute, underside concolorous with the lower marginal zone. Maculae absent. Cilia black, apices initially simple, soon becoming furcate and then very dichotomously branched, 0.05–0.25 × ca. 0.02–0.03 mm, with semi-immersed to sessile bulbate bases ca. 0.05–0.10 mm wide, abundant along the margins and generally contiguous, being scarce only on the apices of the laciniae. Soralia subcapitate, hemispheric to subplane, laminal or subapical, looking somewhat like pustulae at the very beginning of their development, forming small bumps that open soon. Soredia subgranular, 30.0–75.0 µm diam. True pustulae absent, the soralia initially opening from below the upper cortex forcing an opening, and when emptied looking like burst, totally eroded pustulae, leaving the lower cortex exposed or with a few medullary hyphae visible. Isidia absent. Medulla white. Lower surface black, shiny, smooth to subrugose, moderate to densely rhizinate, with some naked parts. Marginal zone brown, attenuate 0.2–0.5 mm wide, occasionally black and indistinct from the center, shiny, smooth, becoming rhizinate at the transition to the center. Rhizines black, initially furcate soon becoming very dichotomously branched, partially with basal bulbs or enlarged bases, 0.10–0.20 (−0.30) × ca. 0.03 mm, frequent to abundant being sparse in some parts, evenly distributed. Apothecia subplane to concave, sessile to adnate, 0.4–2.2 mm diam., laminal, margin and amphithecium smooth, corona, eventually sorediate. Disc brown, epruinose, imperforate, epithecium 5.0–10.0 µm high, hymenium 25.0–35.0 µm high, subhymenium 15.0–20.0 µm high. Ascospores rounded to ellipsoid, (5.0–) 6.0–8.0 × 4.0–6.0 µm, epispore ca. 1.0 µm. Pycnidia scarce, laminal, immersed, with black ostioles. Conidia bacilliform to weakly bifusiform 5.0–7.0 × 0.75 µm.

CHEMISTRY. – Atranorin, gyrophoric acid, variable small quantities of lecanoric and orselinic acids also present according to Sipman and Aubel (1992) (TLC/HPLC); upper cortex K+ yellow, medulla K−, C+ and KC+ rose to reddish rose, UV−.

The presence of lecanoric and orselinic acids was not confirmed here and they could be contaminants as originally suspected by the authors at the time of description. Two labels with the holotype, one from Aptroot and another from Sipman, mention only the presence of gyrophoric acid.

DISTRIBUTION. – South America. Colombia and Guyana. Here reported for the first time from Brazil (States of Amazonas, Mato Grosso, Pará, and São Paulo).

NOTES ON THE TYPE SPECIMEN. – The holotype (fig. 7) consists of several fragments, all in good condition.

COMMENTS. – Currently, there are only two known sorediate species of Bulbothrix (B. imshaugii (Hale) Hale and B. leprieurii), and two known pustulate species (B. pustulata (Hale) Hale and B. oliveirae). The descriptions of B. oliveirae and B. leprieurii called attention to the fact that both appeared to form similar soredia, and that eventually the sorediate pustulae or soralia became excavate exposing the lower cortex. The morphological similarities between the two species and the presence of the same chemical medullary substance (gyrophoric acid), raised the suspicion that they could perhaps represent different stages related to the formation and release of soredia of the same species. However, after study it is clear that they can be distinguished by differences in the development of the vegetative propagules.

As described by Sipman and Aubel (1992), the soralia of Bulbothrix leprieurii vary from capitate to partially plane and excavate (fig. 8). As is noted in the description, I have examined thalli with more hemispherical soralia (fig. 9) and others with plane soralia. At a certain stage, the soralia in all specimens eventually erode and release the soredia, finally becoming excavate and exposing the lower cortex. This ontogeny can be observed in several fragments on the holotype of B. leprieurii.

The bumps or “calluses” that form at the initiation of soralium development cannot always be observed on a given specimen, but typically can be found sparsely on the surface of younger portions of the thallus. If these are examined in section with a transverse cut, it is possible to observe soredia in the immature soralium. Thus these structures are very different from the empty space present in a hollow
pustule. In the later stages of development, when the lower cortex is exposed, the holes left by the emptied
soralia give a very similar appearance to that of pustules that have erupted and fragmented as can be
observed in *Bulbothrix oliveirae*.

Because the soralia of *B. leprieurii* and the pustules of *B. oliveirae* appear almost identical at the
final stages of development, the greatest difficulty in distinguishing the species occurs when all or most of
these structures have eroded. Under these conditions there are few differences left, except for the narrower
laciniae in *B. leprieurii* (0.3−0.7 mm vs. 0.5−1.5 mm wide in *B. oliveirae*), that are also more linear and
frequently sublacinulate, a more continuous (less cracked) upper cortex, and rhizines that are less abundant
in *B. leprieurii* when compared to *B. oliveirae*.

The differences between *Bulbothrix leprieurii* and *B. oliveirae* can be subtle and difficult to
interpret without prior experience. This is evidenced by the fact that all of the specimens cited in the
protologue of *B. oliveirae*, except for the holotype, actually represent typical sorediate specimens of *B.
leprieurii*.

As was mentioned above the only other sorediate species of *Bulbothrix* known is *B. imshaugii*. That species differs from *B. leprieurii* by having wider laciniae with rounded apices (ca. 1.5−4.5 mm wide), a
maculate upper cortex, simple cilia and rhizines, and by the presence of salazinic acid rather than
gyrophoric acid in the medulla. *Bulbothrix coronata* (Fée) Hale is also similar in having dichotomously
branched cilia and rhizines, coronate apothecia and medullary gyrophoric acid. But it differs from *B.
leprieurii* in having wider laciniae (ca. 0.5−1.0 mm wide) and by not forming soralia or any kind of
lichenized propagule.

Additional specimens examined – BRAZIL: AMAZONAS: between Manaus and São Gabriel, along Rio Negro at Temendui Lagoon, campina, ca. 00° 35′S, 64° 40′W, on branch, 30.iv.1979, W.R. Buck 2242 (NY). MATO GROSSO: 842 km N of Cuiabá on Cuiabá-Santaréns highway (BR-163), ca. 8° 45′S, 54° 57′W, ca. 350−500 m, mature forest along stream on sandy soil with deep humus and roadbank vegetation, on roadside Solanaceae, 5.v.1983, L. Brako & M. Dibben 6716 (NY), L. Brako & M. Dibben 6727 (NY). PARA: Serra do Cachimbo, Base Aérea do Cachimbo, ca. 20 km N of the border with Mato Grosso on Cuiabá-Santaréns highway (BR-163), ca. 9° 22′S, 54° 54′W, ca. 430−480m, broad, sandy level plain along Rio Braço de Norte with sandstone exposures, low ridges and valleys to the N & S, 26.iv.1983, L. Brako & M. Dibben 6012 (NY). SÃO PAULO: Ilha Comprida Municipality, Vila das Pedrinhas, at the southern part of the island, clearing in the restinga woods in a place being allotted, 3 m alt., on small tree trunk, 26.ix.2006, M. N. Benatti & M. J. Kitaura 2226 (SP), M. N. Benatti & M. J. Kitaura 2227 (SP); side of the road near the ferry to the Island of Cananéia, on tree trunk at the edge of restinga wood, 3.iv.2004, L.S. Canêz et al. 1229 (SP), on thin tree branch inside the restinga wood, L. S. Canêz et al. 1276 (SP).


**TYPE: BRAZIL: PARÁ:** Serra do Cachimbo, Base Aérea do Cachimbo, ca. 20 km N of the border with Mato Grosso on Cuiabá-Santaréns highway (BR-163), ca. 9° 22′S, 54° 54′W, ca. 430−480m, broad, sandy level plain along Rio Braço de Norte with sandstone exposure, low ridges and valleys to the N & S, 23.iv.1983, L. Brako & M. J. Dibben 5804[c] (NY!, holotype).

**FIGURES 10 AND 11.**

DESCRIPTION. – Thallus sublinear laciniate, greenish gray in herbarium, fragments up to 3.7 cm
diam., submembranaceous, corticulous, upper cortex 12.5−17.5 µm thick, algal layer 15.0−20.0 µm thick,
medulla 60.0−75.0 µm thick, lower cortex 12.5−15.0 µm thick. Laciniae anisotomic dichotomously to
irregularly branched, (0.3)−0.5−1.2 mm wide, contiguous becoming partially crowded at the center, adnate
and appressed, with flat, truncate to subtruncate apices, the margins plane, smooth to sinuious or irregular,
tire to slightly incised, commonly sublacinulate mainly at older parts, the axils oval to partially irregular.
Upper cortex smooth and continuous, with few occasional transversal or irregular fissures, laminal ciliary
bulbs absent. Adventitious marginal lacinulae scarce to abundant, especially on older parts, short, 0.2−0.8 ×
0.1−0.3 mm, plane, simple to fuscate or rarely irregularly branched, apices truncate, lower side concolorous
with the lower marginal zone. Maculae absent. Cilia black, apices initially simple, soon becoming fuscate
and finally dichotomously branched, 0.05−0.25 × ca. 0.03 mm, with semi-immersed to sessile bulbate bases
cr. 0.05−0.10 mm wide, abundant along the margins, spaced up to 0.05 mm from each other to contiguous,
becoming scarce at the apices of the laciniae. Pustulae in the form of rounded to irregular bumps or blisters, laminal to commonly apical or subapical on the laciniae and lacinulae, their walls eroding from the the middle out sometimes forming corticate, coarse granules, leaving a small portion of medullary hyphae with the lower cortex or exposing it totally. Soredia-like grains scarce, subgranular and coarse, partially corticate, originating from the the fragmentation of the walls and external rim of the pustulae and not true soralia. Isidia absent. Medulla white. Lower cortex black, shiny, smooth to subrugose, densely rhizinate with some random open areas. Marginal zone black and indistinct from the center to a dark brown and very narrow band ca. 0.1–0.2 mm wide, shiny, smooth, becoming rhizinate at the transition to the center. Rhizinae black to rarely pale brown, initially furcate commonly becoming very dichotomously branched, partially with bulbate bases, 0.10–0.30 × ca. 0.03 mm, abundant almost like a tomentum, sometimes however being less frequent at random areas, evenly distributed. Apothecia and pycnidia not found.

**CHEMISTRY.** – Atranorin, gyrophoric acid (TLC/HPLC); upper cortex K+ yellow, medulla K−, C+ and KC+ rose, UV−.

**DISTRIBUTION.** – South America: Brazil (Hale 1986).

**NOTES ON THE TYPE SPECIMEN.** – The holotype is composed of three thalli from three different *Bulbothrix* species. When Fletcher (*in* Hale 1986) introduced the name *B. oliveirae* he cited the holotype type as “L. Brako 5804” and did not indicate whether he considered all three thalli to comprise a single specimen. Nonetheless, only a single thallus from the holotype was illustrated in the protologue, and this is the only thallus that corresponds to the description in the protologue. Thus it is assumed here that the remaining two thalli were not used to produce the description and should not be considered part of the type collection. The holotype thallus is in good condition with many pustules at different stages of development and erosion, but most of these structures were already in some stage of disintegration by the time of the collection. The specimen also lacks apothecia and pycnidia. The remaining two fragments represent thalli of *B. amazonensis* and *B. semilunata*, both in good condition. The three fragments present in the holotype were given the letters “a-c” at some point after collection, although no specific letter (i.e., thallus) was cited in the protologue.

**COMMENTS.** – Initially I suspected that *Bulbothrix oliveirae* and *B. leprieurii* might represent the same species, with the former representing a stage with pustulae still intact and barely formed soralia and the latter representing a stage with pustulae fully formed and several eroded soralia. After study of the available material it became clear that my impression was incorrect. Fletcher (*in* Hale 1986) misinterpreted all of the specimens cited in the protologue of *B. oliveirae*, except for the holotype, as having been pustulate rather than sorediate. In fact with the exception of the holotype which is pustulose, all specimens included in *B. oliveirae* by Fletcher (*in* Hale 1986) are sorediate and thus represent *B. leprieurii*. The differences between these two species are discussed in detail above in the entry for *B. leprieurii*. *Bulbothrix oliveirae* is superficially very similar to *B. leprieurii* and some specimens can be difficult to identify with certainty.

The formation of pustules is the main characteristic of *Bulbothrix oliveirae*. These structures can develop all over the upper cortex, but most often occur on the subapical parts of the laciniae and adventitious lacinulae. Initially they appear as swellings or warty bubbles, eventually bursting and gradually eroding, with their walls finally crumbling completely to leave only a hole in the medulla where the lower cortex is exposed. When the walls of the pustules crumble they sometimes form granular to subgranular structures that resemble soredia, but are actually thalline fragments composed of both tissue from both the cortex and medulla. These fragments are in fact coarse and partially corticate granules, and can be seen in varying quantities in the internal rim of the pustulae as they disintegrate.

The final stages of disintegration of the pustules usually leave a thin layer of medullary hyphae on top of the lower cortex, but there are times where this layer also fragments and fully exposes the black lower cortex. The damage caused to the thallus by the development of the pustules, appears to forcibly terminate the development of laciniae beyond that point. In the specimens examined there are relatively fewer pustulae in areas of the cortex where the laciniae or lacinulae continue to grow, which means that the pustulae are formed after the apices have formed new tissue at the growing edge. Propagules such as the soredia of *B. leprieurii*, the laminal lacinulae of *B. pseudocoronata*, or the common isidia found on about half of the species in the genus do not restrict the vegetative growth of the thallus in the manner that is seen in *B. oliveirae* (e.g., Benatti 2011a-b, 2012a-d, 2013a-c).
Figures 10-15. 10, holotype of *Bulbothrix oliveira* (NY). 11. detail of the pustulae from the holotype of *B. oliveira*. 12-15, holotype of *B. sipmanii* (U) showing overall appearance of the specimen (12), detail of laciniae and apothecia (13), detail showing the very narrow laciniae with contiguous bulbate cilia (14), and detail of the bicornute ascospores (15). Scale= 1 cm, except where noted.
The only other species of Bulbothrix known to produce pustules is B. pustulata. Bulbothrix pustulata differs by having wider laciniae (2.5–5.5 mm wide), a more fragile and delicate membranaceous thallus, pustules with a villous, dactyloid aspect that often erupt but do not form of soredia, less frequent cilia and rhizines with larger basal bulbs and simple apices, and by the presence of salazinic acid instead of gyrophoric acid in the medulla. The pustules of B. pustulata are also extensively produced throughout the upper cortex, instead of arising mainly on the apical portions of laciniae.

Additional specimens examined – BRAZIL: SÃO PAULO: Itanhaém Municipality, Balnéário Santa Cruz, near the municipality border between Itanhaém and Peruíbe, low restinga wood ca. 500 m distant from the beach, 1 m alt., 24º 19’S, 47º 00’W, at vacant lots in an area being subdivided, on liana, 14.i.2004, M.N. Benatti et al. 1702 (SP); Cananéia Municipality, Base do Instituto Oceanográfico, 15.ii.1982, on palm tree near the sea coast, M.P. Marcelli 16296 (SP).


Mycobank #460386.

TYPE: GUYANA: East Demenara district, Tihmeri, Dakara Creek, Thompson’s farm, ca. 10 m, coord. 6º 29’N, 58º 15’W, in cultivated, open area, on free standing tree, on branch, 2.ii.1985, H. Sipman & A. Aptroot 18032 (U! holotype; B!, TNS!, US! isotypes).

DESCRIPTION. – Thallus linear laciniate, dusky green in herbarium, up to 1.9 cm diam., submembranaceous, corticolous (on twigs), upper cortex 7.5–12.5 µm thick, algal layer 10.0–12.5 µm thick, medulla 15.0–20.0 µm thick, lower cortex 7.5–10.0 µm thick. Laciniae isometric to anisometric dichotomously to partially irregularly branched, 0.1–0.3 mm wide, contiguous to rarely slightly imbricate, very adnate and strongly appressed, with flat, truncate to acute apices, the margins plane, smooth to subirregular, entire to occasionally slightly incised, scarcely sublacinulate, the axils oval to irregular. Upper cortex smooth and continuous, laminal ciliary bulbs absent. Adventitious marginal lacinulae scarce on older parts, short, 0.1–0.3 × 0.05–0.10 mm, flat, simple to rarely furcate, acute, lower side concolorous with the lower marginal zone. Maculae absent. Cilia black, apices initially simple or furcate, soon becoming very dichotomously branched 0.05–0.15 (–0.20) × ca. 0.03 mm, with semi-immersed to sessile bulbate bases ca. 0.05 mm wide, abundant along the margins, contiguous, becoming absent or scarce only at the apices of the laciniae. Soredia and pustulae absent. Isidia scarce and disposed in small groups, laminal, granular to occasionally smooth cylindrical but still very short, 0.05–0.10 (–0.20) × ca. 0.05 mm, simple, erect, firm, concolorous with the cortex or with dark brownish apices, usually ciliate with small bulbs without apices or with very subtle ones. Medulla white. Lower cortex with variable coloration, brown to dark brown or partially blackish, slightly shiny to opaque, smooth, densely rhizinate. Marginal zone brown to dark brown in a narrow band ca. 0.5 mm wide, often hardly distinguishable from the center, slightly shiny, smooth, slightly less rhizinate than the center. Rhizines black to brown, initially furcate soon becoming very dichotomously branched, very intertwined, partially with subtle bulbate bases, 0.05–0.20 × 0.03–0.05 mm, abundant but less dense near the margins, evenly distributed. Apothecia subconcave to convex, adnate to sessile, 0.2–1.6 mm diam., laminal, margins smooth, coronate (except at very early stages), ampithecia smooth, also with ciliary bulbs and occasionally with few isidia. Disc pale brown, epruinose, imperforate, epithecium 5.0–7.5 µm alt., hymenium 25.0–35.0 µm alt., subhymenium 25.0–35.0 µm alt. Ascospores bicornute, crescent shaped or sigmoid, usually thicker at the apices restricting the lumen to the central portion, (10.0–) 13.0–18.5 × (2.5–) 3.0–4.0 µm, epispore ca. 0.5 µm. Pycnidia scarce, laminal, immersed, with black ostioles. Conidia bacilliform to weakly bifusiform, 5.0–7.5 × 0.5 µm.

CHEMISTRY. – Atranorin and gyrophoric acid (TLC/HPLC). Upper cortex K+ yellow, medulla K−, C+ and KC+ rose, UV−. Spot test reactions are somewhat difficult to interpret because of the thin medulla and very small size of many thalli.

Notes on the type specimen. – All the type material (holotype and isotypes) is composed of very small fragments, 1.0 to 2.0 cm in diameter, over tree bark, which are glued to backings. The very small size of the fragments and the very narrow, delicate and adnate laciniae render it quite difficult to observe the lower cortex without damaging the specimens. The material contains reasonably mature apothecia, although these are small, have coronation and some isidia, as well as mature ascospores. Pycnidia with conidia were also observed. The holotype has the best developed apothecia, where coronation can be easily seen, which is subtle or not perceptible in the isotypes because they are immature. The holotype also has a greater number of adventitious laciniae.

Comments. – Much like Bulbothrix fungicola and B. linteolocarpa Marcelli, this species has linear and very narrow laciniae, being among the smallest known in Bulbothrix species. Aptroot and Aubel (1999) described the laciniae width as 0.2−0.5 mm, although in all of the type material no single lacinia wider than 0.3 mm was found. As described by the authors, the larger laciniae tend to have truncated apices, while the smaller ones and the adventitious laciniae tend to have more acute apices. As they are very narrow, it is difficult to separate laciniae in early stages of development from adventitious laciniae, although the laciniae usually have narrow bases and appear randomly on the margins. This characteristic is similar to B. fungicola.

The cilia and rhizines of Bulbothrix sipmanii tend to be dichotomously branched, assuming this form even in the very early stages of development, and are generally very short in length. Unlike the cilia, which are always dark, the rhizines can occasionally be brown and even paler than the lower surface. The marginal zone of the lower surface is sometimes difficult to distinguish from the center because it is partially dark brown in color, while the bases of the rhizines are paler, and partially bulbate. In the type material the lower surface was predominately brown and dark brown, but some laciniae had a black lower surface.

This species has very small and simple isidia, that are quite sparse and usually found solitary or in small groups that are randomly distributed on the upper surface. The isidia have brown apices as described by Aptroot and Aubel (1999), but in addition my examination revealed that the isidia become ciliate as they mature. The “blackened” apices in some of these isidia are actually ciliary bulbs in an early stage of development. These structures can be detected as small pointy apices, similar to those on marginal cilia near the apices of the youngest laciniae. This pattern of cilia growth on isidia is also similar to that which was observed in B. fungicola (see comments on this species above) and other Bulbothrix species with ciliate isidia.

Bulbothrix sipmanii was compared by Aptroot and Aubel (1999) to two other species, B. schiffneri Zahlbr., which they believed to be the non-isidiate counterpart, and B. semilunata, which has similarly shaped of the ascospores. Of the four species of Bulbothrix with bicornute ascospores, B. sipmanii is the only one currently known to form vegetative propagules. As is the case for B. schiffneri, the apothecia of B. sipmanii have ciliary bulbs on the amphithecia, while the coronation of the margins is subtle on underdeveloped apothecia (different from other species that show clear coronation at the start of the apothecia maturation). Bulbothrix schiffneri is indeed very similar to B. sipmanii as it also contains gyrophoric acid. That species differs by the absence isidia, smaller ascospores (ca. 8.0−13.0 ×3.0−4.0 μm vs. 13.0−18.5 × 3.0−4.0 μm in B. sipmanii), and slightly wider laciniae (ca. 0.2−0.5 mm) (Benatti 2013c). Bulbothrix semilunata also differs from B. sipmanii by not forming isidia, and by the absence of medullary substances (Benatti 2013b). Thalli of B. semilunata have less branched cilia and rhizines (ranging from simple to fuscate to partially subdichotomously branched) than those of B. sipmanii or B. schiffneri, which are generally fuscate to very dichotomously branched, the apices presenting various continuous dichotomies. The tendency of the laciniae of B. sipmanii to have a brown lower cortex is also a difference with these species, which have a black lower cortex.

Bulbothrix fungicola is also similar to B. sipmanii, although it has wider laciniae (ca. 0.2−0.7 mm). When apothecia are lacking, B. sipmanii could be nearly indistinguishable from B. fungicola, due to the very small ciliate isidia which are present in both species. In direct comparison, the shape of the laciniae in B. fungicola tend to be more often sublinear, with more sinuous and crenate margins. The cilia and rhizines of B. fungicola are simple to fuscate (not becoming dichotomously branched), and the lower surface is black with distinct brown margins. When apothecia are present the two species are easily distinguished because the apothecia of B. fungicola do not develop ciliary bulbs in the amphithecia, and the ascospores are ellipsoidal or ovoid, instead of bicornute, as well as smaller (6.5−10.0 × 4.5−6.0 μm).
SPECIES TREATED IN PREVIOUS CONTRIBUTIONS

Mycobank #341606.

**DESCRIPTION.** – For a description, discussion and images, see Benatti and Elix (2012).

**COMMENTS.** – This species was recently resurrected by Benatti and Elix (2012) who removed it from synonymy with *Bulbothrix goebelii*. It is characterized by laciniae 1.0−3.0 mm wide, an emaculate upper cortex, often pycnidiate tortuous isidia, dichotomously branched bulbate cilia and rhizines, a black lower surface with brown margins, occasionally pycnidiate but always ecoronate apothecia, and gyrophoric acid as only medullary substance.

The isidia of *Bulbothrix papyrina* often have embedded pycnidia, resembling black swellings, which were initially interpreted as parasites and later as ciliary bulbs. Occasionally, the pycnidia may also occur in small quantities on the amphithecia as well (the apothecia, however, are ecoronate, not having a bulbate rim). The pycnidiate isidia appear to be common, but not always present in *B. papyrina*. The production of pycnidia is likely a stage of development of the isidia and may even be triggered by environmental conditions.

Mycobank #561687.

**DESCRIPTION.** – For a description, comments and images, see Benatti 2012c.

Comments. – This species is characterized by having sublinear narrow laciniae (usually ≤ 0.5 mm wide), an emaculate upper cortex, dense semi-cylindrical to subcanaliculate or flat laminal lacinulae, simple or furcate cilia and rhizines, black lower surface with brown margins, rhizines with basal bulbs, coronate apothecia, small ascospores 7.0−9.5 × 4.5−5.5 μm, and by the presence of gyrophoric acid as the main medullary substance. It is the species that truly represents the concept of *Bulbothrix suffixa* established by Hale (1976), as the type of *B. suffixa* is a very poorly developed specimen that is impossible to identify with certainty (see description and comments under *B. suffixa* below).

Mycobank #561953.

**DESCRIPTION.** – For a description, discussion and images, see Benatti (2012a).

Comments. – This recently described species is characterized by narrow sublinear laciniae approximately 0.5−1.0 mm wide, an emaculate upper cortex, simple laminal isidia usually ornamented with small bulbate cilia, mostly dichotomously branched marginal cilia and rhizines, a black lower surface with brown margins, rhizines without basal bulbs, coronate apothecia, small rounded ascospores (4.0−6.0 × 4.0−5.0 μm), and the presence of gyrophoric acid. It is similar to *B. fungicola*, which has simple to furcate cilia and rhizines, coronate apothecia, and larger ascospores (8.0−10.0 × 4.5−6.0 μm).

Mycobank #341610.

**DESCRIPTION.** – For a description, comments and images, see Benatti & Elix 2012.

Comments. – This species was recently resurrected in conjunction with establishing the true identity of *Bulbothrix goebelii* (Benatti & Elix 2012). It was one of several names originally recognized by Hale as distinct species, but later placed into synonymy with *B. goebelii* for unknown reasons. *Bulbothrix scortella* is characterized by laciniae approximately 0.5−1.5 mm wide, a maculate upper cortex, eciliate isidia, dichotomously branched bulbate cilia and rhizines, an entirely brown lower surface, coronate apothecia, and the presence of gyrophoric acid.
Bulbothrix scortella is similar to B. subdissecta, differing in the color of the lower surface, absence of lobaric acid as an accessory to gyrophoric acid and somewhat larger ascospores (ca. 7.0–11.0 × 4.0–5.0 µm).

Mycobank #341615.

DESCRIPTION. – For a description, discussion and images, see Benatti and Elix (2012).

Comments. – As with Bulbothrix scortella, this species was recently resurrected in a study dealing with the true identity of B. goebelii. It was one of several names that were initially treated as distinct species but then placed into synonymy with B. goebelii by Hale (see Benatti & Elix 2012).

This species is characterized by laciniae approximately 0.5–1.5 mm wide, a maculate upper cortex, eciliate isidia, dichotomously branched bulbate cilia and rhizines, a black lower surface with distinct brown margins, ecoronate apothecia, and presence of gyrophoric acid usually accompanied by lobaric acid. The species is similar to B. scortella and readers should refer to the discussion under that name for additional notes.

Mycobank #560776.

DESCRIPTION. – For a description, comments and images, see Marcelli et al. (2011).

Comments. – Bulbothrix thomasiana is one of the few species in Bulbothrix known to contain lobaric acid in the medulla, and together with B. apophysata and B. goebelii they are the only species known to have this as main medullary substance. This recently described species is characterized by narrow, sublinear laciniae, a smooth emaculate upper cortex, abundant, apically branched marginal bulbate cilia, simple and ciliate isidia, a usually pale brown lower surface with abundant concolorous rhizines, ecoronate apothecia with small ascospores, and the presence of lobaric acid. The most similar is B. apophysata, which differs in having a black lower surface with dark brown margins, dark rhizines, and completely eciliate isidia.

EXCLUDED OR DOUBTFUL NAMES

(non Parmelia appressa Spreng.).
Mycobank #368527

TYPE: PERU: locality and collector unknown (L!, holotype (as cited by Hale 1976)).

Figure 16 and 17.

Comments. – This name was correctly regarded as a nomen illegitimum according DePriest (1999) as Parmelia “appressa” Zenker is a later homonym of P. appressa Spreng. It is worth noting that Zahlbuckner (1931 p. 704) treated P. appressa Spreng. as a synonym of Physcia applanata (Fée) Zahlbr. (= Dirinaria applanata (Fée) D. D. Awasthi).

The synonymy of Parmelia “appressa” with Bulbothrix coronata accepted by Hale (1976) is confusing because B. coronata has a black lower surface while Zenker (1827) described the lower surface of P. “appressa” as brown. Zenker (1827) mentioned the apothecia in this species as "contiguous, flattened, simple, small, usually with thalline margin and dark brown disks," but there are no apothecia in the type material. In fact none of the fragments have any resemblance to the drawing of Zenker (1827: pl. 21, figs. 8A-E). All thalli in the type material also have many parasitic fungi. Without any apothecia to examine the coronation and ascospores, and due to the scarcity of isidia, it is impossible to determine whether P. “appressa” is conspecific with B. coronata, as was proposed by Hale (1976). Instead it may be an isidiate species distinct from B. coronata with a differently colored lower surface. It is also very similar to B. klementii Hale, differing mainly by the medullary chemistry. Another possibility is that it could correspond to B. scortella, which is also isidiate, with a brown lower surface and gyrophoric acid.
Figures 16-21. 16, all packets comprising the type collection of Parmelia adpressa (L). 17, Detail of the lectotype of P. adpressa. 18-21, lectotype of of Bulbothrix suffixa (BM) showing overall appearance of the specimen (18), details of the upper cortex (19), scarce marginal adventitious lacinulae (20), and isidia (21). Scale bars = 1 cm, except where noted.
Fée (1837) also discussed material of *Parmelia* “*appressa*”, describing cortical maculae and a brown lower surface. Further details are lacking however, and I have not examined any specimens seen by Fée. It appears that he only summarized Zenker’s data in French. Meyen and Flotow (1843) described *P. “appressa*” as having a "whitish membranaceous thallus, sorediate, with a slightly apparent blackish felt hypothallus". Their material almost certainly does not belong to the same species as the type, and if a hypothallus was present it might actually be a species of *Pannaria* or *Parmeliella*. Zahlbruckner (1931 p. 581) included Meyen and Flotow (1843) among the citations for *P. “appressa”* Zenker.


MycoBank #341618.

≡ *Parmelia suffixa* Stirt., Scottish Naturalist 4: 299. 1877–78. **TYPE:** SOUTH AFRICA: Knysna, 2.iv.1878 *J. Knobel s.n.* (BM!, lectotype (selected by Hale 1976); GLAM!, isolectotype).

**FIGURES 18, 19, 20 AND 21.**

**DESCRIPTION (OF THE TYPES).** – Thallus sublinear laciniate, pale dusky gray in herbarium, fragments up to 2.0 cm diam., submembranaceous, corticolous, upper cortex 12.5–17.5 µm thick, algal layer 12.5–15.0 µm thick, medulla 17.5–25.0 µm thick, lower cortex 10.0–15.0 µm thick. Laciniae isotomic to anisotomic or irregularly dichotomously branched, 0.3–0.9 mm wide, contiguous to slightly imbricate, adnate and appressed, with flat, truncate to subtruncate apices, the margins plane, smooth to sinuous, subcrenate or irregular, entire to slightly incised, frequently sublacinulate, the axils oval or rounded. Upper cortex smooth and continuous, laminal ciliary bulbs absent. Adventitious marginal or very rarely submarginal lacinulae common on random parts but more often at older parts, short, 0.15–0.50 × 0.05–0.15 mm, spatuliform, simple to rarely furcate, truncate to subtruncate, initially eciliate but soon developing small marginal ciliary bulbs, lower side concolorous with the lower marginal zone. Maculae weak, almost indistinct, laminal, more visible at younger parts, mixed with scars left by fallen isidia. Cilia black, apices initially simple to furcate, occasionally becoming subdichotomously branched at the axils, 0.05–0.30 (−0.45 at the axils) × ca. 0.03 mm, commonly bent downwards, with semi-immersed to sessile bulbate bases 0.05–0.10 (−0.15) mm wide, abundant along the margins spaced ca. 0.05 mm from each other eventually becoming contiguous, becoming absent only at the apices of the laciniae. Soredia and pustulae absent. Isidia scarce, laminal, granular to smooth cylindrical, very short (apparently at initial stages of development), straight, ca. 0.05 (−0.10) × ca. 0.05 mm, simple, erect, firm, darkened, partially ciliate with tiny bulbs. Medulla white. Lower cortex black to brown or dark castaneous brown, shiny, smooth to subrugose, weakly papillose, densely rhizinate. Marginal zone brown to dark castaneous brown in a narrow band ca. 0.5–1.5 mm wide, shiny to opaque, smooth, weakly papilate, moderate to densely rhizinate. Rhizines black, partially dark brown near the margins or until the transition to the center, initially simple or furcate soon becoming subdichotomously or irregularly branched, commonly with bulbate bases, 0.10–0.50 × ca. 0.03 mm, frequent to abundant almost like a tomentum at some parts, evenly distributed. Apothecia and pycnidia not found.

**CHEMISTRY.** – Atranorin and gyrophoric acid (TLC/HPLC). Upper cortex K+ yellow, medulla K−, C+ and KC+ rose to reddish rose, UV−.


**NOTES ON THE TYPE SPECIMENS:** The lectotype consists of two fragments, each approximately 1.5 cm in diameter, which are on tree bark. The material is in good condition, very little damaged, and has
fairly common marginal adventitious lacinulae, with some sparse submarginal ones close to the margins. The duplicate in GLAM also consists of two fragments, one of 2 cm and the other only 1 cm in diameter, in the same conditions as the lectotype, but with more marginal lacinulae, with some few submarginal ones restricted to a few laciniae. Although the specimens are in good condition, the material is very poorly developed with thalli in the early stages of propagule formation.

Comments. – *Bulbothrix suffixa* is here considered to be a *nomen dubium* because the type material is very small and immature. It has sublinear narrow laciniae, a weakly maculate upper cortex, small adventitious marginal and (rarely) submarginal lacinulae, simple to little branched cilia, a black to brown lower surface with brown margins, branched rhizines with bulbate bases, and gyrophoric acid. Even though these characters could be ascertained, the poor development of other structures makes application of the name uncertain.

The protologue of *Parmelia suffixa* (Stirton 1878) does not mention any lobules, lacinulae, or other similar structure of vegetative propagation. However, there are small structures on the cortex of the type material that resemble undeveloped isidia, occasionally with some small ciliary bulbs. Initially I thought that these isidium initials were the beginning stages of structures that ultimately develop into lacinulae which function as vegetative propagules. There is however, no evidence that this is the case as the lacinulae developed on the thallus are identical to those on the margins which lack the brownish apicies of the immature isidia. These structures appear merely to be regenerating parts of the thallus and are not easily detached, thus they are unlikely to function as vegetative diasporas. Due to the poor state of the type material it is impossible to ascertain with certainty what the morphological characteristics of *Bulbothrix suffixa* are. It is unclear whether the poorly developed structures are akin to the isidia in *B. fungicola*, the laminal lacinulae in *B. pseudocoronata*, or, however unlikely it may be, whether they represent isidia that transform into lacinulae. There are also no apothecia or pycnidia in the type material that would further facilitate identification.

Dodge (1959) attributed specimens to *Bulbothrix suffixa*, but his descriptions were mainly anatomical and not morphological, which make comparison with other species nearly impossible. He even described the material as eciliate, although he mentioned that the specimens seemed ciliate due the presence of simple to branched rhizines, which apparently spilled from the margins. Dodge did not mention lobules, lacinulae or any other similar structure. The apothecia were just described as “smooth”, which might imply the absence of bulbate cilia (coronation). The ascospores were described as ellipsoid and 13.0–14.0 × 6.0–8.0 µm in size, similar to those mentioned by Krog and Swinscow (1988) for specimens they also identified as *B. suffixa*.

The beginning of the modern application of this name likely dates to Hale (1976) where it was described having an upper cortex “becoming densely lobulate, lobules dorsiventral, oblong to spatuliform, marginally bulbate-ciliate”. Neither the description nor the illustration in Hale (1976) correspond to the same species as the type material of *B. suffixa*. The photograph used in that work to illustrate *B. suffixa* corresponds very well to *B. pseudocoronata*, which was considered a synonym of *B. fungicola* by Hale (1976).

II: WORLD KEY TO THE GENUS BULBOTHRIX

1a. Upper cortex yellowish green, with usnic acid (K−) ................................................................. *Relicina*  
1b. Upper cortex greenish gray to grayish, with atranorin (K+ yellow) ...................................................... 2  

2a. Thallus isidiate, lacinulate, sorediate or pustulate .................................................................................. 3  

3a. Thallus sorediate or pustulate .................................................................................................................. 4  

4a. Thallus pustulate, pustulae sometimes bursting, forming granular soredia ........................................... 5  

5a. Laciniae 2.5–5.5 mm wide; cilia and rhizines simple; pustulae rugose to dactyloid; medulla K+ yellow→dark red, P+ yellow (salazinic acid) .............................................................. *B. pustulata*  
5b. Laciniae 0.5–1.5 mm wide; cilia and rhizines dichotomous; pustulae forming small warts; medulla C+ rose, KC+ rose→light orange (gyrophoric acid) ..................................................... *B. oliveirae*  

4b. Thallus sorediate, soralia orbicular to irregular ...................................................................................... 6
6a. Lacinae 2.0–4.5 mm wide; cilia and rhizines simple; medulla K+ yellow→dark red, P+ orange (salazinic acid) ................................................................. B. imshaugii
6b. Lacinae 0.3–0.7 mm wide; cilia and rhizines dichotomous; medulla C+ rose, KC+ rose→light orange (gyrophoric acid) ................................................................. B. leprieurii

3b. Thallus isidiate and/or lacinulate ........................................................................................................... 7

7a. Thallus lacinulate; lacinulae dorsiventral and procumbent, flattened to canaliculate or semicylindrical (like cleaved isidia), ciliate and eventually becoming rhizinate ................................................................. 8

8a. Lacinae 1.0–1.5 (−3.0) mm wide; lacinulae plane to subconvex, dichotomous or irregularly branched; cilia dichotomous or irregularly branched; apothecia ecoronate (fatty acids, all spot tests negative) ......................................................................................... B. lopezii
8b. Lacinae 0.2–1.0 mm wide; lacinulae semicylindrical to canaliculate, simple to furcate; cilia simple to furcate, rarely subdichotomous; apothecia coronate ......................................................................................... 9

9a. Lacinae 0.2–0.5 mm wide; lacinulae often semicylindrical with isidiate aspect at early stages, resembling cleaved isidia and eventually becoming canaliculate; medulla C+ rose, KC+ rose→light orange (gyrophoric acid) ................................................................. B. pseudocoronata
9b. Lacinae 0.3–1.0 mm wide; lacinulae generally flattened from the beginning of their development; medulla with all tests negative (no substances) ......................................................................................... B. caribensis

7b. Thallus isidiate; isidia cylindrical and erect, occasionally subirregular, with or without bulbate cilia of irregular and random disposition ................................................................................................. 10

10a. All medullary spot tests negative (without medullary substances or with colensoinic acid)........... 11

11a. Lacinae subirregular, 1.5–3.0 mm wide; cilia mainly axillary and on incisions, apices simple or absent; rhizines simple; isidia often partially pycnidiate ......................................................................................... B. cassa
11b. Lacinae sublinear, 0.2–1.0 (−1.5) mm wide; cilia conspicuously marginal, apices initially simple to eventually branched; rhizines branched; isidia never pycnidiate ......................................................................................... 12

12a. Upper cortex maculate; laminal ciliar bulbs frequent; cilia simple becoming furcate or trifurcate (isidia usually ciliate) ................................................................................................. B. queenslandica
12b. Upper cortex emaculate; laminal ciliar bulbs absent; cilia furcate becoming dichotomous or irregularly branched ................................................................................................. 13

13a. Lacinae 0.5–1.0 mm wide; lower cortex with brown center and margins; medulla with colensoinic acid (TLC/HPLC) ........................................................................................................... B. klementii
13b. Lacinae 0.2–0.7 mm wide; lower cortex with a black center and brown margins; medulla with traces or without any substances (TLC/HPLC) ......................................................................................... 14

14a. Isidia eciliate; medulla, lower cortex and rhizines with randomly placed spots of a reddish K− pigment; medulla often with traces of gyrophoric acid ................................................................. B. pigmentacea
14b. Isidia ciliate; medulla, lower cortex and rhizines without any pigments; medulla often with traces of an undetermined fatty acid ................................................................................................. B. lyngei

10b. At least one positive medullary spot test reaction (gyrophoric, lecanoric, lobaric, norstictic or salazinic acids) ................................................................................................................................. 15

15a. Medulla K+ yellow→orange, bright or dark red, P+ yellow or orange, with norstictic or salazinic acids ................................................................................................................................. 16

16a. Medulla K+ yellow→orange or bright red, P+ yellow, with norstictic acid (small acicular star shaped reddish orange microcrystals formed in KOH) ......................................................................................... 17

17a. Lacinae 0.3–0.6 mm wide; cilia initially simple, becoming furcated or subdichotomous; lower cortex with black center and brown margins; rhizines dichotomously branched ......................................................................................... B. lordhowensis
17b. Lacinae 0.5–4.5 mm wide; cilia simple or without apices; lower cortex predominantly brown or variably mottled black and brown; rhizines simple ......................................................................................... 18
18a. Thallus corticolous; laciniae subirregular, 1.5−3.0 (−4.5) mm wide; laminal ciliary bulbs common, varying from scarce to abundant; isidia concolorous; lower cortex with variable color, from black to mixed black and brown or totally brown ........................................ B. ventricosa
18b. Thallus saxicolous; laciniae sublinear, 0.5−1.5 (−2.5) mm wide; laminal ciliary bulbs absent; isidia dark brown or blackish; lower cortex pale brown, sometimes the margins darker than the center ........................................ B. cinerea

16b. Medulla K+ yellow→dark red, P+ orange, with salazinic acid (depending on the concentration, bundles of dark red microcrystals might be formed in KOH).........................

19a. Upper cortex very cracked, eventually shedding small pieces (strongly maculate); cilia and rhizines dichotomous; isidia ciliate ........................................ B. subtabacina
19b. Upper cortex continuous or with few irregular cracks, never shedding pieces (emaculate or maculate); cilia and rhizines simple; isidia eciliate ........................................ B. tabacina

20a. Lower cortex black, with black or brown margins, sometimes with small randomly placed dark brown spots .................................................................

21a. Thallus solely saxicolous; laciniae 0.5−3.0 mm wide, with subtruncate apices and sinuous margins; upper cortex emaculate, with frequent cracks; isidia blackish; cilia with simple or absent apices ........................................ B. decurtata
21b. Thallus usually corticolous (rarely saxicolous); laciniae 1.5−5.5 mm wide, with rounded apices and crenate margins; upper cortex weakly to moderately maculate, continuous; isidia concolorous; cilia with simple or double apices ...................... B. tabacina

20b. Lower cortex usually uniformly brown (could have variable shades), occasionally with small random blackish spots .................................................................

22a. Laciniae 0.1−2.0 mm wide, with subtruncate apices and sinuous margins; marginal cilia abundant to contiguous (upper cortex maculate or emaculate) ..................

23a. Laciniae 0.1−0.5 mm wide; lower cortex dark brown ...................... B. microscopica
23b. Laciniae 0.5−2.0 mm wide; lower cortex brown to pale brown ........ B. australiensis

24a. Upper cortex emaculate; isidia usually 0.5−1.0 mm high, generally simple; lower cortex brown with an average tone ........................................ B. subglandulifera
24b. Upper cortex maculate; isidia usually < 0.5 mm high, commonly branched; lower cortex very pale brown ........................................ B. subcorticata

22b. Laciniae 1.5−5.5 mm wide, with subrounded apices and crenate margins; cilia mainly axillary and in the crenulae of the laciniae (upper cortex maculate) ........

25a. Thallus corticolous, submembranaceous; upper cortex weakly to densely maculate; cilia with short apices < 0.3 mm long; rhizines without bulbs ................... B. isidiza
25b. Thallus saxicolous, coriaceous; upper cortex emaculate; cilia with long apices ≥ 0.3 mm long; rhizines with basal or displaced bulbs .................. B. decurtata

15b. Medulla C+ rose to reddish and/or KC+ rose to reddish, with gyrophoric, lecanoric and/or lobaric acids .................................................................

26a. Medulla C−, KC+ rose, UV+ bluish to whitish blue, only lobaric acid ..................

27a. Isidia eciliate; lower cortex black with variably brown margins .................. B. apophysata
27b. Isidia usually ciliate; lower cortex entirely pale brown ........................ B. thomasiana

26b. Medulla C+ and KC+ rose to reddish→light orange, with gyrophoric and/or lecanoric acids, sometimes also containing lobaric acid ..........................

28a. Medulla C+ and KC+ distinctly reddish, with lecanoric acid* .................
29a. Upper cortex, apothecia and isidia eciliate; isidia sometimes with apical portion lost, similar to a pseudocyphellum ..........................................................  B. laevigatula
29b. Upper cortex, apothecia and isidia ciliate; isidia entire ..................................  B. bulbillosa
28b. Medulla C+ and KC+ rose to reddish rose, with gyrophoric acid, with or without lobaric acid (isidia always entire) ........................................................................................................ 30

30a. Lacinae 0.1–0.7 mm wide; isidia usually ciliate .................................................. 31

31a. Lacinae 0.1–0.3 mm wide; lower cortex mottled black and dark brown; ascospores bicornute, 12.0–18.0 × 3.0–4.0 µm ..........................................................  B. sipmanii
31b. Lacinae 0.2–0.7 mm wide; lower cortex black with brown margins; ascospores ellipsoid, 8.0–10.0 × 4.0–6.0 µm .......................................................... 32

32a. Cilia and rhizines simple to furcate; apothecia corona; ascospores ellipsoid 8.0–10.0 × 4.5–6.0 µm ..........................................................  B. fungicola
32b. Cilia and rhizines dichotomous; apothecia eciliate; ascospores rounded 4.0–6.0 × 4.0–5.0 µm ..........................................................  B. pseudofungicola

30b. Lacinae 0.5–3.0 mm wide; isidia ciliate .......................................................... 33

33a. Lacinae 1.0–3.0 mm wide; upper cortex emaculate; isidia straight to tortuous and frequently pycnidiate, amphithecia also sometimes pycnidiate; medulla containing only gyrophoric acid ........................................................................................................  B. papyrina
33b. Lacinae 0.5–1.0 mm wide; upper cortex maculate; isidia only straight, amphithecia never pycnidiate; medulla usually containing gyrophoric and lobaric acids (UV+ faint bluish) .......................................................... 34

34a. Lower cortex light brown, margins often darker than the center; ascospores (6.0–) 7.0–11.0 (−12.5) × 4.0–6.0 µm (some specimens might present only medullary gyrophoric acid) ..................................................................................  B. scortella
34b. Lower cortex black, with dark brown margins and sometimes also a few random spots; ascospores (5.0–) 6.0–8.0 (−9.0) × 4.0–5.0 µm (specimens always with both the gyrophoric and lobaric acids) ..........................  B. subdissecta

2b. Thallus without vegetative propagules or pustulac; apothecia often formed ........................................................................................................ 35

35a. All medullary spot tests negative (medulla without substances, with fatty acids or substances concentrated at the medulla of the apothecia) ........................................................................................................ 36

36a. Lower cortex light brown margins sometimes darker than the center; apothecia with amphithecial bulbs and also occasionally with pycnidia ...........................................  B. subklementii
36b. Lower cortex black, with black or brown margins; apothecia with smooth amphithecia, without bulbs or pycnidia ........................................................................................................ 37

37a. Apothecia corona........................................................................................................ 38

38a. Lacinae 0.2–0.5 mm wide; ascospores bicornute, 12.0–23.0 × 3.0–4.0 µm ......  B. semilunata
38b. Lacinae 0.5–2.5 mm wide; ascospores rounded, 4.5–6.0 × 4.0–5.0 µm ............. 39

39a. Lacinae (1.0–) 1.5–2.5 mm wide; laminal cilar bulbs common, frequent; cilia apices simple to furcate; rhizines subdichotomous .....................................................................  B. bulbochaeta
39b. Lacinae 0.5–1.0 (−1.5) mm wide; laminal cilar bulbs absent; cilia apices simple or absent; rhizines usualy simple ..................................................................................  B. viridescens

37b. Apothecia corona ........................................................................................................ 40

40a. Laminal cilar bulbs absent; cilia and rhizines dichotomously branched; rhizines commonly brown; apothecia medulla KC+ lilaceous, UV+ faint blue (lobaric acid); ascospores 4.0–6.0 (−7.0) × 4.0–5.0 µm ..........................................................  B. goebelii
40b. Laminal cilar bulbs common, also frequent in the amphithecia (not true corona); cilia apices simple or absent; rhizines simple to irregularly branched, black; apothecia medulla KC− and UV−; ascospores 6.0–9.0 × 4.0–5.0 µm ..................................................................................  B. laeviuscula
35b. Medullary spot tests positive, C+ and KC+, K+ and P+, or KC+ and P+ (gyrophoric, lecanoric, norstictic, protocetraric or salazinic acids). ................................................................. 41

41a. Medulla K− and C−, KC+ rose, P+ orange, with protocetraric acid .......... B. chowoensis
41b. Medulla K− and P−, C+ and KC+ rose to reddish, or C− and KC−, K+ yellow→orange or red and P+ yellow to orange, with other substances ............................................. 42

42a. Medulla K− and P−, C+ and KC+ rose to reddish, gyrophoric or lecanoric acids ........ 43

43a. Cilia and rhizines usually simple, sometimes partially furcate (apothecia corone, medulla with gyrophoric acid) ....................................................................................................... 44

44a. Thallus corticolus; laciniae 0.5−1.1 mm wide; ascospores 8.0−10.0 × 4.0−5.0 µm ........ 44b. Thallus saxicolous; laciniae 0.2−0.6 mm wide; ascospores 5.0−7.0 × 4.0−5.0 µm .............................. B. affixa

44c. Thallus corticolus; laciniae 0.5−1.0 mm wide; ascospores ellipsoid, 5.0−10.0 × 3.0−6.0 µm .......... B. silicisrea

43b. Cilia and rhizines initially furcate becoming dichotomous or irregularly branched (apothecia corone or ecoronate; medulla with gyrophoric or lecanoric acids) .................................................. 45

45a. Apothecia corone (medulla with gyrophoric acid). .................................................. 46

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47a. Thallus weakly maculate; 16 ascospores per ascus ........................ B. amazonensis
47b. Thallus emaculate; 8 ascospores per ascus ...................................................... B. coronata

45b. Apothecia ecoronate (medulla with gyrophoric or lecanoric acids) ................. 48

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49a. Laciniae 1.0−2.5 mm wide; with a black lower cortex and brown margins; medulla containing gyrophoric acid ................................................................. B. atrichella
49b. Laciniae 0.5−1.0 mm wide; with a mottled lower cortex, brown to dark brown or black; medulla containing lecanoric acid .................................................. B. confodeatera

42b. Medulla C− and KC−, K+ yellow→orange, bright or dark red, P+ yellow or orange, with norstictic or salazinic acids........................................................... 50

50a. Medulla K+ yellow→orange or bright red, P+ yellow, with norstictic acid (apothecia corone, except for B. haleana) ................................................................................ 51

51a. Thallus saxicolous; apothecia ecoronate (ascospores 5.0−9.0 × 4.0−7.0 µm) ........ 51b. Thallus corticolous; apothecia corone (ascospores of variable sizes) .............. 52

52a. Laciniae 0.5−1.0 mm wide; with a black lower cortex and brown margins; ascospores 5.0−7.5 × 4.5−5.5 µm .................................................................................. B. subcoronata
52b. Laciniae (0.5−) 1.0−3.5 mm wide; lower cortex with variable color, from black to brown with different mixing variations; ascospores 8.0−18.0 × 4.0−11.0 µm .............. B. subcoronata

53a. Upper cortex maculate, often with scarce to frequent laminal ciliary bulbs; cilia with simple apices; ascospores (10.0−) 12.0−18.0 × 7.0−10.0 µm ................................. B. viatica
53b. Upper cortex emaculate, never developing laminal ciliary bulbs; cilia simple but often without apices; ascospores 8.0−12.0 (−14.0) × 4.0−7.0 µm .............................. B. regnelliana

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* A chemotype of Bulbothrix bulbillosa containing gyrophoric acid is morphologically identical to the one containing lecanoric acid. This is a very peculiar and unique case in Bulbothrix, as even the spot test reactions to C and KC on B. bulbillosa are usually bright red for the specimens containing gyrophoric acid (what is normally expected for lecanoric acid) instead of pale pink (the usual for gyrophoric acid).

### III: INDEX TO CURRENTLY ACCEPTED NAMES IN BULBOLETRIX

<table>
<thead>
<tr>
<th>Year</th>
<th>Original name</th>
<th>Current status</th>
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<td>≡ B. papyrina (Fée) Hale</td>
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<td>1885</td>
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<td>Parmelia subcoronata Müll. Arg.</td>
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<td>Parmelia bicornuta Müll. Arg.</td>
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<td>Parmelia coronata var. denudata Vain.</td>
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<td>Parmelia hypocraea Vain.</td>
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<td>Parmelia schiffneri Zahlbr.</td>
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<td>Parmelia continua Lynge</td>
<td>\textit{Bulbothrix continua} (Lyenge) Hale</td>
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<td>Parmelia fungicola Lynge</td>
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<td>Parmelia marginalis Lynge</td>
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<td>Parmelia semilunata Lynge</td>
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<td>Parmelia viridescens Lynge</td>
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<td>Parmelia isidiza var. domingensis Vain.</td>
<td>\textit{Bulbothrix ventricosa} (Hale &amp; Kurok.) Hale</td>
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<td>1926</td>
<td>Parmelia leptascea Stein. &amp; Zahlbr.</td>
<td>\textit{Bulbothrix hypocraea} (Vainio) Hale</td>
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<td>1926</td>
<td>Parmelia sensibilis Stein. &amp; Zahlbr.</td>
<td>\textit{Bulbothrix sensibilis} (Stein. &amp; Zahlbr.) Hale</td>
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<td>Parmelia demangei Harmand</td>
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<td>1928</td>
<td>Parmelia recurviscens Harmand</td>
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<td>Parmelia ochrovestita Zahlbr.</td>
<td>\textit{Bulbothrix tabacina} (Mont. &amp; Bosch) Hale</td>
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<td>1938</td>
<td>Parmelia proboscidea var. saxicola Sambo</td>
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<td>1947</td>
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<td>Parmelia apophysata Hale &amp; Kurok.</td>
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<td><em>Hypotrachyna tuskiformis</em> (Elix) Benatti &amp; Marcelli</td>
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2000 *Bulbothrix yunnana* Wang, Chen & Elix  
2000 *Bulbothrix pinguicida* Louwhoff & Elix  
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2008 *Bulbothrix regnelliana* Jungbluth, Marcelli & Elix  
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2011 *Bulbothrix lyngei* Benatti & Marcelli  
2012 *Bulbothrix laeviuscula* (Rasänen) Benatti & Marcelli  
2012 *Bulbothrix substcortea* (Asahina) Marcelli & Benatti  
2012 *Bulbothrix pseudocoronata* (Gyeln.) Benatti & Marcelli  
2012 *Bulbothrix pseudofungicola* Benatti & Marcelli  
2012 *Bulbothrix silicisrea* Marcelli & Benatti  
2013 *Bulbothrix bulbillosa* Benatti, Spielmann & Bungartz  

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