

A review of the genus *Bulbothrix* Hale: the species with medullary salazinic acid lacking vegetative propagules

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Abstract

Descriptions are presented for the seven known *Bulbothrix* (Parmeliaceae, Lichenized Fungi) species with salazinic acid in the medulla and without vegetative propagules. *Bulbothrix continua*, previously considered as a synonym of *B. hypocraea*, is recognized as independent species. The current delimitations are confirmed for *B. enormis*, *B. hypocraea*, *B. meizospora*, *B. linteolocarpa*, *B. sensibilis*, and *B. setschwanensis*. New characteristics and range extensions are provided.

Key words

Parmeliaceae, *Parmelinella*, norstictic acid, bulbate cilia

Introduction

The genus *Bulbothrix* Hale was proposed for the group of species called *Parmelia* Series *Bicornutae* (Lynge) Hale & Kurokawa (Hale 1974). This group is characterized by small, lacinate and usually adnate thalli, bulbate marginal cilia, an upper cortex containing atranorin, with pored epicortex, without pseudocyphellae, with isolichenan in the cell walls, simple to branched cilia and rhizinae, smooth to coronate apothecia, hyaline unicellular ellipsoid to bicornute ascospores 5.0–21.0 × 4.0–12.0 μm, and bacilli-form to bifusiform conidia 5.0–10.0 × 0.5–1.0 μm (Hale 1976a, Elix 1993, Elix 1994).

Crespo et al. (2010) present a revised generic concept of Parmelioid lichens based on molecular, morphological and chemical evidences. They show that *Bulbothrix* is nested in the *Parmelina* clade and some species are grouped with *Parmelinella*, making

the genus paraphyletic. The *Bulbothrix* species with salazinic acid, the subject of this study, may actually belong to the genus *Parmelinella*, or even be another small genus closely related to it (Divakar et al. 2006, Crespo et al. 2010). A new generic arrangement of *Bulbothrix* species is not the subject of the present study, however. The type species of *Bulbothrix* is *B. semilunata* (Lynge) Hale, characterized by narrow sublinear laciniae, apically branched cilia and rhizines, coronate apothecia, and bicornute ascospores. This species also lacks medullary substances.

During an unpublished revision of the genus *Bulbothrix* (Benatti 2010) the type specimens and additional material of all *Bulbothrix* species were studied. They appeared to have cilia with hollow basal bulbs, which contain differentiated cells and a characteristic oily substance (Hale 1975, Feuerer and Marth 1997, Benatti 2011). The first published part of Benatti's (2010) thesis concerns new combinations of four species, *Hypotrachyna tuskiiformis* (Elix) Benatti & Marcelli, *Parmelinopsis pinguiacida* (Louwhoff & Elix) Marcelli & Benatti, *P. subinflata* (Hale) Benatti & Marcelli and *Parmotrema yunnanum* (Sheng L. Wang, J.B. Chen & Elix) Marcelli & Benatti, previously placed in *Bulbothrix* (Benatti and Marcelli 2010) and excluded due to the lack of true bulbate cilia. The second part treats the species containing medullary norstictic and protocetraric acids (Benatti 2012). This paper is the next in the series and presents the results for the seven species with medullary salazinic acid [*Bulbothrix continua* (Lynge) Hale, *B. enormis* (Hale) Krog, *B. hypocraea* (Vainio) Hale, *B. linteolocarpa* Marcelli, *B. meizospora* (Nylander) Hale, *B. sensibilis* (Steiner & Zahlbruckner) Hale and *B. setschwanensis* (Zahlbruckner) Hale], that do not form isidia, soredia, lacinulae or pustules.

For a comprehensive understanding and easy assessment of all the data on the review of this genus comprising ca. 60 species gathered in an unpublished review study by Benatti (2010), is planned to be divided in six parts. The different parts are as follows: (I) the species containing medullary norstictic and protocetraric acid (already published see Benatti 2012), (II) the species containing salazinic acid lacking vegetative propagules (this paper), (III) the species containing salazinic acid with vegetative propagules, (IV) the species containing fatty acids or no medullary substances, (V) the species containing the gyrophoric/lobaric/lecanoric acids lacking vegetative propagules, and (VI) the species containing the gyrophoric/lobaric/lecanoric with vegetative propagules, ultimately resulting in a synthesis of the whole genus followed by a world wide key.

The descriptions of the species treated here can also be found somewhere else in the literature such as Hale (1976a). Nonetheless, the present study includes detailed examinations (morphological and chemical) of all the type species; I mean the types of all the synonymous names under a species; details of basal bulb of the cilia including characteristics of oily substances; and detailed discussion. Additionally, I examined hundreds of specimens distributed world wide, which are not mentioned in previous studies. I found worth providing detailed species descriptions here because I found several specimens erroneously identified in dozens of herbaria including some at genus level, for example *Bulbothrix* specimens was identified as *Hypotrachyna*, *Parmelinella*

or *Parmelinopsis*. Perhaps, this could be due to short descriptions available in the literature that may lead to misinterpretation of species names or their characteristics. The review in this level of detail also aims to help as much as possible giving very detailed descriptions including fine morphological feature not elsewhere found on literature that might even help correlating with molecular data. This is not restrict for the species treated here, but to the whole genus, as all papers will aim to explain the peculiar problems regarding each species group.

Material and methods

Type material and additional specimens were studied from BM, FH, GLAM, H, HUFSCAr, LD, LG, M, NY, S, SP, TNS, TUR, US, W, and WU, originating from Asia, Africa, and South America. Added is a considerable material collected in Brazil 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 methodology and conventions are detailed in Benatti (2012). Bulbs on cilia, rhizines, apothecia and other thallus parts were checked using the clarification method following Benatti (2011). 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 left with the specimens. The chemical constituents of the types were examined by Prof. J. A. Elix (Canberra) using high performance liquid chromatography (HPLC), following the methods described in Elix et al. (2003).

The presence of salazinic acid is indicated by a K+yellow→dark red spot test reaction, not unlike that of norstictic acid, but turning darker red even with different KOH concentrations (10% and 30%) in *Bulbothrix* specimens. It also reacts P+ yellow, and does not react to C or KC, neither reacts to UV light. Its presence can also be indicated by the formation of bundles of thin elongated crystals of a deep reddish color, visible under a light microscope after the transfer of a small piece of the thallus or of the apothecia onto a microscope slide and dropping the reagent on the fungal material. However, as compared with the much more obvious crystals of norstictic acid (Benatti 2012), the crystals of salazinic acid need a higher concentration of the substance and take longer to crystallize.

The species selected for comparisons are those who show close morphological or chemical similarities, and those most often compared by other authors due to peculiar characteristics (e.g., Elix 1994, Divakar and Upreti 2005, Hale 1976a, Marcelli 1993, Sérusiaux 1984, Swinscow and Krog 1988). The species containing soredia, isidia and pustulae [*Bulbothrix australiensis* Hale, *B. decurtata* (Hale & Kurokawa) Hale, *B. imshaugii* (Hale) Hale, *B. isidiza* (Nylander) Hale, *B. microscopica* Elix, *B. pustulata* (Hale) Hale, *B. subglandulifera* (Hue) Hale, *B. subscortea* (Asahina) Marcelli & Benatti, *B. subtabacina* (Elix) Elix and *B. tabacina* (Montagne & Bosch) Hale] are the subject of a future treatment.

Results and discussion

The study confirmed all seven previously known species containing salazinic acid that do not form vegetative propagules or pustules. Four species, *Bulbothrix continua*, *B. linteolocarpa*, *B. sensibilis* and *B. setschwanensis* are corticolous, while *B. enormis* is saxicolous. *Bulbothrix hypocraea* and *B. meizospora* are predominately corticolous, rarely saxicolous and in the case of *B. meizospora*, also rarely terricolous. All species are described in detail and discussed below.

Table 1 summarizes the main characteristics (usual averages found) used for differentiate the species in this paper and most commonly accepted in literature (see e.g. list in the Introduction).

Table 1. Comparative diagnostic characteristics of *Bulbothrix* species containing salazinic acid that do not reproduce by vegetative propagules. The data refer to the most typical range found.

Species	Laciniae width	Maculae	Marginal bulb size	Lower cortex color	Ascospore size
<i>B. continua</i>	1–2.5 mm	absent	ca. 0.05–0.15 mm wide	brown to pale brown	9.0–13.5 × 5.0–7.5 μm
<i>B. enormis</i>	1.5–8 mm	absent	ca. 0.05–0.20 mm wide	mostly pale brown	7.0–11.5 × 5.0–7.0 mm
<i>B. hypocraea</i>	1–2.5 mm	present (abundant)	ca. 0.10–0.30 mm wide	pale brown to ivory	7.0–14.0 × 5.0–8.0 mm
<i>B. linteolocarpa</i>	< 1 mm	absent	ca. 0.05–0.10 mm wide	pale brown	9.0–16.0 × 6.5–8.0 μm
<i>B. meizospora</i>	1.5–6 mm	present (weak)	ca. 0.10–0.30 mm wide	black center and most margins	10.0–22.0 × 7.5–14.0 μm
<i>B. sensibilis</i>	1.5–5 mm	present (variable)	ca. 0.05–0.25 mm wide	black center with brown margins	7.0–13.0 × 5.0–7.0 μm
<i>B. setschwanensis</i>	1–5 mm	absent	ca. 0.05–0.25 mm wide	pale brown center and margins	10.0–19.0 × 6.0–10.0 μm

The species

***Bulbothrix continua* (Lyngé) Hale. Phytologia 28(5): 480. 1974.**

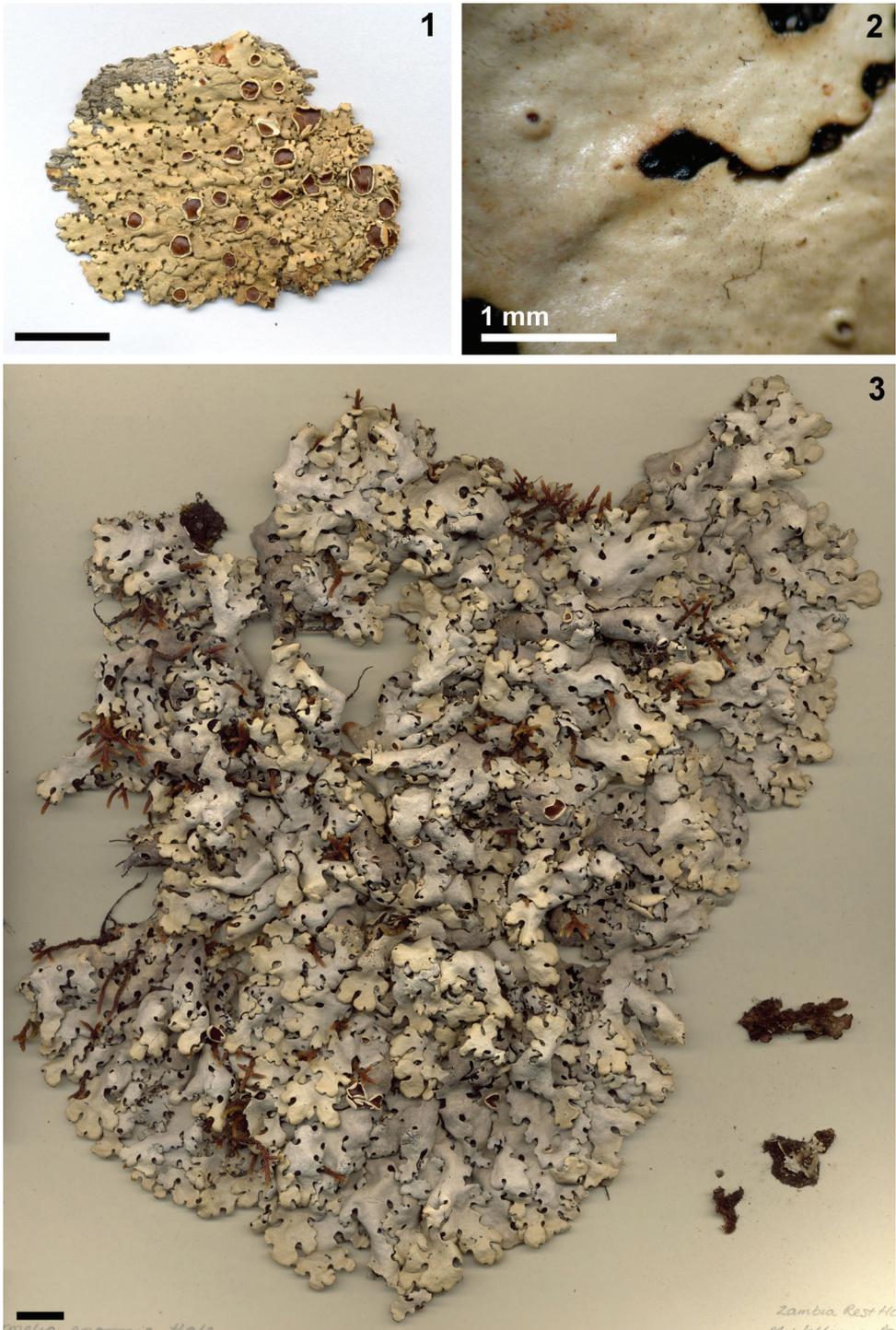
Mycobank: MB 341595

Figures 1–2

Basionym: *Parmelia continua* Lyngé. Arkiv för Botanik 13(13): 109. 1914.

Holotype. Brasiliae civit Matto Grosso, Serra da Chapada, Buriti, leg. Malme s.n., 19-VI-1894 (S!).

Description. Thallus subirregularly lacinate, grayish green in the herbarium, up to 3.8 cm diam., subcoriaceous, corticolous; upper cortex 15.0–22.5 μm thick, algal layer 25.0–37.5 μm thick, medulla 67.5–85.0 μm thick, lower cortex 20.0–25.0 μm thick.



Figures 1–3. 1 Holotype of *Bulbothrix continua* 2 Detail of the shiny emaculate upper cortex 3 Holotype of *Bulbothrix enormis*. Scale bars = 1 cm (1,3), 1 mm (2).

Laciniae anisotomically to irregularly dichotomously branched, 0.8–1.9 (–2.3) mm wide, slightly imbricate, rarely becoming crowded at the center, adnate and adpressed, with flat, subtruncate apices; margins plane, smooth and sinuous to crenate, entire, occasionally sublacinulate; axils oval. Upper surface smooth and continuous, becoming rugose and irregularly cracked in some parts; laminal ciliary bulbs absent. Adventitious marginal lacinulae scarce and restrict to older parts, short, 0.2–0.5 × 0.1–0.5 mm, plane, simple to rarely furcate; apices truncate; lower side concolorous to the lower marginal zone. Maculae absent. Cilia black, without or with simple apices, commonly bent downwards, 0.05–0.40 × ca. 0.03 mm, with semi-immersed to emergent bulbate bases 0.05–0.15 (–0.25) mm wide, abundant throughout the margin spaced 0.05–0.10 mm from each other to contiguous, solitary or in small groups at the crenae and axils, scarce at the apices of the laciniae. Soredia, Pustulae and Isidia absent. Medulla white. Lower surface brown to pale brown, shiny to opaque, smooth to subrugose, weakly papillate, moderately rhizinate. Marginal zone brown to pale brown, indistinct from the center, shiny to opaque, smooth, weakly papillate, weakly to densely rhizinate. Rhizinae black to pale brown, partially white or with whitish apices when close to the margins, simple or sometimes irregularly branched, commonly with bulbate bases, 0.10–0.65 × 0.03–0.10 mm, frequent but becoming abundant close to the margins or scarce at some other parts, sometimes agglutinated, evenly distributed. Apothecia concave to plane or convex, adnate to sessile and distended over the laciniae, 0.4–3.7 mm diam., laminal; margin smooth to subcrenate, ecoronate; amphithecium smooth, without ornamentations. Disc pale brown, epruinose, imperforate; epithecium 15.0–20.0 mm high; hymenium 50.0–62.5 μm high; subhymenium 15.0–22.5 μm high. Ascospores ellipsoid to oval, 9.0–13.5 × 5.0–7.5 μm; epispore ca. 1.0 mm. Pycnidia common, laminal, immersed, with black ostioles. Conidia bacilliform 5.0–7.5 × 1.0 μm.

TLC/HPLC: cortical atranorin, medullary salazinic and consalazinic acids (see also Hale 1976).

Distribution. South America: Brazil: State of Mato Grosso (Lynge 1914). Here is reported new for the Brazilian State of São Paulo.

Additional specimens examined. Brazil, Mato Grosso State, Santa Anna da Chapada, Buriti Municipality, leg. G. O. Malme s.n., 19-IV-1894 (US). Idem, São Paulo State, 6 km SW of Jaboticabal, 21°35'S, 48°35'W, on trees in “cerradão” (savannah), leg. A. Fletcher 10108, 1-V-1975 (BM). Idem, São Manuel Municipality, Fazenda Palmeira da Serra, unofficial private cerrado (savannah) reserve, on tree trunk in the cerrado, leg. M. P. Marcelli & S. B. Barbosa 35232, 03-VI-2003 (SP, paratype of *B. vainioi*). Idem, Santa Rita do Passa Quatro Municipality, Fazenda Vassununga, km 259 of Anhanguera Highway, 760 m, transition from cerrado to “cerradão” (savannah), trees with signs of old burns, on a tree thin twig, leg. M. P. Marcelli & S. B. L. Morretes 16055, 21-IX-1978 (SP). Idem, Moji-Guaçu Municipality, Fazenda Campininha, Estação Biológica de Moji-Guaçu, illuminated, dry savannah, on tree thin twig, leg. M. P. Marcelli 15885, 29-VI-1979 (SP).

Comments. The holotype (Figs 1–2) consists of a small, entire thallus, in good condition. The material contains several apothecia at different stages of maturity with well developed ascospores, and some pycnidia. It is on a small piece of tree bark but

with the laciniae apices free from the substrate, and is not glued to cardboard. There is no trace of true maculae in the upper cortex or in the amphithecia, although the cortex is in fact somewhat pale and shiny.

Hale (1960) mentioned that '*Parmelia*' *continua* was an unusual member of the section *Hypotrachyna* Vainio, without soredia or isidia and producing salazinic acid, believing at first that it might be a non-isidiate variety of '*Parmelia*' *cinerascens* Lynge. Latter, Hale and Kurokawa (1964) included '*P.*' *continua* in the key for the '*Parmelia*' species that composed the Subsection *Bicornutae* Series *Bicornutae*, separating '*P.*' *continua* from '*P.*' *hypocraea* Vainio by the absence vs. presence of cortical maculae, respectively.

Shortly after the recombination of '*Parmelia*' *continua* into *Bulbothrix* (Hale 1974), Hale (1976a) placed *B. continua* in the synonymy of *B. hypocraea* (Vainio) Hale, without any explanation. Most probably, Hale decided to synonymize them because of their great morphological similarity. However, I am inclined to accept Hale's first interpretation (1974), since the presence of maculae implies a fundamentally different anatomic conformation of the medullary hyphae, as observed by Barbosa and Marcelli (2010, 2011) in the genus *Parmotrema*.

Compared with the specimens of *B. continua*, those of *B. hypocraea* are always quite maculate, and their thalli often form wider laciniae than those of *B. continua*. Hale (1976a) mentioned that the discs of the apothecia in *B. hypocraea* have a burnt amber color. However, Marcelli (1993) cited a disc color, shape and distribution of cilia different than those described by Hale, more similar to *B. continua*.

Bulbothrix linteolcarpa Marcelli differs by the much narrower laciniae, barely exceeding 0.5 mm, that are also more linear with contiguous cilia forming long apices. As they mature, apothecia of *B. linteolcarpa* continually adapt to the conformation of the surface, settling on the laciniae as if they were spreading over them. Two specimens of uncertain identity cited by Marcelli (1993) among the examined material of *B. linteolcarpa* were actually found to be of *B. continua*.

Bulbothrix sensibilis (Steiner & Zahlbruckner) Hale differs from *B. continua* equally by the presence of cortical maculae and moreover by the shiny black lower cortex with dark brown margins. *Bulbothrix setschwanensis* (Zahlbruckner) Hale differs by the larger laciniae (ca. 1.5–5.0 mm wide) and by the size of the ascospores (usually 12.0–19.0 × 7.0–10.0 µm).

***Bulbothrix enormis* (Hale) Krog. *The Lichenologist* 25(3): 299. 1993.**

Mycobank: MB 360209

Figure 3

Basionym: *Parmelia enormis* Hale. *Phytologia* 23(4): 344. 1972.

Synonym: *Parmelina enormis* (Hale) Hale. *Phytologia* 28: 482. 1974.

Holotype. Zambia, Zambia Rest House area, Nyika Plateau, 7600 ft., on granite rocks, M. Jellicoe s.n., VII-1968 (BM!, isotypes at TNS n.v. and US!).

Description. Thallus sublinearly to subirregularly sublaciniate, gray with dusky green distal parts in herbarium, up to 24.1 cm diam., coriaceous, saxicolous; upper cortex 15.0–22.5 μm thick, algal layer 52.5–80.0 μm thick, medulla 120.0–150.0 μm thick, lower cortex 15.0–25.0 μm thick. Laciniae isotomically or anisotomically to irregularly dichotomously branched, (1.3–) 3.2–6.0 (–7.8) mm wide, imbricate to crowded, slightly to not adnate and loose, occasionally almost subcanaliculate, with involute to revolute or sometimes plane, subrounded to subtruncate apices; margins plane to subundulate or slightly involute, smooth and sinuous to occasionally subcrenate, entire, rarely little sublacinulate; axils oval. Upper surface smooth and continuous, rarely with some random irregular cracks; laminal ciliary bulbs absent. Adventitious marginal lacinulae scarce on random parts, short, 0.5–1.7 \times 0.3–1.1 mm, usually involute, simple or sometimes irregularly branched; apices truncate to subtruncate; lower side concolorous to the lower marginal zone. Maculae absent. Cilia black to dark brown, with simple to partially double or furcate apices, occasionally bent downwards, 0.10–1.20 (–1.80) \times ca. 0.05 (–0.10) mm, with semi-immersed to emergent bulbate bases 0.05–0.20 (–0.35) mm wide or partially not bulbate, sometimes disposed on a distinct black line, frequent to abundant throughout the margins, in small groups in the axils and adjacent parts spaced 0.10–0.40 mm from each other, becoming absent or scarce at the apices of the laciniae and adjacent parts. Soredia, Isidia and Pustulae absent. Medulla usually white, but pinkish in some random parts and below the hymenial discs. Lower surface pale brown, occasionally with random small dark brown or black spots, shiny, smooth, moderate to densely rhizinate. Marginal zone brown, indistinct from the center or sometimes interrupted by blackish spots, shiny, smooth, weakly papillate, gradually becoming rhizinate following the center. Rhizinae black to variably brown, occasionally whitish or with whitish apices, simple to occasionally furcate or irregularly branched, without bulbate bases or with subtle basal or displaced bulbs, 0.20–1.80 (–2.30) \times 0.05–0.10 mm, frequent to abundant, evenly distributed. Apothecia subconcave to urceolate or occasionally plane, becoming folded when old, adnate to substipitate, 1.1–10.0 mm diam., laminal to submarginal, ecoronate; margin smooth to subcrenate and fissured; amphithecium smooth, without ornamentations. Disc brown to dark brown, epruinose, imperforate; epithecium 7.5–17.5 μm high; hymenium 20.0–55.0 μm high; subhymenium 12.5–22.5 μm high. Ascospores ellipsoid to oval or subrounded, 7.0–11.5 \times 5.0–7.0 μm ; epispore (0.5–) 1.0–1.5 mm thick. Pycnidia laminal to submarginal, frequent, immersed, with brown or black ostioles. Conidia bacilliform to weakly or distinct bifusiform 5.0–8.0 \times 0.75 μm .

TLC/HPLC: cortical atranorin and chloroatranorin, medullary salazinic and consalazinic acids (see also Hale 1972, 1976b).

Distribution. Africa: Zambia (Hale 1972, 1976b, Krog 1993), Malawi, and Tanzania (Krog 1993).

Additional specimen examined. Zambia, Zambia Rest House area, Nyika Plateau, leg. M. Jellicoe s.n., IV-1969 (FH).

Comments. The holotype consists of a large specimen more than 20 cm in diameter, glued to board, in excellent condition and containing several apothecia and pyc-

nidia. There are some loose fragments from 3 to 10 cm diam., allowing visualization of the lower cortex details. The isotype from US consists of several loose fragments such as those with the holotype, also in good condition, with mature apothecia and pycnidia. There are no remains of the rocky substrate of where the materials were collected, indicating that the thalli were not strongly adhered to the substrate.

Originally, Hale (1972) did not notice the presence of bulbs in the cilia of this species, and recombined it (Hale 1974) into *Parmelina* Hale without any comment. Hale (1972) first commented that the presence of cilia located in the axils would situate it in Section *Imbricaria*, even though he said that the species superficially resembled a *Hypotrachyna* species due the shape of the laciniae, what he again emphasized in the genus monograph (Hale 1976b). Although the general appearance of the thalli indeed resembles a large specimen of *Hypotrachyna* as he said, the presence of marginal cilia and the simple rhizines easily differentiate *B. enormis* from this other genus.

Most of the cilia seen in the specimens studied are bulbate, but some of them are not, even including some of the largest cilia. However, the bulbs have the typical anatomical structure of *Bulbothrix* species, with an oily substance and idioblasts cells (Hale 1975, Feuerer and Marth 1997, Benatti 2011). They vary from the more typical globose aspect to an oval shape, stretching following the growth and detachment of the apices. Some have slightly extended bases, perhaps an early stage of development of the cavity.

While Hale (1972, 1976b) mentioned an overall brown lower cortex, it should be noticed that although this is the predominant color, darker or even blackish spots may occur, occasional and randomly scattered (these were not seen in the FH specimen). The rhizines may also vary from paler to darker than the cortex, or be blackish.

Krog (1993) realized that this species did not fit well in the concept of the genus *Parmelina* due to the configuration of the lobes, and recombined it into *Bulbothrix*, having confirmed the presence of marginal bulbate cilia in the holotype and other specimens. The author realized that her material from Southern Africa fitted the description of *Parmelina enormis*, and she observed bulbate cilia in this species.

Bulbothrix hypocraea (Vainio) Hale and *B. setschwanensis* (Zahlbruckner) Hale were compared to *B. enormis* by Krog (1993) because they shared a pale brown lower cortex, simple rhizines and medullary salazinic acid. The author distinguished these species by their less robust thalli, usually adnate on bark, with crenate lobes with a more or less irregular pattern of branching. Besides the differences mentioned by Krog (1993), *B. hypocraea* also has narrower laciniae ca. 1.5–4.0 mm wide, an evidently maculate upper cortex, overall clearly bulbate cilia with short apices that appear solitary at the crenae and axils of the laciniae. *Bulbothrix setschwanensis* also differs by the narrower laciniae (ca. 1.0–3.5 mm wide), cilia in crenae or axillary with overall globose, evident bulbate bases and short apices, and by the larger ascospores (12.0–19.0 × 7.0–10.0 μm).

Bulbothrix haleana Sérusiaux (LG!, US!) differs by the thallus aspect, with narrow subirregular laciniae 1.0–3.5 mm wide, the overall globose and always evidently bulbate cilia with shorter apices, and by the smaller ascospores 5.0–9.0 × 4.0–7.0 μm. Further it contains norstictic acid, rather than salazinic acid as stated in the original description (Benatti 2012).

Another relatively similar species, *B. meizospora* (Nylander) Hale, also differs by the narrower laciniae (ca. 1.5–4.0 mm wide), larger ascospores (12.5–22.0 × 9.0–14.0 µm) and a black lower cortex with brown margins.

Hale (1972) compared *Bulbothrix enormis* also to *P. usambarensis* Steiner & Zahlbruckner [= *Pseudoparmelia usambarensis* (Steiner & Zahlbruckner) Krog & Swinscow (REN!, lectotype)], another similar African saxicolous species, but this species forms isidia, has a black lower cortex, and although he cited eciliate margins, it does have marginal cilia, just not in abundance.

***Bulbothrix hypocraea* (Vain.) Hale. Phytologia 28(5): 480. 1974.**

Mycobank: MB 341600

Figures 4–9

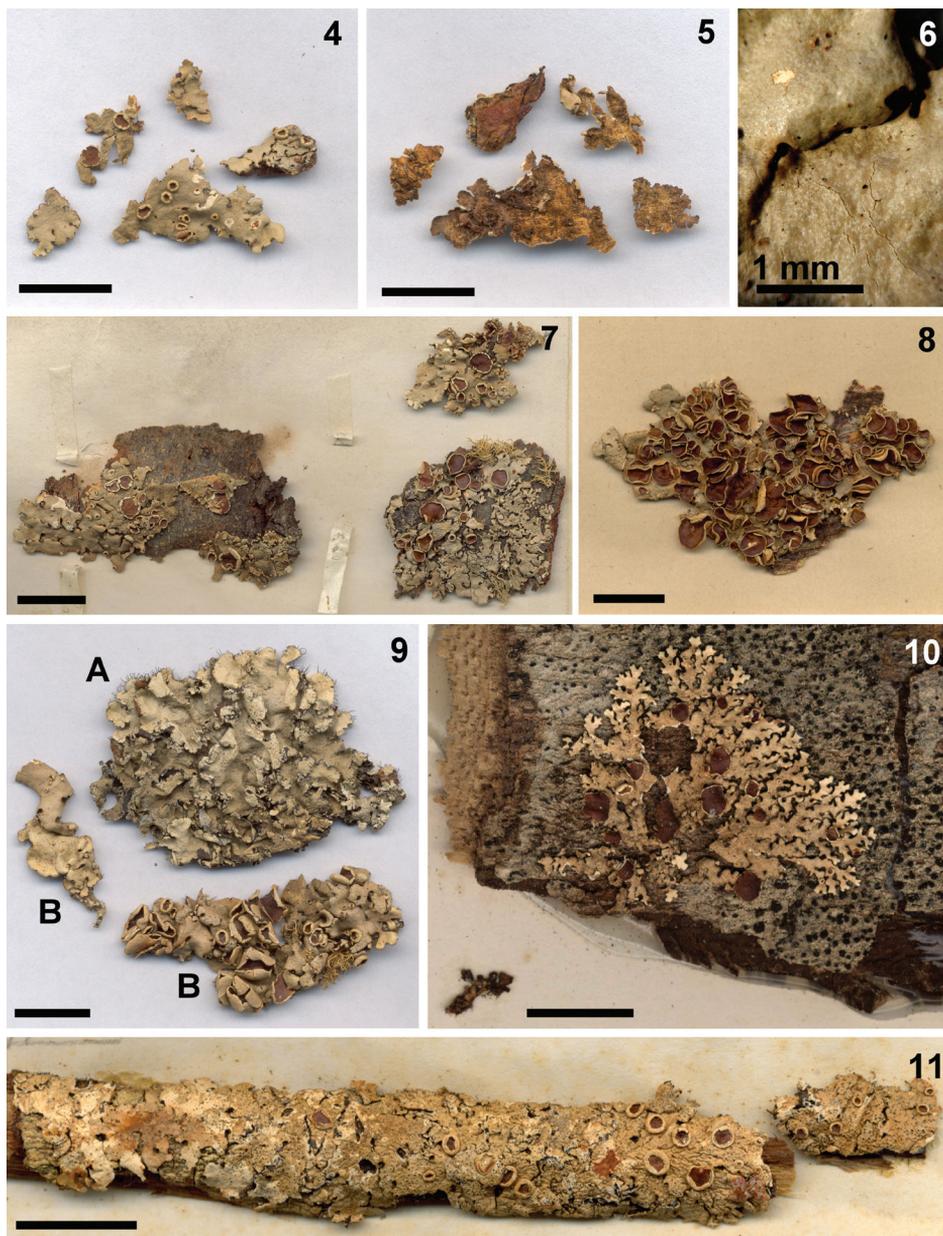
Basionym: *Parmelia hypocraea* Vainio. Catalogue of the African Plants Collected by F. Welwitsch 2(2): 400. 1901.

Synonyms: ? *Parmelia leptascea* Stein. & Zahlb. Botanische Jahrbücher für Systematik 60: 514. 1926.

Parmelia proboscidea var. *saxicola* Cengia Sambo. Nuovo Giornale Botanico Italiano 45: 380. 1938.

Lectotype. Angola, Huilla (3800 ad 5500 ped. s. m.), ad corticem arborum Leguminosarum in sylvis densis juxta flumen Monino, ca. 14°16'S, leg. Welwitsch 32 pro parte, IV-1860 (TUR-V!, duplicate at BM!).

Description. Thallus sublinearly to subirregularly laciniate to sublaciniate, light dusky gray in the herbarium, in fragments up to 5.2 cm diam., coriaceous to subcoriaceous, corticolous or rarely saxicolous; upper cortex 15.0–25.0 µm thick, algal layer 25.0–42.5 µm thick, medulla 75.0–125.0 µm thick, lower cortex 12.5–20.0 µm thick. Laciniae anisotomically dichotomously to irregularly branched, (0.5–) 0.9–2.6 (–3.0) mm wide, contiguous to slightly imbricate, rarely crowded at the center, ±adnate and loosely adpressed, with plane to slightly involute or revolute, truncate, subtruncate or subrounded apices; margins plane to subplane, smooth to sinuous and subcrenate or subirregular, entire to slightly incised, not lacinulate; axils oval to irregular. Upper cortex mostly continuous, occasionally with some irregular cracks on older parts, smooth to subrugose; laminal ciliary bulbs absent. Adventitious marginal lacinulae absent, even on old parts. Maculae usually distinct, punctiform to efigurate, laminal on the thallus or on the amphithecia of the apothecia. Cilia black or rarely brown, without or with simple apices, often bent downwards, 0.05–0.65 × 0.03–0.05 mm, with semi-immersed to emergent, bulbate bases (0.05–) 0.10–0.30 mm wide (these partially enlarged or occasionally absent), frequent throughout the margins, solitary or in small groups in the crenae and axils spaced 0.05–0.20 mm from each other to occasionally contiguous, becoming absent or scarce at the apices of the laciniae and adjacent parts, usually absent or scarce in the apices of the laciniae and adjacent



Figures 4–11. 4 Lectotype of *Bulbothrix hypocraea* 5 Detail of the lower side of the lectotype 6 Detail of the maculate upper cortex 7 Duplicate of *Bulbothrix hypocraea* 8 Holotype of *Parmelia leptascea* 9 Lectotype of *Parmelia proboscidea* var. *saxicola* (marked B) 10 Holotype of *Bulbothrix linteolocarpa* 11 Holotype of *Bulbothrix meizospora*. Scale bars = 1 cm (4, 5, 7, 8, 9, 10, 11), and 1 mm (6).

parts. Soredia, Isidia and Pustulae absent. Medulla white. Lower surface pale brown to ivory, opaque to slightly shiny, smooth, moderately rhizinate, sometimes up to the margins. Marginal zone indistinctly delimited from the center to slightly attenuate,

0.5–2.0 mm wide, pale brown to ivory, opaque to slightly shiny, smooth, weakly papillate, often rhizinate. Rhizinae ivory or light to dark brown, occasionally blackish, whitish or with white apices, simple or sometimes irregularly branched, partially with blackish bulbate bases or displaced bulbs, $0.10\text{--}0.80$ ($\text{--}1.10$) \times $0.05\text{--}0.10$ mm, frequent, sometimes agglutinated, evenly distributed. Apothecia subconcave to subplane, becoming folded when old, sessile to adnate to substipitate, $0.3\text{--}8.2$ mm diam., laminal to submarginal, ecoronate; margin subcrenate; amphithecia smooth occasionally fissured, without ornamentations. Disc pale brown to reddish brown, epruinose, imperforate; epithecium $7.5\text{--}17.5$ μm high; hymenium $32.5\text{--}70.0$ μm high; subhymenium $10.0\text{--}37.5$ μm high. Ascospores ellipsoid to oval or subrounded, $7.0\text{--}14.0$ \times (5.0--) $6.0\text{--}8.0$ μm ; epispore ca. 1.0 mm. Pycnidia laminal, frequent mainly at the distal parts of the laciniae, immersed, with black ostioles. Conidia baciliform to weakly bifusiform (4.0--) $5.0\text{--}9.0$ \times 0.75 μm .

TLC/HPLC: cortical atranorin and chloroatranorin, medullary salazinic and consalazinic acids (see also Hale 1976).

Distribution. Africa (Zahlbruckner 1926): Angola (Vainio 1901, Hale 1976a), South Africa (Hale 1976a), Kenya, Tanzania (Sambo 1938, Swinscow and Krog 1988), Uganda (Hale 1976a, Swinscow and Krog 1988), Rwanda (Killmann and Fischer 2005, Bock et al. 2007), Rhodesia (nowadays Zimbabwe), Zaire, and Zambia (Hale 1976a). South America: Venezuela (López-Figueiras 1986, Marcano et al. 1996,) Brazil – States of Minas Gerais, Mato Grosso (Hale 1976a), Paraná (Eliasaro and Adler 1997, Eliasaro 2001), São Paulo (Hale 1976a, Marcelli 1993) and Tocantins (Eliasaro and Adler 1997).

Additional specimens examined. Africa, Bakoba am Victoriasee, auf Baumrinden, Schröder 319 (W!, holotype of *Parmelia leptascea*). Rhodesia (Zimbabwe), District Salisbury, Chindamora Reserve, Ngomakukira, epiphyte on *Julbernardia globiflora*, *Swatzia madagascariensis* etc., leg. H. Wild 5806, 10-VI-1962 (NY). Kenya, K4, Nth. Nyeri ($1^{\circ}30'S$, $37^{\circ}30'E$), Lew Downs Ranch, 0 km W of Isiolo, Acacia woodland, leg. H. Ballev 660c, 4-XII-1981 (NY). Tanzania, Mahulo, Kipengere, loc. c. s. on rock, with *Usnea densirostra*, very mixed, leg. Eusébio 13 bis, 02-III-1935 (FI!, lectotype of *Parmelia proboscidea* var. *saxicola*, designate here as “B”). Brazil, Mato Grosso State, Serra do Roncador, riverine forest, 46 km north of Chavantina, Rio Vau, epiphyte, abundant, leg. G. T. Prance & N. T. Silva 59380A, 11-X-1964 (NY). Idem, Minas Gerais State, Lagoa Santa, leg. Warming s.n (M). Idem, São Paulo State, Brotas Municipality, NW side of intersection of road to Campo Alegre with the Brotas-Itirapina road, arboreal semi-closed cerrado woodland, $22^{\circ}17'S$, $47^{\circ}56'W$, 750 m, leg. G. Eiten et al. 2976c, 16-VI-1961 (US). Idem, Santa Rita do Passa Quatro Municipality, fazenda Vassununga, km 259 of Anhanguera highway, on woody stem of vine, leg. M. P. Marcelli & B. L. Morretes 15628, 03-VI-1978 (SP). Idem, São Manuel Municipality, Fazenda Palmeira da Serra, non official particular cerrado (savannah) reserve, on tree trunk at the woods, leg. M. P. Marcelli & S. B. Barbosa 35680, 03-VI-2003 (SP).

Comments. The lectotype (Fig. 4–5) consists of three small fragments on bark glued to cardboard, and some smaller fragments packed in paper, free of substrate. The duplicate (Fig. 7) consists of three fragments, all on bark, one of them glued to cardboard (fragments free from substrate were used to see the features of the lower cortex). The type material has several pycnidia, restricted to the distal parts of the laciniae.

Bulbothrix hypocraea has the most strongly maculate thalli of the genus (Fig. 6). However, in very old herbarium material, such as the type, the maculae may become difficult to be seen due to the darkening of the upper cortex and the staining of the medulla by the oxidized salazinic acid. In this case, a bright illumination and wetting the thalli make the maculae more visible.

Most cilia have an evident bulbate base, their apices are usually bent downwards and sometimes barely visible from above. Some cilia, however, have no basal bulb, but just a thickened, tapering base (possibly an early stage in the development of the cavity).

The color of the lower cortex varies from brown to ivory or cream, the marginal zone being slightly darker than the center (Fig. 5). The ivory color is the least common, and is similar to that observed in the lower margin of other Parmeliaceae (like *Parmotrema* species) which are white ivory when fresh, eventually changing color after time in the herbarium.

The swellings seen in the rhizines along its length are not actually endociliary pycnidia, as first suspected by Marcelli (1993), but basal or displaced bulbs. No conidia were found inside, but instead an oily substance like the one found in the marginal cilia. These structures have been noted already by Jungbluth (2006), who also called them bulbs. The color of the rhizines is somewhat variable, as in some thalli darker rhizines are commoner while in others these are of lighter tones. The bulbs are more difficult to see in blackish rhizines, since in this species they are usually thick.

Vainio (1901) mentioned a whitish color for the upper cortex (which suggests that the maculae of the type material were much more evident when the specimen was collected). He described the laciniae with a larger width (1.5–5.0 mm wide) than seen here. Hale (1976a) described *B. hypocraea* with a more similar laciniae shape, branching pattern and width (1–3.5 mm) like was seen here.

The ascospore measurements provided by Hale (1976a), Swinscow and Krog (1988), Marcelli (1993), Eliasaro (2001), and Jungbluth (2006) do not vary significantly and are in agreement with those of Vainio (1901) and those obtained here.

The description by Eliasaro (2001) has narrower laciniae compared to others (0.5–1.0 mm wide), but agrees in all other characteristics. Eliasaro reports occasional small amounts of norstictic acid in her specimens. This is probably contamination, since it was not reported by other authors and not found in the specimens studied.

Swinscow and Krog (1988) described African material of *B. hypocraea* that deviated by being emaculate or weakly maculate, with cilia often seen only as “black nodes” in the margins and with ascospores 8.0–10.0 × 3.0–5.0 μm, including some saxicolous specimens. From their perspective, it is close to the type of *Parmelia leptascea* Zahlbruckner and Steiner (W!). Unfortunately, this material was not sent on loan from O

for comparison, although requested several times. The authors present an illustration showing small cilia composed solely of the bulbs. Jungbluth (2006) supposed that these specimens might belong to a different taxon, for which the name *P. leptascea* might be available as seen here. Indeed no marginal cilia in the *P. leptascea* holotype (Fig. 8) have apices, even the most developed, usually restricted only to bulbs. These are also more abundant than those seen in typical specimens of *B. hypocraea*. However, besides the saxicolous habit, the laciniae usually crowded and with a larger maximum width, and the cilia aspect, no other significant differences were found with *B. hypocraea*, although the maculae are evident despite the dark tone acquired in herbarium. The variations found may be merely due to the substrate. More material is needed for a decision about the status of this material and a proposition of a new combination regarding *Parmelia leptascea*.

The type collection of *Parmelia proboscidea* var. *saxicola* Cengia Sambo (FI!) consists of a ciliate *Parmotrema* specimen with submarginal, pustular soralia, and two fragments of *B. hypocraea* (Fig. 9, marked B) that make up the majority of the collection. Therefore the latter are appointed here as the lectotype, as it is in accordance to the species protologue. The comments of Cengia Sambo (1938) suggest that she did not realize that the parts were from two different species. The author did not describe the material in detail, only commenting that the laciniae were variable, the smaller thalli being so because of being saxicolous.

Bulbothrix setschwanensis (Zahlbruckner) Hale differs by the absence of cortical maculae and by larger ascospores $12.0\text{--}19.0 \times 6.0\text{--}9.0 \mu\text{m}$. Hale (1976a) distinguished this species from *B. hypocraea* in his key also by the width of the laciniae, but although there is a tendency for specimens of *B. setschwanensis* to have wider laciniae, there are specimens with laciniae the same width typically found in specimens of *B. hypocraea*, such as the holotype. Basically, the largest laciniae of *B. hypocraea* are of about the same width as the smallest of *B. setschwanensis*. The absence of maculae and the spore size are reliable characters to differentiate between the two species.

Bulbothrix linteolocarpa Marcelli was compared to *B. hypocraea* by Jungbluth (2006). It differs clearly by the much narrower linear laciniae $0.2\text{--}0.5\text{--}(0.8)$ mm wide, by the emaculate upper cortex, and by the cilia with smaller bulbate bases and longer apices. The apothecia are also different in shape, being flatter and usually stretched over the laciniae.

Among other similar species, *Bulbothrix sensibilis* (Steiner & Zahlbruckner) Hale was compared to *B. hypocraea* by Hale (1976a) and Jungbluth (2006), and it differs by the black lower cortex with brown margins and by the weaker maculae of the upper cortex. *Bulbothrix subcoronata* (Müller Argoviensis) Hale (G!) was compared to *B. hypocraea* by Eliasaro (2001). The type material differs by a black lower cortex with brown margins, coronate apothecia containing smaller ascospores ($5.0\text{--}7.5 \times 4.0\text{--}5.5$ mm) and medullary norstictic acid. *Bulbothrix meizospora* (Nylander) Hale was compared by Jungbluth (2006), and differs by the weaker maculae of the upper cortex, a black lower cortex with brown or black margins, and by the larger ascospores ($12.0\text{--}22.0 \times 9.0\text{--}14.0 \mu\text{m}$).

***Bulbothrix linteolocarpa* Marcelli. Acta Botanica Brasilica 7(2): 42. 1993.**

Mycobank: MB 458790

Figure 10

Holotype. Brazil, Mato Grosso State, between Jaciara and São Vicente, km 313 of BR-364 highway, ca. 100 km ESE of Cuiabá, cerradão (savannah), on tree trunk, leg. Marcelli 8446, 2-VII-1980 (SP!).

Description. Thallus sublinear laciniate, dusky gray in the herbarium, up to 2.6 cm diam., subcoriaceous, corticolous; upper cortex 20.0–30.0 μm thick, algal layer 55.0–75.0 μm thick, medulla 25.0–35.5 μm thick, lower cortex 10.0–15.0 μm thick. Laciniae irregularly to anisotomically dichotomously branched, 0.2–0.6 (–0.8) mm wide, contiguous to occasionally slightly imbricate, adnate and adpressed, with flat, truncate apices; margins flat, smooth to sinuous or subirregular, entire to slightly incised and rarely sublacinulate; axils oval to irregular. Upper cortex continuous, smooth to subrugose; laminal ciliary bulbs absent. Adventitious marginal lacinulae scarce on older parts, short, 0.1–0.6 \times 0.05–0.20 mm, plane, simple; apices truncate; lower side concolor to the lower marginal zone. Maculae absent. Cilia black to brown, with simple to partially furcate apices, often bent downwards, 0.05–0.45 \times ca. 0.03 mm, with semi-immersed to emergent bulbate bases ca. 0.05–0.10 mm wide, frequent along the margins, spaced 0.5–1.0 mm from each other rarely becoming contiguous at the axils, usually absent or scarce on the apices of the laciniae. Soredia, Isidia and Pustulae absent. Medulla white. Lower surface pale brown, shiny, smooth, weakly papillate, moderately rhizinate. Marginal zone pale brown, slightly darker than the center, shiny, attenuate, 0.5–1.0 mm wide, smooth, weakly papillate, slightly rhizinate. Rhizinae light to dark brown or almost blackish, simple to occasionally furcate or irregularly branched, often with dark basal or displaced bulbs, 0.05–0.60 \times ca. 0.03–0.05 mm, frequent, becoming scarce at some parts, partially agglutinated, evenly distributed. Apothecia subconcave, becoming plane or convex, stretching over the laciniae while maturing, adnate, 0.3–3.4 mm diam., laminal, ecoronate; margin smooth to incised and subcrenate; amphitecium smooth, without ornamentations. Disc brown, epruinose, imperforate; epithecium 12.5–20.0 mm high; hymenium 37.5–45.0 μm high; subhymenium 15.0–20.0 μm high. Ascospores ellipsoid to oval, (9.0–) 10.0–16.0 \times 6.5–8.0 μm ; epispore ca. 1.0 μm . Pycnidia not found.

TLC/HPLC: cortical atranorin and chloroatranorin, medullary salazinic, consalazinic and secalonic A acids (label from J. A. Elix with the holotype, 19-VII-1995).

Distribution. South America. Brazil – States of Mato Grosso and São Paulo (Marcelli 1993).

Additional specimens examined. Brazil, Mato Grosso State, between Jaciara and São Vicente, ca. 100 km ESSE of Cuiabá, 750 m alt., on thin twig at the cerrado (savannah), leg. M.P. Marcelli 8445, 02-VII-1980 (SP). Idem, São Paulo State, Moji-Guaçu Municipality, Fazenda Campininha, Estação Biológica de Moji-Guaçu, illuminated and dry cerradão (savannah), on thin twig, leg. M.P. Marcelli 15812, 07-XII-1976 (SP). Idem, Santa Rita do Passa Quatro Municipality, fazenda Vassununga,

km 259 of the Anhanguera Highway, 760 m alt., transition from cerrado to cerrado (savannah), trees with signs of old burnings, on tree thin twig, leg. M.P. Marcelli & SB. L. Morretes 15626, 23-VI-1978 (SP). Idem, São Carlos Municipality, Campus of the Universidade Federal de São Carlos - UFSCar, cerrado (savannah), on a wooden fence near a firebreak, 22°1'S, 47°53'W, alt. 855 m, on *Eucalyptus* sp. trunk, leg. G. G. Batista & M. N. Benatti 115B, 04-IX-2006 (HUFSCar).

Comments. The holotype (Fig. 10) consists of small thalli about 2.5 cm diameter, in good condition, on tree bark and over a crustose lichen with blackened perithecia. It was necessary to detach some laciniae for proper observation of the lower cortex. The upper cortex is emaculate, and there are several apothecia with ascospores in different stages of maturation.

A peculiar anatomical characteristic is that the algal layer is always thicker than the medulla in all examined material of *B. linteolcarpa*, and usually appears to be in the middle of the medulla, separating it in two portions, instead of being situated in its upper portion just below the cortex.

Some of the specimens analysed by Marcelli (1993) were confirmed to have wider laciniae (1.0–2.5 mm), a darker brown lower cortex, cilia with very globose basal bulbs and longer apices, and simple rhizines simply without basal bulbs. These specimens, that the author suspected to belong to a similar but different taxon, are actually *B. continua* (Lyngé) Hale.

Bulbothrix continua (Lyngé) Hale is the closest species to *B. linteolcarpa* in overall characteristics. However, *B. linteolcarpa* has much narrower laciniae than *B. continua* (0.2–0.5 against 1.0–2.5 mm), cilia with smaller, less globose bulbate bases (0.05–0.10 mm vs. 0.05–0.25 mm), and always with apices that are also partially furcate, a darker lower cortex, and less abundant, more variably branched rhizines.

Marcelli (1993) compared *B. linteolcarpa* to *B. hypocraea* (Vainio) Hale and to *B. sensibilis* (Steiner & Zahlbruckner) Hale. As to *B. hypocraea*, see under that species. *Bulbothrix sensibilis* has larger laciniae (ca. 1.0–4.0 mm larg.) that are often imbricated or crowded, cilia without apices or with simple short apices, normally restricted to the crenae and axils of the laciniae, concave to urceolate apothecia, a black lower cortex with brown margins, and averagely smaller, often subrounded ascospores (7.0–12.0 × 5.0–7.0 µm).

An apparently common species on cerrado (savannah) areas, *Bulbothrix linteolcarpa* was mentioned by Mistry (1998) in an article on bioindicators of fires.

***Bulbothrix meizospora* (Nyl.) Hale. Phytologia 28(5): 480. 1974.**

Mycobank: MB 341605

Figures 11–14

Basionym: *Parmelia tiliacea* var. *meizospora* Nyl. Synopsis Methodica Lichenum 1: 383. 1860.

Synonyms: *Parmelia meizospora* (Nylander) Nyl. Flora 52: 292. 1869.

Parmelia amplexens Stirton. Scottish Naturallist 4: 201. 1878.

Bulbothrix vainioi Jungbluth, Marcelli & Elix. Mycotaxon 104: 59. 2008.

Holotype. India, Nilgherries Montains, Watt s.n. (H-NYL 35107!).

Description. Thallus subirregular laciniate to sublaciniate, dark dusky gray in the herbarium, up to 7.3 cm diam., subcoriaceous to submembranaceous, corticolous (rarely on rocks or soil); upper cortex 15.0–20.0 μm thick, algal layer 25.0–35.0 μm thick, medulla 85.0–110.0 μm thick, lower cortex 15.0–20.0 μm thick. Laciniae irregularly to almost anisotomically dichotomously branched, 1.6–6.1 mm wide, contiguous to slightly imbricate, becoming crowded at the center, \pm adnate and adpressed, with flat to slightly involute, subrounded to subtruncate or rarely truncate apices; margins flat to slightly involute, crenate to or irregular, entire, rarely sublacinulate; axils oval to irregular. Upper cortex smooth and continuous at younger parts, becoming rugose and irregularly cracked at older parts; laminal ciliary bulbs absent. Adventitious marginal lacinulae absent to scarce on older parts, short, 0.2–0.8 \times ca. 0.1–0.3 mm, plane, simple; apices truncate; lower side concolorous with the lower marginal zone. Maculae weak, punctiform, laminal or in the amphithecium, usually common but hard to see on darkened specimens (such as the type). Cilia black, without or with simple or double apices, short and bent downwards, 0.05–0.30 (–0.60) \times 0.03–0.05 mm, with semi-immersed to emergent bulbate bases 0.10–0.30 mm wide (these partially enlarged or occasionally absent), often withered and becoming reniform at the axils, scarce along the margins but more frequent at the crenae and axils, spaced 0.05–0.15 mm from each to occasionally contiguous, solitary or in small groups, becoming absent at the apices and adjacent parts of the laciniae. Soredia, Isidia and Pustulae absent. Medulla white. Lower cortex black, occasionally dark brown at the transition from the margins to the center, slightly shiny to opaque, smooth to rugose, moderately rhizinate. Marginal zone black and indistinct from the center to brown or dark brown and attenuate, 0.5–4.0 mm wide, opaque to slightly shiny, smooth to rugose, weakly papillate, scarcely rhizinate at the transition to the center. Rhizinae black, occasionally dark brown close to the margins, initially simple to rarely furcate, without basal or displaced bulbs, 0.10–0.40 (–0.70) \times ca. 0.05 mm, usually frequent but varying from scarce to abundant at a few parts or near the margins, evenly distributed. Apothecia urceolate to concave or subconcave, partially becoming fissured and folded when old, adnate to subpedicelate, 0.8–6.2 mm diam., laminal to submarginal, ecoronate; margin smooth; amphithecium smooth becoming subrugose, without ornamentations. Disc light to dark brown, epruinose, imperforate; epithecium 10.0–20.0 μm high; hymenium 50.0–80.0 μm high; subhymenium 15.0–37.5 μm high. Ascospores ellipsoid to oval or rounded, (10.0–) 12.5–19.0 (–22.0) \times (7.5–) 9.0–11.0 (–14.0) μm ; epispore (0.5–) 1.0–1.5 μm . Pycnidia frequent, laminal to submarginal, immersed, with black ostioles. Conidia baciliform to weakly or distinctly bifusiform (4.0–) 5.0–9.0 \times 0.75 μm .

TLC/HPLC: cortical atranorin and chloroatranorin, medullary salazinic and consalazinic acids (see also Hale 1976).



Figures 12–16. 12 Lectotype of *Parmelia amplexens* 13 Holotype of *Bulbothrix vainioi* 14 Detail of the lower cortex of *B. vainioi* 15 Holotype of *Bulbothrix sensibilis* 16 Holotype of *Bulbothrix setschwanensis*. Scale = 1 cm (14, 15, 16), 2 mm (17), 1 mm (18), and 20 μ m (19).

Distribution. Asia: India (Nylander 1860, Stirton 1878, Hale 1976a, Divakar and Upreti 2005), Pakistan (Hale 1976a), Nepal (Hale 1976a, Kurokawa 1993), and Thailand (Wolseley et al. 2002). Africa: Camarões (Hale 1976a), Kenya (Swinscow and Krog 1988), and Tanzania (Krog 2000). South America: Brazil - State of São Paulo (Marcelli 1993, Jungbluth 2006). Accordingly to Elix (1994), the species was erroneously cited for Australia (Knight 1882), and does not occur in that region. Here it is cited as new for Malawi.

Additional specimens examined. India, Mussoorie, northwest Himalaya, 7000 ft., leg. R. R. Stewart s.n., VII-1931 (NY 12298). Idem, Nilgherries Montains, *Watt* s.n. (lectotype of *Parmelia amplexens*, BM!, duplicate at GLAM!). Pakistan, Lower Topa, Murree hills, on bark of *Pinus excelsa*, leg. S. H. Iqbal 835, 11-VII-1967 (US). Malawi, Cholo Mt., dead branchlets of rain-forest trees, 1200 m alt., leg. L. J. Brass s.n. 24-IX-1946 (NY 17788). Brazil, São Paulo State, Itirapina Municipality, Estação Experimental de Itirapina, IF, leg. P. Jungbluth, L. S. Canêz & A. A. Spielmann PJ881, 26-III-2004. Idem, Santa Rita do Passa Quatro Municipality, Fazenda Vassununga, km 259 of the Anhanguera Highway, leg. M. P. Marcelli & B. L. Morretes 15653, 03-VI-1978 (SP). Idem, São Manuel Municipality, Fazenda Palmeira da Serra, non official particular cerrado (savannah) reserve, on tree trunk, leg. M. P. Marcelli & S. B. Barbosa 35693, 03-VI-2003 (SP). Idem, Botucatu Municipality, beside the highway that connects the city to the highway Castello Branco (SP-280), km 3, private cerradão forest inside Fazenda Morro do Ouro, 22°53'S, 48°26'W, 804 m alt, on a tree trunk, leg. M. P. Marcelli & S. B. Barbosa 35696, 4-VI-2003 (holotype of *Bulbothrix vainioi*, SP!).

Comments. The holotype (Fig. 11) consists of a single thallus on bark. It is partially detached from the substrate and in poor condition. Part of the upper cortex is absent, the medulla is much stained by oxidized salazinic acid, and the thallus is brittle and fragile. There are several apothecia in different stages of maturation, some of them also damaged, though they have ascospores. The thallus has many pycnidia, some containing conidia.

Nylander wrote on a label with the type specimen voucher “ascospores 14.0–18.0 × 7.0–11.0 mm”, but mentioned as measures 14.0–21.0 × 8.0–11.0 mm at the work in which he described *Parmelia tiliacea* var. *meizospora* (Nylander 1860), and as 11.0–21.0 × 8.0–11.0 mm in the work that raised the variety to the rank of species (Nylander 1869).

Nylander (1885) mentioned bifusiform conidia for Indian material, measuring 5.0 × 0.5–0.7 μm (he was one of the first authors to note bifusiform conidia in *Bulbothrix*). Divakar and Upreti (2005) and Jungbluth (2006) also mentioned bifusiform conidia for *B. meizospora*.

Hale (1976a) mentioned that the size of ascospores was variable in the species, and that is confirmed by the material cited below, in which ascospores may have any measure starting from 12.0–15.0 × 7.0–10.0 μm up to 12.0–22.0 × 8.0–12.0 μm. Marcelli (1993) and Jungbluth (2006) mentioned ascospores 12.0–16.5 × 8.0–10.0 μm. Ascospores under 12.0 μm are usually quite rare and look not fully developed.

Cilia in *B. meizospora* are usually infrequent, and a portion of them in a same thalli apices might not present apices, while some others do not have bulbs. Often the bulbs become withered or reniform, which is more evident in the axillary cilia.

Regarding the presence and intensity of cortical maculae, Swinscow and Krog (1988) and Marcelli (1993) cited specimens of *B. meizospora* with absence of cortical macules, while Hale (1976a) and Divakar and Upreti (2005) mentioned that the species can be weakly to moderately maculate, and Jungbluth (2006) mentioned distinct maculae.

Apparently, as mentioned by Benatti (2010), there are no *Bulbothrix* species with variable presence of maculae, but that are always either emaculate such as *B. continua* (Lynge) Hale, or always maculate as *B. hypocraea* (Vainio) Hale. What seems to happen is that certain species, such as *B. meizospora*, have variable maculae intensity, more subtle and scarce in some thalli (which makes it difficult to see them) and somewhat more evident in others.

Bulbothrix setschwanensis (Zahlbruckner) Hale was compared to *B. meizospora* by Hale (1976a) and Divakar and Upreti (2005). It differs by the more constantly bulbate cilia with distinct apices that appear more abundantly at the margins, and by the pale brown lower cortex.

Bulbothrix sensibilis (Steiner & Zahlbruckner) Hale was compared by Swinscow and Krog (1988), and differs from *B. meizospora* only by the smaller ascospores, which vary from $7.0\text{--}9.0 \times 4.0\text{--}7.0$ to $8.0\text{--}12.0 \times 6.0\text{--}8.0$ μm , as cited by Zahlbruckner (1926), Hale (1976a), and Swinscow and Krog (1988) and as seen in the present work. Hale (1976a) used the laciniae aspect and width to differentiate the species, I found that these features are not very helpful in the case of these two species, with only the tendency of smaller sizes to be more common in *B. sensibilis*. Although Hale (1976a) used the shape and width of the laciniae for differentiation, comparisons between *B. sensibilis* and *B. meizospora* gave almost identical measurements, with slight variations in width, the specimens of *B. sensibilis* frequently tending to have narrower, more often sublinear laciniae. Besides the sole significative difference of ascospore sizes, recent analyses of DNA sequences corroborate the distinction of the species (Divakar et al. 2010).

Bulbothrix hypocraea (Vainio) Hale was compared to *B. meizospora* by Jungbluth (2006). It differs by having a distinctly maculate upper cortex, narrower and sublinear laciniae (ca. $1.0\text{--}3.0$ mm wide), a pale brown lower cortex and smaller ascospores (usually $7.0\text{--}14.0 \times 5.0\text{--}8.0$ μm).

Recognition of *B. meizospora* as a *Bulbothrix* species can sometimes be difficult, as commented already by Marcelli (1993), due to the relatively large size of the thalli when compared to other species of the genus, and because the bulbs are not very evident in the cilia or sometimes partially absent. Notably *Canoparmelia amazonica* (Nylander) Hale, present in the same habitats, was compared by Marcelli (1993) to *B. meizospora*, suggesting that in certain circumstances they could be mistaken in field. *Canoparmelia amazonica* can be distinguished by the complete absence of marginal cilia and by the presence of medullary protocetraric acid.

The type material (Fig. 12) of *Parmelia amplexens* Stirton (BM! lectotype, GLAM! duplicate) has cilia with more distinct bulbs and somewhat longer apices, and it is difficult to recognize maculae due its poor condition. However, the further characteristics agree with those of *B. meizospora* as accepted by Hale (1976a). Stir-

ton (1878) described ellipsoid ascospores $15.0\text{--}18.0 \times 9.0\text{--}12.0 \mu\text{m}$ and cylindrical straight conidia $6.0 \times 0.7 \mu\text{m}$, which are also in agreement with measurements obtained here from the type (ascospores $12.0\text{--}19.0 \times 10.0\text{--}12.0 \mu\text{m}$; conidia nearly identical) and those normally found in *B. meizospora*. The lectotype is a relatively large thallus (about 10 cm wide) in poor condition, the cortex and several of the marginal ciliary bulbs badly damaged. It is less brownish than the duplicate, but also with the medulla stained by oxidized salazinic acid, and several apothecia have lost their hymenia. The duplicate is composed of two larger fragments a few cm wide and several smaller fragments, and it is very dusky brown.

Bulbothrix vainioi (Fig. 13–14) Jungbluth, Marcelli and Elix was described by Jungbluth et al. (2008) based on specimens with ascospores over $12 \mu\text{m}$ long included by Hale (1976a) provisionally in *B. sensibilis*. However, apparently they overlooked the possibility that their material could belong to *B. meizospora*, the ascospores with the minimum common diameter for that species. As was checked here, all specimens assigned to *Bulbothrix vainioi* are morphologically identical with *B. meizospora* and have the same chemistry. Consequently *Bulbothrix vainioi* is not a species similar to *B. sensibilis* with larger ascospores, as the authors assumed, but typical *B. meizospora* with ascospores $12.0\text{--}16.0 \mu\text{m}$ long, a size range well inside the limits found for this species, and with the same cilia.

Hale (1976a) and Divakar and Upreti (2005) mentioned that thalli of *B. meizospora* can occasionally be found on rocks, and rarely on soil. Divakar and Upreti (2005) mentioned pycnidia usually confined to peripheral areas of laciniae, but in the holotype and other material studied they can be seen all over the thallus.

***Bulbothrix sensibilis* (Stein. & Zahlb.) Hale. Phytologia 28: 481. 1974.**

Mycobank: MB 341612

Figure 15

Basionym: *Parmelia sensibilis* Stein. & Zahlb. Afrikanische Flechten (Lichenes), Englers Botanische Jahrbücher für Systematik 60: 522. 1926.

Holotype. British East Africa, Bei-Bura (Kenia), auf Baumzweigen, leg. Schröder 285 (W!).

Description. Thallus subirregularly to sublinearly sublaciniate, dusky gray in the herbarium, up to 6.9 cm diam., subcoriaceous, corticolous or ramulicolous; upper cortex $12.5\text{--}25.0 \mu\text{m}$ thick, algal layer $15.0\text{--}27.5 \mu\text{m}$ thick, medulla $87.5\text{--}120.0 \mu\text{m}$ thick, lower cortex $12.5\text{--}17.5 \mu\text{m}$ thick. Laciniae irregularly to occasionally anisotomically dichotomously branched, 1.3–5.2 mm wide, slightly imbricate, becoming crowded at the center, weakly adnate and loosely adpressed, with flat, subrounded to subtruncate apices; margins flat, slightly sinuous to crenate or irregular, entire to slightly incised, occasionally sublacinulate; axils oval to irregular. Upper cortex smooth and continuous, becoming subrugose with occasional irregular cracks only on older parts; laminal ciliary bulbs absent. Adventitious marginal lacinulae scarce on older parts, short, 0.2–1.2

× 0.1–0.2 mm, plane, simple to irregularly branched; apices truncate; lower side concolor with the lower marginal zone. Maculae weak to distinct, punctiform, laminal, more evident at distal parts of the thallus. Cilia black, without or with simple and short apices, occasionally bent downwards, 0.05–0.20 (–0.30) × ca. 0.03 mm, with emerse bulbate bases 0.05–0.25 mm wide, occasionally withered and reniform, scarce along the margins, becoming frequent at the crenae and axils spaced ca. 0.05–0.15 mm from each other to eventually contiguous, solitary or in small groups becoming absent or scarce at the apices and adjacent parts of the laciniae. Soredia, Isidia, and Pustulae absent. Medulla white. Lower cortex black, with random dark brown spots at the transition to the center, slightly shiny, smooth to subrugose or subvenate, moderately rhizinate. Marginal zone mostly brown, attenuate, ca. 0.5–2.0 mm wide, partially black and indistinct from the center, slightly shiny, smooth to subvenate, weakly rhizinate until the transition to the center. Rhizinae black, sometimes partially dark brown close to the margins, simple to rarely furcate, without basal or displaced bulbs, 0.10–0.30 (–0.40) × ca. 0.05 mm, usually frequent but scarcer at the margins and at the transition to the center, evenly distributed. Apothecia concave to subplane, sessile to adnate, 0.2–4.3 mm diam., laminal, ecoronate; margin and amphitecia initially smooth becoming subrugose, without ornamentations. Disc pale brown, epruinose, imperforate; epithecium 10.0–17.5 µm high; hymenium 30.0–47.5 µm high; subhymenium 20.0–30.0 µm high. Ascospores ellipsoid to oval, (7.0–) 8.0–12.0 (–13.0) × 5.0–7.0 µm; epispore ca. 0.75 µm. Pycnidia frequent, laminal, immersed, with black ostioles. Conidia baciliform to weakly bifusiform 5.0–9.0 × 0.75 µm.

TLC/HPLC: cortical atranorin, medullary salazinic and consalazinic acids (see also Hale 1976).

Distribution. Asia: Sri Lanka (Awasthi 1976), India (Awasthi 1976, Divakar and Upreti 2005), and Thailand (Pooprang et al. 1999); África: Kenya (Zahlbruckner 1926, Dodge 1959, Swinscow and Krog 1988), Tanzania (Swinscow and Krog 1988), Angola, Guinea, Malawi, Zaire, Zambia (Hale 1976a), Madagascar (Aptroot 1990), and Rwanda (Killmann and Fischer 2005, Bock et al. 2007); South America: Venezuela (Hale 1976a, López-Figueiras 1986), Brazil - State of São Paulo (Marcelli 1993).

Additional specimens examined. Venezuela, Táchira, Via Rubio, Brámon, 800–1100 m, leg. M. E. Hale & M. López Figueiras 45727, 24-III-1975 (US). Brazil, São Paulo State, 6 km SW of Jaboticabal, 21°35'S, 48°35'W, on trees in cerradão, leg. A. Fletcher 10138, 03-V-1975 (BM). Idem, Pirassununga, Rawitscher Reserve, Cerrado auf Zweigen, leg. H. Walter & E. Walter Br 58, 30-IX-1965 (M).

Comments. The holotype of *B. sensibilis* (Fig. 15) consists of a small thallus ca. 6.0 cm in diameter on tree branch, in a reasonable state of preservation, although several parts and apothecia are badly damaged. The material is glued to the card voucher, and it was necessary to free some laciniae for observation of the lower cortex. There are apothecia containing ascospores in good condition and there are several pycnidia with conidia.

Steiner and Zahlbruckner (Zahlbruckner 1926) described the species as having no cilia, but mentioning of what they interpreted as a constant presence of parasites with inflated bases or converted into bulbs (“non rare planta parasitica inclusis, basin ver-

sus semel vel bis bulbiformiter inflatis vel bulbum tantum formantibus”). The authors also noted the occurrence of brown patches in certain parts of the center of the thallus lower cortex, and not just at the margins. Dodge (1959) commented on the tendency of laciniae in the central parts of the thalli to become with a more wrinkled and broken surface. The author also did not perceive the bulbate cilia, though he did mention something like small papillate rhizines along the margins. Interestingly, he described the apothecia as perforate, what was not found on the material examined here. Awasthi (1976) was the first author to describe bulbate cilia for the species. The characteristics he described are in accordance with the type material, only his measures of the laciniae being even wider (2.0 to 6.0 mm). The ascospore descriptions and measurements of the specimens studied by Dodge (1959), Awasthi (1976), Swinscow and Krog (1988) and Divakar and Upreti (2005) are all in accordance with the type of material of *B. sensibilis*.

The material attributed by Marcelli (1993) to *B. sensibilis*, described as emaculate with a overall black lower cortex, sparse rhizines sparse and ascospores $12.6\text{--}14.4 \times 7.2\text{--}8.1 \mu\text{m}$ are in fact weakly, sparsely maculate specimens of *B. meizospora* with laciniae and ascospore of minimum dimensions found in the species, but not below those considered normal.

Hale (1976a) attributed examined specimens from several African countries and Venezuela to *Bulbothrix sensibilis*, with a first citation of the species for the Americas. Overall, the material described is in accordance with the type material. However, in two keys (Hale and Kurokawa 1964, Hale 1976a) were cited ascospores sizes as $7.0\text{--}9.0 \mu\text{m}$ long, much smaller than the size $7.0\text{--}18.0 \times 5.0\text{--}12.0 \mu\text{m}$ that Hale mentioned in the description of the species in his monograph (Hale 1976a).

Hale (1976a) cited in his key subirregular laciniae for *B. meizospora* and sublinear for *B. sensibilis*, the opposite of what is in his descriptions, where *B. meizospora* is the species described as having sublinear laciniae, not *B. sensibilis*. Although he used different widths in the key laciniae as to differences for separate them, he also described the same size for both. Jungbluth et al. (2008) discussed in the description of *B. vainioi* on the possible identity of the South American material of *B. sensibilis* seen by Hale (1976a). The authors believed in the hypothesis of the involvement of two taxa, one composed of African and Indian specimens with ascospores less than $12.0 \mu\text{m}$ long corresponding to the true *B. sensibilis*, and the other composed of the South American specimens with ascospores larger than $12.0 \mu\text{m}$ long that they described as *B. vainioi*.

It is possible that Hale (1976a) may have been confused when typing measurements closer to those of the ascospores of *B. meizospora* in the description of *B. sensibilis*, since the differences he used in the key are exactly as seen here. Another hypothesis is that Hale may have mistaken the material of Venezuela with *B. sensibilis* due to the similarity between the African specimens with his South American specimen. As found by analyzing material of *B. vainioi* and *B. meizospora*, even differences of cilia cited in the comments under *B. vainioi* are minimal and usually found in the same species, even in a same specimen.

Bulbothrix hypocraea (Vain.) Hale differs by being more evidently maculate than *B. sensibilis*, by the pale brown lower cortex with slightly darker margins, and by the

brown rhizines with dark basal or displaced bulbs. Hale (1976a) noted that although the african-american pattern of distribution, *B. sensibilis* was a much rarer species, believing that *B. sensibilis* should either be or resemble the parental form of *B. tabacina* (Mont. & Bosch) Hale. In turn, *B. tabacina* (L! lectotype, duplicate at PC!) differs by the formation of laminal isidia, a uniformly black lower cortex, and by the averagely larger ascospores $9.0\text{--}16.0 \times 5.0\text{--}8.0 \mu\text{m}$.

Bulbothrix bulbochaeta (Hale) Hale (LWG! holotype, US! isotype) differs by the narrower laciniae ca. 1.0–2.5 mm wide, the branched cilia and rhizines, the constant presence of laminal ciliary bulbs, the coronate apothecia containing very small and rounded ascospores $4.0\text{--}6.0 \times 3.0\text{--}4.0 \mu\text{m}$ and by the absence of medullary substances.

Bulbothrix linteolcarpa Marcelli was compared to *B. sensibilis* by Marcelli (1993), and differs by the linear, narrower and truncated laciniae 0.2–0.6 (–0.8) mm wide, the brown lower cortex, the very adnate, distended plane apothecia containing larger ascospores $12.0\text{--}16.0 \times 6.0\text{--}8.0 \mu\text{m}$, and by the frequent cilia with smaller bulbs (similar in size and aspect to those found in *Bulbothrix* species containing gyrophoric acid) and longer apices.

Bulbothrix meizospora (Steiner & Zahlbruckner) Hale differs by the laciniae usually more irregularly branched and with rounded apices, and by the always larger ascospores, measuring $12.0\text{--}22.0 \times 8.0\text{--}12.0 \mu\text{m}$. Comparatively, thalli of *B. sensibilis* are also more evidently maculate.

***Bulbothrix setschwanensis* (Zahlb.) Hale. Phytologia 28: 481. 1974.**

Mycobank: MB 341613

Figure 16

Basionym: *Parmelia setschwanensis* Zahlb. Symbolae Sinicae 3: 184. 1930.

Holotype. China, Prov. Setschwan austro-occid., in regionis siccae subtropicae convalis fluminis Yalung ad septentriones oppidi Yneyünen infra castelum Kwapi ram *Pistacia weinmannifolia* supra vic. Otang, alt. 2400–2500 m., leg. Handel-Mazzetti 2739, 30-V-1914 (WU!).

Description. Thallus subirregularly to sublinearly lacinate, greenish gray in the herbarium, up to 7.0 cm diam., subcoriaceous, corticolous or ramulicolous; upper cortex $15.0\text{--}20.0 \mu\text{m}$ thick, algal layer $30.0\text{--}47.5 \mu\text{m}$ thick, medulla $87.5\text{--}110.0 \mu\text{m}$ thick, lower cortex $12.5\text{--}20.0 \mu\text{m}$ thick. Laciniae irregularly to partially to anisotomically dichotomously branched, contiguous to imbricate, 1.1–3.5 (–5.0) mm wide, adnate and adpressed, with \pm flat, subrounded to subtruncate apices; margins flat, smooth and sinuous to crenate or or irregular, entire to slightly incised, occasionally sublacinulate; axils oval or irregular. Upper cortex mostly smooth and continuous, occasionally becoming subrugose and irregularly cracked; laminal ciliary bulbs absent. Adventitious marginal lacinulae scarce on older parts, short, $0.2\text{--}1.0 \times 0.1\text{--}0.6 \text{ mm}$, plane, simple to irregularly branched; apices truncate or acute; lower side concolor with the lower marginal zone. Maculae absent. Cilia black, without or with simple apices, $0.05\text{--}0.30$ (–0.50) \times ca.

0.03 mm, with semi-immersed to emerge bulbate bases 0.05–0.25 mm wide, frequent to abundant along the margins, spaced 0.05–0.15 mm from each other to rarely contiguous, solitary or in small groups at the crenae and axils becoming scarce at the apices of the laciniae. Soredia, Isidia and Pustulae absent. Medulla white. Lower surface pale brown, opaque, smooth to subrugose, moderately rhizinate. Marginal zone pale brown, indistinctly delimited from the center, opaque, smooth to subrugose, weakly papillate, variably rhizinate. Rhizines brown or cream colored, simple, rarely with subtle displaced blackish bulbs, 0.05–0.80 × 0.03–0.05 mm, frequent becoming abundant near the margins, evenly distributed. Apothecia subconcave to plane, adnate to subpedicelate, 0.4–4.1 mm diam., laminal to submarginal, ecoronate; margin smooth to subcrenate or fissured; amphitecia smooth, without ornamentations. Disc light to dark brown, epruinose, imperforate; epthecium 7.5–12.5 mm high; hymenium 35.0–42.5 µm high; subhymenium 12.5–20.0 µm high. Ascospores ellipsoid to oval, (10.0–) 12.0–19.0 × 6.0–9.0 (–10.0) µm; epispore ca. 1.0 µm. Pycnidia laminal, frequent, immerse, with black ostioles. Conidia baciliform to weakly bifusiform (4.0–) 5.0–8.5 × ca. 0.75 µm.

TLC/HPLC: cortical atranorin and chloroatranorin, medullary salazinic and consalazinic acids (see also Hale 1976).

Distribution. Asia: China (Zahlbruckner 1930, Hale 1976a), India (Hale 1976a, Divakar and Upreti 2005), Nepal (Hale 1976a, Kurokawa 1993, Divakar and Upreti 2005) and Thailand (Wolseley and Aguirre-Hudson 1997, Wolseley et al. 2002, Ramkhamhaeng University Herbarium 2006).

Additional specimens examined. India, Oriental India, prov. Central, Chavradar, Manra distr., 3500 ft., leg. J. Masten s.n., XII-1900 (NY). Idem, Kolhapur, Maharashtra, Panhala Forest, leg. P. G. Pahvardhan & R. A. V. Prabhu 74.1007, 13-X-1974 (US). Idem, Índia, E. Himalayas, Darjeeling, West Bengal, Manibhanjan, 7700 ft., leg. C. G. Dharne & K. N. R. Chaudhuri 82, VI-1966 (SP). Pakistan, Lower Topa, Murree hills, on bark of *Pinus excelsa*, leg. S. H. Iqbal 844(?), 11-VII-1967 (US).

Comments. The holotype (Fig. 16) consists of a thallus on a tree twig, together with other bark fragments containing smaller pieces. It is in a reasonable state of preservation, with some lobes and apothecia badly damaged. The material contains several apothecia at different stages of maturity with ascospores in good condition, and many pycnidia with conidia. There are some loose fragments, on which the lower cortex was observed.

Zahlbruckner (1930) described the species as not ciliate (“in marginibus non ciliatis”), since like Lynge (1914) thought that the bulbate cilia on the margins were rhizines. Zahlbruckner (1930) described the lower cortex as black with brown margins (subtus niger, excepta parte angusta marginali castaneo-fusca), but the analysis of the type material confirmed the statements of Hale (1976a) and Divakar and Upreti (2005) on the color to be pale brown (almost cream in some parts) from the center to the margins.

Zahlbruckner (1930) also mentioned ellipsoid to suboval ascospores 12.0–18.0 × 6.0–10.0 mm, but there is a note from Hale with the lectotype citing 12.0–15.0 × 7.0–8.0 mm, and the ascospores found measure (10.0–) 12.0–15.0 × 7.0–9.0 mm. The syntype was not located (W, according to Hale 1976a), and accordingly to his data probably should have ascospores 12.0–18.0 × 6.0–12.0 µm. Measurements made

by Hale (1976a) and Divakar and Upreti (2005) respectively mention ascospores $12.0\text{--}19.0 \times 6.0\text{--}9.0$ and $10.0\text{--}19.0 \times 6.0\text{--}9.0$ μm encompassing the measurements mentioned above. The other specimens examined here have similar sized ascospores, generally above 12.0×7.0 μm . The occurrence of a similar ascospores size variety also occurs in *B. meizospora* (Nylander) Hale.

Among similar species, *Bulbothrix meizospora* is morphologically close to *B. setschwanensis* including the ascospores of similar size, but the has a distinct black lower cortex with brown margins, as cited by Hale (1976a) and Divakar and Upreti (2005).

Hale (1976a) compared *Bulbothrix setschwanensis* to *B. hypocraea* (Vainio) Hale. This species differs by evident maculae in the upper cortex, the narrower laciniae width (ca. 0.5–2.5 mm wide) and by the smaller sizes of the ascospores ($8.0\text{--}14.0 \times 6.0\text{--}8.0$ mm). *Bulbothrix sensibilis* (Steiner & Zahlbruckner) Hale and *B. meizospora* cortices both differ from *B. setschwanensis* by the black lower cortex with brown margins, presence of cortical maculae, and in the case of *B. sensibilis*, also by the smaller ascospores $8.0\text{--}12.0 \times 5.0\text{--}7.0$ μm . *Bulbothrix linteolocarpa* Marcelli differs by the much narrower sublinear laciniae ca. 0.2–0.5 mm wide, and by the cilia with small bulbs and more evident apices that are more widespread along the margins rather than restricted to the crenae and axils of the laciniae.

Bulbothrix continua (Lynge) Hale differs by the narrower laciniae ca. 1.0–2.0 mm wide and by the smaller ascospores $9.0\text{--}13.5 \times 5.0\text{--}7.5$ μm . in direct comparison, morphologically its aspect more closely resembles that of *B. hypocraea*, although the maculations are absent, while that of *B. setschwanensis* is more akin to that of *B. meizospora*. In a key in Hale and Kurokawa (1964) *B. continua* was separated from *B. setschwanensis* solely by the laciniae width and by the geographical distribution, the first thought to be endemic to South America and the other to Asia.

Originally described from China, the species is also known from India and Nepal (Hale 1976a, Divakar and Upreti 2005), where it is endemic to the Himalayan mountain region. *Bulbothrix setschwanensis* has been used in *in vitro* experiments for the production of secondary metabolites and reduction of inhibitory activity or reduction of enzymes (Behera and Makhija 2001, 2002, Behera et al. 2000).

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Molecular data support placement of *Cameronia* in Ostropomycetidae (Lecanoromycetes, Ascomycota)

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Abstract

The phylogenetic position of the Tasmanian endemic genus *Cameronia* Kantvilas is studied using partial sequences of nuclear LSU and mitochondrial SSU ribosomal DNA. Monophyly of the genus is supported, as is its placement in Ostropomycetidae, although its position within this subclass remains uncertain. Given the lack of close relatives to *Cameronia* and its morphological differences compared to other families with perithecioid ascomata in Ostropomycetidae, the new family Cameroniaceae Kantvilas & Lumbsch is proposed.

Keywords

Cameroniaceae, lichens, new family, Tasmania, taxonomy

Introduction

The lichen flora of Tasmania has a remarkable number of unique species, as well as several genera that are unknown or very rarely found in other regions. Examples include the genera *Jarmania* Kantvilas (Kantvilas 1996), *Meridianelia* Kantvilas & Lumbsch (Kantvilas and Lumbsch 2009), *Siphulella* Kantvilas, Elix & P. James (Kantvilas et al. 1992), *Tasmidella* Kantvilas, Hafellner & Elix (Kantvilas et al. 1999), and several species of *Cladia* (Kantvilas and Elix 1987, 1999) and thelotremoid Graphidaceae (Kantvilas and Vezda 2000; Mangold et al. 2009). In general, endemism can be either the result of survival of relict taxa (palaeoendemism) or recent speciation events (neoendemism) (Brandley et al. 2010; Brooks et al. 2006; Goldberg et al. 2005; Jans-

sen et al. 2008; Kier et al. 2009; Kraft et al. 2010; Lamoreux et al. 2006; Olson et al. 2001; Qian 2001). The reasons for the relatively large amount of endemic taxa in Tasmania are not well understood. In the genus *Cladia*, for example, molecular data are consistent with a recent speciation and suggest neoendemism (Lumbsch et al. 2010; Parnmen 2011), but for most endemic taxa there are currently insufficient data available to test whether they represent relict lineages or are the product of recent speciation events. In some cases, however, lichens that were believed to be endemic to Tasmania, were subsequently also discovered in New Zealand, e.g. *Bunodophoron flaccidum* (Wedin 1993; Wedin 2001).

Lichen taxa unique to Tasmania include the genus *Cameronia* (Kantvilas 2012), which was recently described with an unclear systematic position and placed tentatively in Ostropomycetidae. The genus includes two species that occur on siliceous rocks at high elevations. Although its thallus is superficially similar to that of a species of *Lecanora* or *Pertusaria*, the genus is readily distinguished by the presence of eumuriform ascospores in thick-walled, broadly obovate, hemiamyloid asci with a non-amyloid tholus, formed in a hamathecium consisting of richly branched, anastomosing paraphysoids. The ascomata are perithecioid. Secondary metabolites present in the genus include the 9-*O*-methylpannaric acid chemosyndrome and an unknown triphenyl.

Thick-walled asci having a hemiamyloid wall and non-amyloid tholus, anastomosing paraphysoids and muriform ascospores are all characters reminiscent of Arthoniales (Ertz and Tehler 2011; Grube 1998; Tehler 1990), but the perithecioid ascomata, chlorococcoid photobiont, and morphological details of the ascus differ from this order (Kantvilas 2012). Perithecioid ascomata and thick-walled asci in a hamathecium consisting of anastomosing paraphysoids are characteristic for Protothelenellaceae and Thelenellaceae in Ostropomycetidae (Fryday and Coppins 2004; Mayrhofer 1987a,b; Mayrhofer and Poelt 1985; Schmitt et al. 2005). However, these families differ in having cylindrical asci and, furthermore, Thelenellaceae lacks any amyloid reactions of the asci, whereas Protothelenellaceae have an amyloid tholus. Because phenotypic characters do not place *Cameronia* in any group unambiguously and the placement in Ostropomycetidae was tentative, we used freshly collected material of the two species of *Cameronia* to generate DNA sequences of two loci (mtSSU and nuLSU rDNA) to test the monophyly of *Cameronia* and its placement of *Cameronia* in Ostropomycetidae, and to identify the closest relatives of the genus and place it in a family.

Materials and methods

Taxon sampling and molecular methods

The study is based on fresh material collected by GK and deposited in the Tasmanian Herbarium (HO) and the Field Museum of Natural History (F), and on DNA sequences downloaded from Genbank. Sequences of Umbilicariaceae were included as outgroup since this family has been shown previously to be sister to Lecanoromycetidae

+ Ostropomycetidae (Lumbsch et al. 2007a; Miadlikowska et al. 2006; Spatafora et al. 2006; Wedin et al. 2005). Sequence data of the two species of *Cameronia* were assembled with sequences of mitochondrial small subunit (mtSSU) and nuclear LSU rDNA downloaded from Genbank (Table 1). Sample preparation, DNA isolation, PCR and direct sequencing were performed as described previously (Mangold et al. 2008; Rovas-Plata and Lumbsch 2011). Primers for amplification were: mr SSU1 (Zoller et al. 1999) and MSU7 (Zhou and Stanosz 2001) for mtSSU, and AL2R (Mangold et al. 2008) and nu-LSU-1125-3' (= LR6) (Vilgalys and Hester 1990) for nuLSU rDNA. Sequence fragments obtained were assembled with SeqMan 4.03 (DNASTAR) and manually adjusted.

Table 1. Sequences obtained from Genbank for the study. Family or generic group as in figure 1, largely following (Lumbsch and Huhndorf 2010). Newly obtained sequences are indicated in bold.

Species	Family/generic group as in Fig. 1	nuLSU	mtSSU
<i>Acarosporina microspora</i>	Stictiaceae	AY584643	AY584612
<i>Agyrium rufum</i>	-	EF81824	EF81821
<i>Ainoa mooreana</i>	-	AY212850	AY212828
<i>Anzina carneonivea</i>	-	AY212829	AY212851
<i>Arctomia delicatula</i>	Arctomiaceae	AY853307	AY853355
<i>Arctomia teretiuscula</i>	Arctomiaceae	DQ007346	DQ007349
<i>Aspicilia caesiocinerea</i>	Megasporaceae	DQ780303	DQ780271
<i>Aspicilia cinerea</i>	Megasporaceae	DQ780304	DQ780272
<i>Aspicilia contorta</i>	Megasporaceae	DQ986782	DQ986876
<i>Aspicilia hispida</i>	Megasporaceae	DQ780305	DQ780273
<i>Baeomyces placophyllus</i>	-	AY300878	AF356658
<i>Baeomyces rufus</i>	-	DQ871008	DQ871016
<i>Belonia russula</i>	Gyalectaceae	FJ941887	AY648888
<i>Bryophagus gloeocapsa</i>	Gyalectaceae	AF465440	AY300880
<i>Cameronia pertusarioides</i> 6504	-	JX977114	JX977110
<i>Cameronia pertusarioides</i> 6505	-	JX977115	JX977111
<i>Cameronia pertusarioides</i> 6506	-	JX977116	JX977112
<i>Cameronia tecta</i>	-	JX977117	JX977113
<i>Chapsa phlyctidioides</i>	Graphidaceae	JX465300	EU675275
<i>Chapsa pulchra</i>	Graphidaceae	EU075619	EU075571
<i>Coccomycetella richardsonii</i>	Odontotremataceae	HM244761	HM244737
<i>Coccotrema cucurbitula</i>	Coccotremataceae	AF274092	AF329161
<i>Coccotrema pocillarium</i>	Coccotremataceae	AF274093	AF329166
<i>Coenogonium leprieurii</i>	Coenogoniaceae	AF465442	AY584698
<i>Coenogonium luteum</i>	Coenogoniaceae	AF279387	AY584699
<i>Coenogonium pineti</i>	Coenogoniaceae	AY300834	AY300884
<i>Cryptodiscus pallidus</i>	Stictiaceae	FJ904677	FJ904701
<i>"Cryptodiscus" rhopaloides</i>	-	FJ904685	FJ904707
<i>Dibaeis baeomyces</i>	Icmadophilaceae	AY789291	AY584704
<i>Diploschistes cinereocaesius</i>	Graphidaceae	AY300835	AY300885
<i>Diploschistes scruposus</i>	Graphidaceae	AF279389	AY584692
<i>Dyplolabia afzelii</i>	Graphidaceae	HQ639628	HQ639594
<i>Elixia flexella</i>	-	AY853368	AY853320

Species	Family/generic group as in Fig. 1	nuLSU	mtSSU
<i>Fissurina insidiosa</i>	Graphidaceae	DQ973045	DQ972995
<i>Glyphis cicatricosa</i>	Graphidaceae	HQ639630	HQ639610
<i>Graphis scripta</i>	Graphidaceae	AY853322	AY853370
<i>Gregorella humida</i>	Arctomiaceae	AY853329	AY853378
<i>Gyalecta flotowii</i>	Gyalectaceae	AY300838	AY300889
<i>Gyalecta hypoleuca</i>	Gyalectaceae	AF465453	HQ659180
<i>Gyalecta truncigena</i>	Gyalectaceae	HM244766	HM244743
<i>Gyalecta ulmi</i>	Gyalectaceae	AF465463	AY300888
<i>Gyalectaria gyalectoides</i>	Coccotremataceae	GU980983	GU980975
<i>Gyalectaria jamesii</i>	Coccotremataceae	GU980984	GU980976
<i>“Gyalidea” praetermissa</i>	-	HM244768	HM244745
<i>Hymenelia lacustris</i>	Hymeneliaceae	AY853371	AY853323
<i>Icmadophila ericetorum</i>	Icmadophilaceae	DQ883694	DQ986897
<i>Lobothallia radiosa</i>	Megasporaceae	DQ780306	DQ780274
<i>Myriotrema olivaceum</i>	Graphidaceae	EU075627	EU075579
<i>Nadvornikia hawaiiensis</i>	Graphidaceae	AY605080	EU075581
<i>Ocellularia chiriquiensis</i>	Graphidaceae	EU075629	EU075582
<i>Ocellularia endoxantha</i>	Graphidaceae	AY605082	EU075589
<i>Ochrolechia androgyna</i>	<i>Ochrolechia</i>	AY300846	AY300897
<i>Ochrolechia balcanica</i>	<i>Ochrolechia</i>	AF329171	AF329170
<i>Ochrolechia frigida</i>	<i>Ochrolechia</i>	AY300847	AY300898
<i>Ochrolechia oregonensis</i>	<i>Ochrolechia</i>	DQ780308	DQ780276
<i>Ochrolechia pallescens</i>	<i>Ochrolechia</i>	DQ780310	DQ780277
<i>Ochrolechia parvella</i>	<i>Ochrolechia</i>	AF274097	AF320173
<i>Ochrolechia peruensis</i>	<i>Ochrolechia</i>	DQ780311	DQ780279
<i>Ochrolechia turneri</i>	<i>Ochrolechia</i>	AY568002	AY567982
<i>Ochrolechia yasudae</i>	<i>Ochrolechia</i>	DQ986776	DQ986902
<i>Ochrolechia</i> sp.	<i>Ochrolechia</i>	DQ986777	DQ986886
<i>Odontotrema phacidiellum</i>	Odontotremataceae	HM244769	HM244748
<i>Odontotrema</i> sp.	Odontotremataceae	HM244772	HM244751
<i>Orceolina antarctica</i>	Trapeliaceae	AY212852	AF274115
<i>Orceolina kerguelensis</i>	Trapeliaceae	AY212830	AF381561
<i>Paschelkiella pini</i>	Stictidaceae	HM244762	HM244738
<i>“Pertusaria” albescens</i>	Variolaria-group	AF329176	AF329175
<i>“Pertusaria” amara</i>	Variolaria-group	AF274101	AY300900
<i>Pertusaria coccodes</i>	Pertusariaceae	AF2741095	AY567984
<i>“Pertusaria” corallina</i>	Variolaria-group	AY300850	AY300901
<i>“Pertusaria” corallophora</i>	Variolaria-group	DQ780316	DQ780285
<i>Pertusaria coronata</i>	Pertusariaceae	AY300851	AY300902
<i>Pertusaria gibberosa</i>	Pertusariaceae	DQ780322	DQ780289
<i>Pertusaria lecanina</i>	Pertusariaceae	AF274296	AY567991
<i>Pertusaria leioplaca</i>	Pertusariaceae	AY300852	AY300903
<i>“Pertusaria” mammosa</i>	Variolaria-group	AY212831	AY212854
<i>Pertusaria mesotropa</i>	Pertusariaceae	DQ780325	DQ780292
<i>“Pertusaria” ophthalmiza</i>	Variolaria-group	AY568006	AY567993
<i>Pertusaria paramerae</i>	Pertusariaceae	DQ780326	DQ780293
<i>Pertusaria pertusa</i>	Pertusariaceae	AF279300	AF381565
<i>Pertusaria plittiana</i>	Pertusariaceae	DQ780328	DQ780294

Species	Family/generic group as in Fig. 1	nuLSU	mtSSU
<i>Pertusaria pustulata</i>	Pertusariaceae	DQ780332	DQ780297
" <i>Pertusaria</i> " <i>scaberula</i>	Variolaria-group	AF274099	AF431959
" <i>Pertusaria</i> " <i>subventosa</i>	Variolaria-group	AY300854	AY300905
<i>Phlyctis agelaea</i>	Phlyctidaceae	AY853381	AY853332
<i>Phlyctis argena</i>	Phlyctidaceae	DQ986771	DQ986880
<i>Phyllobaeis erythrella</i>	-	DQ986780	DQ986888
<i>Placopsis cribellans</i>	Trapeliaceae	DQ871010	DQ871018
<i>Placopsis gelida</i>	Trapeliaceae	AY212836	AY212859
<i>Placopsis santessonii</i>	Trapeliaceae	AY212845	AY212867
<i>Placynthiella icmalea</i>	Trapeliaceae	AY212846	AY212870
<i>Placynthiella uliginosa</i>	Trapeliaceae	DQ986774	DQ986877
<i>Protothelenella corrosa</i>	Protothelenellaceae	AY607734	AY607746
<i>Protothelenella sphinctrinoidella</i>	Protothelenellaceae	AY607735	AY607747
<i>Pycnotrema pynoporellum</i>	Graphidaceae	JX421615	JX421295
<i>Rhexiophiale rhexoblephara</i>	-	AY853391	AY853341
<i>Schizoxylon albescens</i>	Stictidaceae	DQ401144	DQ401142
<i>Siphula ceratites</i>	Icmadophilaceae	AY853394	AY853344
<i>Schaereria corticola</i>	-	AY300909	AY300859
<i>Stegobolus subcavatus</i>	Graphidaceae	EU075641	EU075595
<i>Stictis populorum</i>	Stictidaceae	AY527327	AY300882
<i>Stictis radiata</i>	Stictidaceae	AY300864	AY584727
<i>Thamnolia vermicularis</i>	Icmadophilaceae	AY853345	AY853395
<i>Thecaria quassicola</i>	Graphidaceae	HQ639667	JF828971
<i>Thelotrema lepadinum</i>	Graphidaceae	AY300866	AY300916
<i>Thelotrema subtile</i>	Graphidaceae	DQ871013	DQ871020
<i>Thelotrema suecicum</i>	Graphidaceae	AY300867	AY300917
<i>Topeliopsis decorticans</i>	Graphidaceae	EU075654	EU075609
<i>Trapelia chiodectonoides</i>	Trapeliaceae	AY212847	AY212873
<i>Trapelia placodioides</i>	Trapeliaceae	AF274103	AF431962
<i>Trapeliopsis flexuosa</i>	Trapeliaceae	AF274118	AY212875
<i>Trapeliopsis granulosa</i>	Trapeliaceae	AF274119	AF381561
<i>Trapeliopsis percrenata</i>	Trapeliaceae	AF279302	AY212876
<i>Umbilicaria crustulosa</i>	Umbilicariaceae	AY300869	AY300919
<i>Umbilicaria decussata</i>	Umbilicariaceae	HM161603	HM161628
<i>Umbilicaria hyperborea</i>	Umbilicariaceae	AY853399	AY853349
<i>Varicellaria hemisphaerica</i>	<i>Varicellaria</i>	AF381563	AF381556
<i>Varicellaria lactea</i>	<i>Varicellaria</i>	AF381557	AF381564
<i>Varicellaria velata</i>	<i>Varicellaria</i>	AY300855	AY300906
<i>Waweia fruticulosa</i>	Arctomiaceae	DQ007347	DQ871023

Sequence alignments and phylogenetic analysis

We assembled partial sequences using Geneious Pro 5.4.3 (Drummond et al. 2011) and edited conflicts manually. Alignments were done using Clustal W (Thompson et al. 1994). Ambiguously aligned regions were removed manually. The single locus and concatenated alignments were analyzed by maximum likelihood (ML) and a Bayesian approach (B/MCMC). To test for potential conflict, ML bootstrap analyses were per-

formed on the individual data sets, and 75% bootstrap consensus trees were examined for conflict (Lutzoni et al. 2004). Maximum likelihood analyses were performed using the program GARLI (Zwickl 2006), employing the general time reversible model of nucleotide substitution (Rodriguez et al. 1990), including estimation of invariant sites, and assuming a discrete gamma distribution with six rate categories as in Lumbsch et al. (2007b). Bootstrapping (Felsenstein 1985) was performed based on 2000 replicates. The B/MCMC analysis was conducted on the concatenated data set using MrBayes 3.1.2 (Huelsenbeck and Ronquist 2001), with the same substitution model as in the ML analysis. The dataset was partitioned into two (mtSSU, nuLSU) and each part was allowed to have its own parameters (Nylander et al. 2004). A run with 20,000,000 generations, starting with a random tree and employing 4 simultaneous chains, was executed. Every 100th tree was saved. The first 500,000 generations (i.e. the first 5000 trees) were deleted as the “burn in” of the chain. We used AWTY (Nylander et al. 2007) to compare split frequencies in the different runs and to plot cumulative split frequencies to ensure that equilibrium was reached. Of the remaining trees, a majority rule consensus tree with average branch lengths was calculated using the sumt option of MrBayes. Posterior probabilities were obtained for each clade. Only clades that received bootstrap support equal or above 70% under ML and posterior probabilities ≥ 0.95 were considered as strongly supported. Phylogenetic trees were depicted using the program FigTree 1.3.1 (Rambaut 2009).

Results and discussion

Eight new sequences were generated for this study and aligned with sequences downloaded from Genbank (Table 1). The single gene locus trees did not show any conflicts and hence the concatenated data set was analyzed. Our combined data set included 1313 unambiguously aligned positions, 370 of which were constant. The ML tree had a likelihood value of -26318.540 and in the B/MCMC analysis of the combined data set, the likelihood parameters in the sample had the following mean (Variance): $\text{LnL} = -27045.138$ (0.35). The ML tree and the tree from the B/MCMC tree sampling were almost identical, with no differences in well-supported clades. Furthermore, taxon sampling was very similar to that of previous studies focusing on the phylogeny of Ostropomycetidae (Baloch et al. 2010; Lumbsch et al. 2007a; Lumbsch et al. 2007b; Wedin et al. 2005). Thus, only a simplified ML tree, with samples of well-supported families, genera or generic groups collapsed, is shown here (Fig. 1). Individual OTUs are shown only for the species of *Cameronia* and its sister groups. In our analysis, the four samples of the two *Cameronia* species form a strongly supported, monophyletic group within the well-supported Ostropomycetidae, confirming the monophyly of the genus and its placement in Ostropomycetidae. The genus *Cameronia* is another example of a group of lichenized ascomycetes with perithecioid ascomata in this subclass, with others being Porinaceae (Baloch and Grube 2006; Grube et al. 2004), Protothelenellaceae and Thelenellaceae (Schmitt et al. 2005). There are additional families

in this subclass that also include taxa with more or less perithecioid ascomata, such as Coccotremataceae, Gyalectaceae, Pertusariaceae and Graphidaceae (Baloch et al. 2010; Lumbsch and Schmitt 2002; Lumbsch et al. 2001; Rivas-Plata et al. 2012; Rovas-Plata and Lumbsch 2011; Schmitt et al. 2010; Schmitt and Lumbsch 2004). The diversity of ascomatal morphologies in this subclass has been linked to the hemiangiocarpous type of ascoma development in the group as a whole (Schmitt et al. 2009).

The backbone of the Ostropomycetidae tree largely lacks support and the relationships of *Cameronia* within Ostropomycetidae remain unclear. *Cameronia* is the sister-group of Baeomycetaceae (*Ainoa*, *Baeomyces*, *Phyllobaeis*) but this relationship lacks support. This clade forms a sister-group to a well-supported clade that includes *Anzina* and Protothelenellaceae, but again, this relationship lacks support.

Although the molecular data support the placement of *Cameronia* in Ostropomycetidae, they fail to identify any close relatives of the genus, which is also reflected in the similarities of Blast searches of the newly generated sequences (maximal identity - nuLSU: 94%, mtSSU: 93%). *Cameronia* is distinguished by several characters that are generally used to characterize families, as shown in Table 2 where salient features of *Cameronia* and other families of Ostropomycetidae with perithecioid ascomata (Porinaceae, Protothelenellaceae, Thelenellaceae) are compared. The ascus type is very different from any of the other perithecioid Ostropomycetidae and also different from the apotheciate Baeomycetaceae, which have cylindrical asci (Gierl and Kalb 1993). Nor is the rudimentary exciple seen in *Cameronia* found in any of the other perithecioid families. Morphologically, the most similar family in Ostropomycetidae is Protothelenellaceae, with which *Cameronia* shares a hamathecium of richly branched paraphysoids and a lack of periphyses. However, Protothelenellaceae have a different exciple, different asci with an amyloid apical apparatus in the tholus and an ocular chamber, and halonate ascospores. Furthermore, Protothelenellaceae form a well-supported clade with *Anzina* (Fig. 1) and are only distantly related to *Cameronia*. The isolated position of *Cameronia* is consistent with the hypothesis that this genus is a case of paleoendemism. It will be an exciting project to test this hypothesis at a later stage when more sequence data from Ostropomycetidae become available.

Given the dissimilarity in morphological characters and the lack of close relatives in the phylogenetic tree, we propose a new family Cameroniaceae below to accommodate the genus *Cameronia*. The new family is placed in Ostropomycetidae with unclear ordinal position.

Cameroniaceae Kantvilas & Lumbsch, fam. nov.

Mycobank: MB 802404

Type: *Cameronia* Kantvilas, Lichenologist 44: 92. 2012.

Description. Thallus crustose, photobiont a coccoid green alga. Ascomata perithecioid, immersed in the thallus, proper exciple rudimentary, hamathecium consisting of richly branched, anastomosing paraphysoids, interspersed with oil droplets, containing

Table 2. Diagnostic features of families with perithecioid ascomata in Ostropomycetidae (Baloch and Grube 2006; Fryday and Coppins 2004; Grube et al. 2004; Kantvilas 2012; Mayrhofer 1987b,2002; Mayrhofer and Poelt 1985; McCarthy 1995; McCarthy 2000).

Characters	<i>Cameronia</i>	Porinaceae	Protothelenellaceae	Thelenellaceae
Proper exciple	rudimentary	Well developed, consisting of periplektenchymatous cells	Well developed, consisting of periplektenchymatous to isodiametric cells	Well developed, consisting of periplektenchymatous cells
Hamathecium	Richly branched, anastomosing paraphysoids, no periphyses	Simple to sparsely branched Paraphyses, no periphyses	Richly branched, anastomosing paraphysoids, no periphyses	Richly branched, anastomosing paraphysoids, periphyses present
Asci	Broadly obovate	cylindrical	cylindrical	cylindrical
Tholus	Well-developed	Poorly developed	Well-developed	Poorly developed
Ascus amyloidity	Outer wall hemiamyloid, tholus non-amyloid	Non-amyloid	Outer and wall and tholus amyloid	Non-amyloid
Ocular chamber	-	-	+	+/-
Ascospores	Hyaline, non-halonate, thick-walled, muriform	Hyaline, halonate, thin- to thick-walled, transversely septate to muriform	Hyaline, halonate, thick-walled muriform	Hyaline to brownish, halonate, thin-walled, muriform
Chemistry	Dibenzofuranes, triphenyl	Nil or pigments	nil	nil

hymenial algae, periphyses absent. Asci broadly obovate, with outer wall hemiamyloid and with a well-developed, non-amyloid tholus; ocular chamber lacking. Ascospores hyaline, non-halonate, eumuriform. Conidiomata immersed in the thallus, forming baciliform to bone-shaped conidia.

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An appraisal of megascience platforms for biodiversity information

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Abstract

The megascience platforms Biodiversity Heritage Library (BHL), Catalogue of Life (CoL), Encyclopedia of Life (EOL), Global Biodiversity Information Facility (GBIF), International Barcode of Life (iBOL), International Nucleotide Sequence Database Collaboration (INSDC) and JSTOR Plant Science, all belong to a group of global players that harvest, process, repurpose and provide biodiversity data on all kinds of organisms. Each of these platforms primarily focus on one data domain, for instance, taxonomy and classification, occurrence, morphology, ecology, and molecular data.

The present contribution describes aspects of processing and provision of biological research data on these platforms, focusing on the technical implementation of data exchange, copyright issues, and data sharing policies as well as their implications for data custodians, owners, providers, and publishers. With the exception of JSTOR Plant Science, most international initiatives seek long-term business models and funding mechanisms to provide online data openly and free of charge. For example, currently GBIF depends on governmental commitments for its funding, and CoL is financed by EU or national grants, as well as being based on Species 2000, a British non-for-profit company, and ITIS. These business models are compared with that of JSTOR Plant Science, the commercial portal of the Global Plant Initiative (GPI). All initiatives currently meet challenges of sustainability with regard to data curation as well as software development for maintaining the complexity of their services. All platforms discussed here also harvest and provide mycological and lichenological research data.

Keywords

Internet Platforms for Natural Sciences, BHL, CoL, EOL, GBIF, iBOL, JSTOR Plant Science, INSDC, DDBJ, EMBL, GenBank, Barcoding, Data Flow, Research Data

Introduction

In biodiversity research, data driven approaches, relying on internet resources that provide huge amounts of quality information, are increasingly important. In the late 1990s, most biodiversity websites offered more or less static web content and were operated by individual scientists or research groups. At that time, only a limited number of data access portals, mostly addressing data collections of homogenous structure, existed. Today, web-based information sources are almost overwhelmingly complex, heterogeneous, and seemingly exponentially growing. To find useful and reliable biodiversity information, several general approaches exist: (a) web sites where individual scientists or scientific community members curate categorized link collections, e.g., The Mycology.Net (<http://www.mycology.net>), (b) global search providers such as Google, Bing, or Yahoo and others that provide solutions with advanced generic search tools, and (c) so-called megascience platforms which have been set up in a scientific community context. The present contribution will analyse the latter approach and the probable challenges these will have to face in the future. It will focus on seven large platforms for biodiversity, which are relevant for lichen research data at a global scale.

Some major biodiversity data projects and platforms which have a geographically limited scope such as the Atlas of Living Australia (ALA; <http://www.ala.org.au/>) and the envisaged European LifeWatch project (<http://www.lifewatch.eu>) are not subject of this paper. Some other limited time projects, e.g., EDIT (<http://www.e-taxonomy.eu/>) or 4D4Life (<http://www.4d4life.eu/>), are not discussed in detail here because their results are contributing or have contributed to other platforms (e.g., 4D4Life results are injected into CoL).

Finally, several new initiatives or platforms are under active technical development and might attract relevant amounts of biodiversity and ecology research data in the near future. They are, however, not yet suitable for a comparison of the kind intended here. ViBRANT (<http://vbrant.eu/>) develops web-based virtual research communities for biodiversity science. Based on Scratchpads (<http://scratchpads.eu/>) and the Biowikifarm (<http://biowikifarm.net>), individual research communities share data management, curation, analysis and publishing services. This allows to improving effectiveness of research and supports long term data preservation and re-use in several of the platforms discussed here. pro-iBiosphere (<http://www.pro-ibiosphere.eu/>) is a coordination project to provide for a global generic organismic knowledge publishing and curation platform that brings the traditional Flora and Fauna editorial efforts into the digital world. The Map of Life (MOL; <http://www.mappinglife.org/about/>) project is an initiative that is just starting. Supported by content data from GBIF and EOL, it focuses on occurrence maps along with tools for querying and transforming related data.

History and scope of megascience platforms processing biodiversity information

Starting in the early 1990s, researchers in biology recognized the importance of the internet for disseminating data for research purposes. Work groups dedicating themselves on nucleic acid sequence data were the first to initiate domain-specific data projects covering all organism groups at a global level. Three platforms, EMBL-Bank (<http://www.ebi.ac.uk/embl/>), GenBank (<http://www.ncbi.nlm.nih.gov/genbank/>), and DDBJ (<http://www.ddbj.nig.ac.jp>) emerged, which in 1992 formed the International Nucleotide Sequence Database Collaboration (INSDC; <http://www.insdc.org>). Today, this consortium provides access to several databases focussing on molecular data.

Ten years later, in 2001, two other megascience platforms were initiated by scientists with the objective to collect and curate organismic biodiversity information. The first was the Catalogue of Life (CoL) that aims to produce a global quality-assured checklist of all species of plants, animals, fungi and other macro- and micro-organisms known to science (<http://www.catalogueoflife.org>). Currently, this data pool is supplied by data sets of more than 100 taxonomic databases and checklists and is annually updated. CoL currently contains authoritative names and synonyms for about 8,000 lichen species obtained from the Global Species Database LIAS (Rambold 2012; <http://www.catalogueoflife.org/col/details/database/id/79>).

In the same year, 2001, the Global Biodiversity Information Facility (GBIF) was initiated. It provides species distribution data in the form of occurrence records along with names and classifications, as well as links to additional information (<http://data.gbif.org/tutorial/tutorial>). GBIF makes data from more than 400 so-called 'data publishers' from all over the world openly and freely available. Occurrence records with geographical coordinates are visualized in global distribution maps. For instance, for Lecanoromycetes 3,281,898 occurrence records exist (last visited: 31-10-2012).

In 2003, the precursor project ('API – African Plant Initiative') of the Global Plant Initiative (GPI; <http://gpi.myspecies.info>) was started. The output of the efforts of GPI is accessible via the JSTOR Plant Science portal providing access to foundational content concerning plant type specimen data, taxonomy, references, high-resolution images of type specimens, and related literature (<http://plants.jstor.org/action/about>). JSTOR Plant Science makes available data that are shared by more than 220 partner herbaria worldwide. Certain lichen type collections, like those of BM, G, H, LINN and M, are accessible as well.

Subsequently in 2005, the Biodiversity Heritage Library (BHL) consortium was founded. BHL is a consortium of libraries with a focus on natural history and botanical literature that cooperate in digitizing and making legacy literature of biodiversity accessible under open access (<http://www.biodiversitylibrary.org>; last visited: 26-06-2012). Currently, more than 60,000 titles and 100,000 volumes are available. Scientific organism names in the literature are recognized by means of the uBio NameBank (including lichen species names from LIAS and Index Fungorum, see <http://names.ubio.org/browser/details.php?namebankID=3871575>). The BHL is not the only ini-

tiative or project digitalising historical biology literature (more than 40 are listed by Kasperek 2010), but so far it is the largest one.

In 2007, the CBOL (the Consortium for the Barcode of Life) started the International Barcode of Life (iBOL <http://ibol.org>) initiative. The original idea is a consequence of the barcoding proposal published by Hebert et al. (2003). The initiative is devoted to the collection of DNA barcoding sequence data <http://www.barcodinglife.com/> stored in the Barcode of Life Data System (BOLD). BOLD contains 156,461 taxa species with barcode sequences and a total of 1,702,485 specimens with barcode sequences, (last visited: 26-06-2012); about 1,250 of these are Lecanoromycete specimens (http://www.barcodinglife.com/index.php/Taxbrowser_Taxonpage?taxid=262560; last visited: 04-11-2012). The primary mission of iBOL is to extend the geographic and taxonomic coverage of the barcode reference library to store the resulting barcode records, to provide community access to the knowledge they represent, and to create new devices to ensure global access to this information. The work of iBOL is carried out by a research alliance spanning 25 nations with varying levels of investment and responsibilities (<http://www.barcodeoflife.org/content/about/what-ibol>). The overall task of the iBOL research participants is to collect and curate specimens, to extract DNA, to gather barcode data (records of group-specific DNA marker gene sequences), and to build up an informatics platform being required for storing and providing these records for species identification.

In the same year when iBOL was launched, 2007, another highly ambitious megascience initiative was launched: The Encyclopedia of Life (EOL; <http://eol.org/discover>), which collects and freely provides information about all species at a global scale including classifications, multimedia data, maps of occurrences. This initiative created more than 3.3 million pages: 1,079,652 pages with some amount of content, including 94,467 with considerable contents, being called ‘rich pages’ (http://eol.org/statistics/page_richness?date_one_set=2012-10-12&date_two_set=2012-10-31data.gbif.org).

Data domains

Each of the major biodiversity data platforms profiled here has its own scope (Table 1). Aside, each has a focus on one of the three central information segments: names and classification, occurrence, and descriptive or trait data.

Name data primarily include accepted names, synonyms, and proposed higher classification (usually reflecting a phylogenetic concept). Data from this domain may be classified as being either unequivocal (or ‘objective’, like the validity of a name according to the relevant nomenclatural code as well as the obligate synonymy), or equivocal (‘subjective’, e.g. depending on a phylogenetic concept, like the assignment of a heterotypic synonym to a currently accepted taxon name). Relevant databases for lichenology which provide taxon names as well as taxonomic concepts are LIAS names (<http://liasnames.lias.net/>; Triebel et al. 2010), Species Fungorum (<http://www.speciesfungorum.org/>), MycoBank (<http://www.mycobank.org/>), and, in future, the

Table 1. Contents and scopes of megascience platforms providing and processing biodiversity information

Megascience platform	Content and scope	Year of launch	Logo
International Nucleotide Sequence Databases (INSDC)	Nucleic acid sequences	1992	
Catalogue of Life (CoL)	Taxonomic checklists	2001	
Global Biodiversity Information Facility (GBIF)	Occurrences and records	2001	
JSTOR Plant Science	Type specimens, multimedia objects	2003	
Biodiversity Heritage Library (BHL)	Biodiversity literature, multimedia objects	2005	
Barcode of Life (iBOL)	DNA barcoding sequences	2007	
Encyclopedia of Life (EOL)	Knowledge data, species fact sheets, multimedia objects	2007	

evolving Chinese Portal for fungal names (<http://www.fungalinfo.net/fungalname/fungalname.html>). EOL, GBIF, BOLD for iBOL, and INSDC use the names and classifications from these and other name providers. Name data are also essential for the BHL site which provides access to digital images of biodiversity literature resources. BHL extracts scientific names from the digitized documents by a taxonomic name recognition algorithm and offers extended search techniques for these names. JSTOR Plant Science needs taxonomic names and information on classification to improve search tools and provide basic data on type specimens including multi-media objects important for taxonomy and systematics.

Occurrence data may be split into two major categories: collection and observation data. Collection data are correctly considered as more reliable when compared to observational records. However, for many groups of taxa, with sufficient quality con-

trol of observer expertise and combined with digital photographs or other multimedia data, the relevance of observational data has dramatically increased in recent years. The central platform for collection and occurrence data is GBIF. GBIF set up various kinds of tools and APIs to mobilise, visualize, and analyse the distribution patterns of taxa (<http://tools.gbif.org>), preferably with the data contents available through GBIF.

Descriptive data may be split in various specific ones, referring to a) morphological and anatomical characters and character states, b) to chemical properties (in the case of lichens, e.g. the highly diverse secondary metabolites), and c) to nucleic acid sequences, from DNA sequences of various genes (including the so-called ‘barcoding genes’) to full genome sequences d) to behavioural and ecological features. The central platform for descriptive data under a), b), and d) is EOL with the limitation that the descriptions of species are generated by individuals and partners with heterogeneous content data (e.g., FishBase), and do not derive from structured database contents. One major phenotypic trait database with structured descriptive data for lichen species is LIAS light (<http://liaslight.lias.net>), covering the morpho- and chemodiversity of about two thirds of all known lichen species (> 9,000 taxa). The most outstanding nucleic acid sequence database repository with three partners is the INSDC consortium with EMBL-Bank, NCBI-GenBank, and DDBJ.

Business models and consortial structures

In the case of the INSDC consortium, the collaborating institutions (DDBJ, EMBL-ENA, and NCBI-GenBank) have established data-sharing policies for more than twenty years. Responsibility for the quality and accuracy of the records, however, has been assigned to the submitting authors or institutions (<http://www.insdc.org/policy>). The three well-established partner institutions agreed to maintain a common technical core infrastructure for submission and archiving nucleic acid sequence data worldwide (Cochrane et al. 2010).

The Catalogue of Life (CoL) consortium is a cooperation of two partners being the autonomous federation of database organizations and taxonomic database custodians ‘Species2000’ (registered as a not-for-profit, limited by guarantee company in the UK), and ITIS, a partnership of federal agencies and other organizations from the United States, Canada, and Mexico. The CoL secretariat is currently located at University of Reading (UK) and mainly financed by grants and financial support from one of the two partners, Species2000. Data are provided by experts from 115 taxonomic databases from around the world, each responsible for a defined group of organisms (<http://www.catalogueoflife.org/col/info/about>). Data quality is assured by peer-review mechanisms.

The Global Biodiversity Information Facility (GBIF) is an intergovernmental organization. GBIF members or ‘GBIF participants’ (<http://www.gbif.org/participation/being-a-part-of-gbif/>) are about 60 nations (China not included) and approximately 50 international organizations. The voting participants provide financial contribution

to the GBIF secretariat, the advisory committee structure and the work program on a yearly basis (<http://www.gbif.org/governance/finance/>). They are responsible for the national support of the GBIF network, which is primarily a non-centralised system with national participant nodes (<http://www.gbif.org/participation/>). Data are provided by more than 420 mainly institutional publishers, being responsible for data quality and accuracy. GBIF is developing a decentralised network of 'biodiversity information facilities' (BIFs) established and maintained by its participants which, e.g., are countries or international organisations that have signed the GBIF Memorandum of Understanding (MoU) (<http://www.gbif.org/participation/participant-nodes>).

JSTOR Plant Science has been funded and spearheaded by the Andrew W. Mellon Foundation through the project 'Global Plant Initiative' (<http://about.jstor.org/content/jstor-plant-science>). Content partners and publishers are represented by more than 200 institutions from over 50 countries. The major goal of the initiative is to digitise herbarised type specimens (mainly plants, but also bryophytes, algae, fungi, and lichens) and provide access to images and metadata at a global scale. The digitised and quality-controlled data is published under non-exclusive license conditions by JSTOR (<http://about.jstor.org/10things>). JSTOR itself is a not-for-profit organization with a commercial segment being based on the income from subscriptions fees by foundations, university institutions, libraries and individuals for accessing the information. A considerable number of scholarship institutions have access for free, but the majority of individual scientists who are not affiliated to such institutions can use only a limited amount of the research data from JSTOR Plant Science for free.

The Biodiversity Heritage Library (BHL) is a consortium of 12 partner libraries from US and UK natural history collections, supported by grants from several foundations. Its primary funding came from the Encyclopedia of Life initiative (<http://biodivlib.wikispaces.com/Funding+Sources>), a close co-operation partner of this initiative. The BHL project is focussed on digitising legacy literature related to biodiversity. Since 2009, it has expanded globally, e.g. by an EU funded project with 28 institutions involved, as well as BHL nodes in China, Australia, and Brazil.

The International Barcode of Life (iBOL) initiative with its central node in Canada is funded mainly and by the Ontario government, two Canadian Foundations, and the Genome Canada association. The international research program is coordinated by a team at the University of Guelph and supports barcoding activities of the iBOL partners to a certain degree. The governance board consists of senior staff from Genome Canada, a science advisory committee, and an international scientific collaboration committee with members drawn from nations with funded barcoding projects linked to iBOL (<http://ibol.org/funding-shortfall-brings-changes-at-ibol/>). iBOL is structured and organized in four major nodes (Canada, China, Europe, US), several regional and national nodes, as well as partner organizations from 27 nations (<http://ibol.org/about-us/partner-nations/>).

The Encyclopedia of Life (EOL) is an international consortium, financially supported by 16 institutions and 6 foundations. Its contents are provided by more than 220 partner content data platforms and more than 62,000 so-called 'members'. Data

is quality-controlled by about 300 active EOL curators on a voluntary basis (<http://eol.org/statistics>; access 2012-10-31). The EOL executive committee provides governance and decision-making at the policy level. The senior individuals represent GBIF, BHL, foundations in the USA, and cornerstone institutions in the USA, Australia, China, Egypt, and Mexico (<http://eol.org/info/3#SC>).

In conclusion, only three to four of the seven initiatives have sufficient technical infrastructure backbone that can be regarded as independent from third-party grants to scientists or scientific institutions, which are INSDC, GBIF, JSTOR Plant Science, and probably EOL. For four of the seven initiatives discussed here, financing the creation of content data is not the central issue of the business model. Only JSTOR Plant Science, iBOL and BHL-US directly back this kind of activity by financial support. The remaining ones mainly rely on the motivation of volunteers and individual enthusiasts (EOL, CoL), or on national funding programs to support generation of data and its delivery (GBIF, iBOL).

Data flows, cross-linkages

Each of the seven platforms has its own profile with respect to data domains, providers and scope of contents, and user communities, but strong dependencies between the platforms (e.g. between BHL and EOL) exist. Furthermore, there is cooperation between the four platforms GBIF, iBOL, EOL and JSTOR Plant Science to visualise occurrence data and to link data from biodiversity literature. They therefore require a common name data backbone, provided by a jointly developed technical structure in the frame of a common project, the Global Names Architecture (GNA; <http://www.globalnames.org/>) project. For sequence data which is produced in the iBOL context, the INSDC consortium with NCBI GenBank has agreed to stand by as the general data repository and backup archive.

The cooperation and linkages between the seven megascience platforms themselves as well as between the seven initiatives and their primary data providers is assumed to be facilitated by relying on open source principles and on contents provided under creative commons or open database licences conditions or – at least – data sharing policies on a non-exclusive basis. With growing content, the data flow and cross-linkages between the seven platforms is visible (Fig. 1). In parallel, the backtracking of multimedia data with corresponding metadata, e.g., from EOL and from thematic portals like EDIT (<http://search.biocase.org/edit/>: this is mirroring the GBIF index database), back to the primary providers or publishers of scientific data is possible.

The data life cycle and data flow starts with data production. The megascience platforms are harvesting infrastructures which are part of a ‘food chain’ that starts with the primary-content producers to primary and secondary harvesters and ends up with data users, consumers and digesters. Data harvesters like GBIF and CoL, which are typically fed by research data from individual scientists and institutions, may alternatively also be supplied by primary data collecting infrastructures, e.g. by the World Regis-

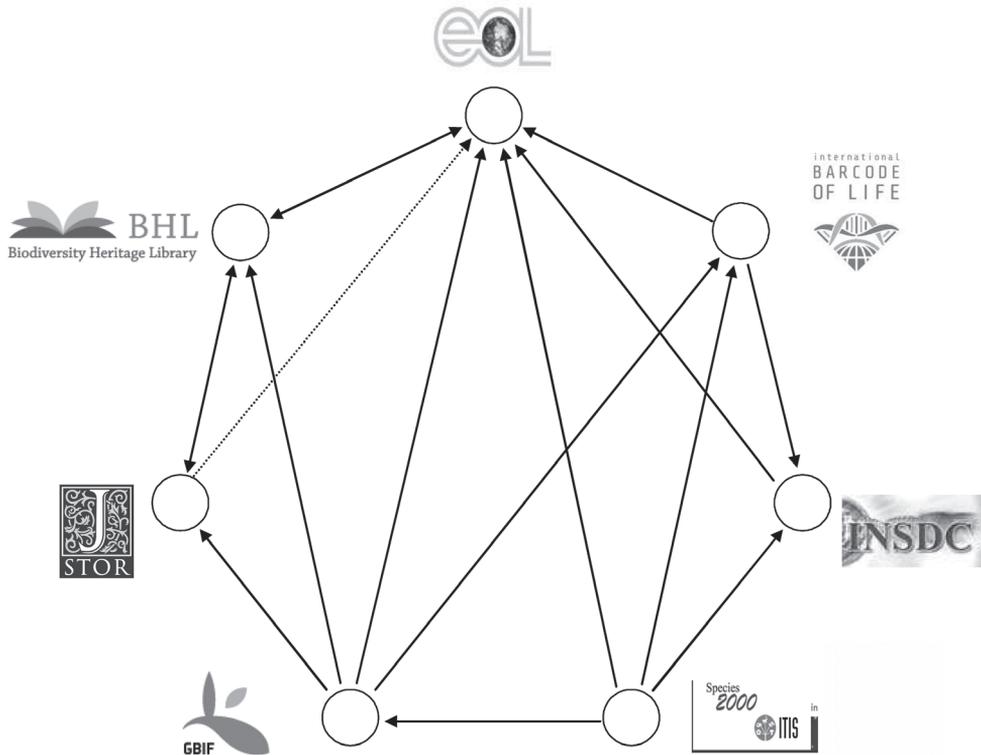


Figure 1. Biodiversity megascience platforms – cross-linkages and data exchange.

ter of Marine Species (WoRMS; <http://www.marinespecies.org/>), Species Fungorum (<http://www.speciesfungorum.org/>), and FishBase (<http://www.fishbase.org/>).

Names data, taxonomy, and classifications are of essential interests for all biodiversity platforms. Thus the comprehensive and reliable species databases offered by CoL form one of the multiple taxonomic backbones of EOL, GBIF, iBOL, BHL, and the INSDC data platforms.

Concerning taxonomic names and classifications, the data flows will be even more complicated in the future because there are overlapping and competing name thesauri for taxonomic and biological groups worldwide. As an example: Lichen names and synonym data are actually being collected by three different major sites (Index Fungorum/Species Fungorum; <http://www.indexfungorum.org>, LIAS names, and MycoBank), and are either directly forwarded to several megascience platforms, or indirectly via CoL.

Another type of data flow starts with the occurrence data harvested by the megascience platform GBIF. Several initiatives or projects like EDIT and BioCASE established data flow structures with mirrors of the GBIF index database. Based on these cache databases, they forward large amounts of GBIF occurrence data to various thematic search portals (<http://search.biocase.org/>; <http://search.biocase.org/edit/>; Holtschek et al. 2009).

Data harvesting, data exchange, and data quality

Different data harvesting strategies are required (a) for the initial content building from facts not yet available in aggregated form, and (b) for harvesting data that are already aggregated and available as databases, digital publications. In the latter case this may be organized as a unidirectional, perhaps hierarchical data flow, or as reciprocal exchange (partial or full data replication).

In both cases, the goal of megascience platforms is to attract data from a large number of potential provider groups, researchers and research groups, citizen scientists, and established infrastructure and science institutions. With regard to the data domains in focus of JSTOR Plant Science and BHL, institutions are the main data providers, whereas INSDC attract individual researchers and EOL – at least – intends to attract individual researchers and ‘citizen scientists’ to contribute with their data. Currently, however, the majority of data in EOL comes from other databases: Wikipedia, FishBase, Plazi, etc.

GBIF and CoL address large and small data aggregators, both institutional and individual, but not accept single data records from individual scientists. They require a certain level of aggregation and the capacity to follow structured information transfer protocols according to data exchange standards.

All seven platforms have to be attractive for their data provider communities and use easy-to-use upload techniques, modern web presentation, analysis and visualisation techniques and at least have started the implementation of download options. To facilitate massive collaboration with data providers, data users, and the data exchange between platforms of other data domains, the use of creative commons licenses for data content is urgently recommended (Hagedorn et al. 2011).

EOL was initiated as a funded project and will depend on third-party funds for continued operation. With its strong dependency on biodiversity communities and the activities of individuals and other project content partners, it will always be confronted by new user requirements due to the changing internet world and the rapid enhancement of web technologies. EOL relies mainly on the aggregation and harvesting of external content and uses established web technologies and community solutions to mobilise and cache data. Active input by users is guided via community user interfaces (e.g., until 2010 through so called LifeDesks, now by endorsing ViBRANT scratchpads).

With the growth of content and the rapid enhancement of web technologies, new technical challenges will have to be met to keep large amounts of data manageable and available. Thus the analysis options of the content data for scientific purposes actually are not (yet) in the focus of this platform.

The Wikipedia platform (as well as the associated Wikispecies) goes a citizen science driven and interactive way to mobilise species-related description data and images and provide them to public. Wikispecies currently comprises more than 343,862 content pages (mostly taxon pages, <https://species.wikimedia.org/wiki/Special:Statistics>), the contents of which is limited to nomenclature, taxonomic hierarchy, or names in various languages. The English Wikipedia contains approximately 213,661 taxon pag-

es (<http://toolserv.org/~jarry/templatecount/index.php?lang=en&name=Template%3ATaxobox#bottom>), most of which with substantial content.

INSDC is the only platform which has an explicit mandate from the scientific community to harvest and present data. This is achieved through alliances with publishers. Today, the editorial rules of most journals consider INSDC deposition of nucleotide or protein sequences and the citation of the resulting INSDC accession numbers as mandatory, a practice which “arose not passively, but through the efforts of INSDC member institutions and other proponents of open data sharing” (Cochrane et al. 2010). The technical mechanism of the data exchange in the INSDC consortium (with regard to nucleic acid sequence data submission and provision) is the pooling of the original data into one joint data management system, managing this newly established system at one institution and mirroring the database to the consortial partners. iBOL is using the INSDC consortial infrastructure for data archiving.

The large number of providers for occurrence data (from the monitoring community as well as the natural history collection community) and the large amount of data packages which are regularly updated determine the harvesting strategy of the GBIF network. It was originally planned for continuous connectivity and distributed queries, but the technical limitations were difficult to master. GBIF therefore now uses harvesting of a limited set of data instead (called ‘indexing’), such that the index is centrally maintained and can be directly queried. With the new GBIF integrated publishing toolkit (IPT) GBIF has been able to support a much wider range of content providers with less technical expertise. The updating of the harvested data may occur at short intervals, or only when a provider publishes a new version. In that way, they underline the decentralized approach of the network with independent data holders or publishers and a mediating role of the national GBIF participant nodes. The new harvesting network of CoL follows a similar strategy.

Data curation and quality control of harvested data is a main issue for all megascience platforms (e.g., Costello et al. 2012). All have to consider quality (in the sense of Chapman 2005) of the original data and address the life cycle of data. They do it in different ways:

GBIF, iBOL, JSTOR Plant Sciences, and probably INSDC, work to establish feedback mechanism to their primary data providers to improve quality of data. GBIF and CoL are planning to realise technical workflows to obtain high-quality data from primary sites by dynamic periodic and event-based data harvesting. Thus, they are likely to provide relatively up-to-date data, as far as the connected primary sites are maintained by domain experts. Platforms like iBOL rely on the direct input and curation efforts of the contributing scientific community and single researchers to ensure and improve the quality of data – similar as INSDC does. Besides relying on the quality of the harvested data from large content partners, EOL has established an own system of single EOL curators, who are expected to improve the harvested EOL content. There is, however, no regular feedback option to the primary data providers.

In addition, copies of harvested data occur which might be harvested again by EOL (or other megascience platforms and thematically focussed portals). Thus, it can

happen that the secondary information becomes ranked higher in internet searches than the original, well-curated information from the primary information site. Information duplication of this kind is most easily visible with Latin taxon names. For instance, a Google search of “*Rimularia exigua*”, a hitherto extremely rarely collected crustose lichen from Australia, only having been treated in the context of one monograph and occurring in only one primary species checklist, results in 330 hits, nearly all from secondary and tertiary data harvesters and portals like Cybertruffle (<http://www.cybertruffle.org.uk>) and SinBiota 2.0 (<http://sinbiota.biota.org.br>) which spread names data obtained, e.g., from CoL. Unfortunately, not only correct names are disseminated but also misspelled or otherwise erroneous names, even if they are corrected already at a primary information site.

Benefits for data producers, primary data providers and data consumers

Data producers and primary data providers are individuals or organizations that contribute with their data to the content of megascience platforms. They may profit in decidedly different ways from such an activity. The member institutions of JSTOR Plant Science are paid for their digitalisation efforts and contribution to the initiative by the A. Mellon foundation. With regard to GBIF, data providers directly profit from an established data pipeline that allows publishing data sets by using the integrated IPT publishing toolkit as recommended by the GBIF secretariat. In that context, the source data are getting processed and published in standard-compliant Darwin Core Archive (DwC-A) and Ecological Modeling Language (EML v2.1.1) formats (<http://www.gbif.org/informatics/infrastructure/publishing/>). Various feed-back mechanisms at the GBIF central node support quality control at the primary data site.

The easy access to useful and reliable high-quality data for open and free “data-driven” research purposes (with the aim to publish in high-ranked scientific journals) may be primarily of interest to the platform users and consumers, but not necessarily to the operators and content providers. The content maintenance of a scientific data platform therefore has to be considered as a valuable achievement of the data generators (and maintainers) *per se*. Recently, ‘data publishing’ through scientific information portals is combined with new kinds of mechanisms to provide additional incentives to data owners that provide their original data to others. The so-called ‘data papers’, currently promoted by GBIF and EOL community members and publishers like Pensoft (Chavan and Penev 2011), are suggested as an option to form a link between biodiversity data publishing via megascience platforms or portals and the scholarly publishing in peer-reviewed journals with DOI assignment and provision of impact factors. The process of data-paper-publishing uses a common GBIF/Pensoft workflow of data publishing and automated generation of data paper manuscripts using the GBIF integrated publishing toolkit, followed by the editorial workflow via the Pensoft online editorial system and resulting in a regular scholar

publication in online publication like the 'Biodiversity Data Journal' (<http://www.biomedcentral.com/1471-2105/12/S15/S2>) and MycoKeys.

Reliable and quality-controlled data are a prime interest of data consumers. The data publishing mechanism in the context of INSDC is the best example for that. It requires the active submission of the respective data sets by individuals or organisations which receive an INSDC accession number for every submitted nucleic or amino acid sequence. This identifier is requested by peer-reviewed journals for submission of manuscripts and allows for the backtracking of information to the data producer.

A similar solution is presently being established for the improvement of data content of fungal names thesauri which – regarding the data flow – will secondarily positively influence CoL data. A group of mycologists and database operators gained influence on the fungal scientific community and achieved that the new ICN code (ratified in Melbourne 2011) dictated, that, as of 1 January 2013, each new fungal name must be registered in a recognized repository prior to publication (Norvell 2011, Norvell and Redhead 2012). From a technical point of view, such obligations are probably unnecessary. It seems to make more sense to realise technical solutions for harvesting this type of data from open access (and access-limited) journals, all by now being available in digital form. To do this effectively, markup standards for scientific publishing should be developed, a topic presently dealt with by pro-iBiosphere.

Primary data providers also profit to some degree from seed money projects being funded by platform initiatives and consortia like GBIF, EOL, and CoL. At least, during the first years, iBOL proved to be an excellent opportunity for natural history collections to receive free DNA barcoding data of specimens in their own collections.

Primary data providers usually are also users of their own data and profit from various kinds of analysis options. As data are generally openly accessible (except those in JSTOR; see above), analysis of own data against a wider data background has become a standard use case. Most published phylogenies are based on nucleic acid sequence data of the data producer (or primary provider) combined with otherwise published background sequence data. The situation is similar for occurrence data, where freely available bioinformatics and biodiversity informatics tools for data analysis (INSDC, GBIF, iBOL, and BHL) and visualisation (GBIF, JSTOR, BHL, and EOL) enlarge benefit for platform users.

The benefit for scientists mainly depends on the amount and quality of openly and freely available information. Established megascience information platforms with a history of more than ten years like INSDC already comprise a considerable number of records. However, due to missing or insufficient data curation services by INSDC, insufficient mechanisms to improve and enrich previously submitted (meta-)data, uncritical use of INSDC cannot be recommended. For that reason, a considerable number of thematically focused secondary data platforms have evolved, providing quality-controlled data. In the context of nucleic acid sequence data especially valuable examples are the 'ITS2 Database' at Würzburg University, Germany (<http://its2.bioapps.biozentrum.uni-wuerzburg.de>), several RNA databases (e.g.,

net/Databases/RNA_Databases/), or, as an example of a full genome sequence database, the *Saccharomyces* genome database (<http://www.yeastgenome.org>).

In some cases, the quality of a data may also decrease with time. For instance, data being linked with taxonomic names may degenerate, as taxonomic opinions and phylogenetic concepts are not stable over time. The reasons for this are the discovery of new taxa, the reappraisal of old or discovery of new phenetic traits or of additional gene markers, or the application of improved data analysis algorithms. It entails that under insufficient and inadequate data curation conditions that insufficiently provide for data updates from the original data sources, even well-established megascience platforms are liable to become outdated sooner or later. With regard to taxonomic and nomenclature data flow mechanisms, two major preconditions need to be considered. Firstly, that external taxonomy sources, providing synonymy and classification, are up-to-date and second, that feed-back mechanisms between data sources and platforms need to provide mechanisms for correcting recognized inconsistencies. Both issues are presently not satisfactorily realized even for the oldest megascience platform INSDC, despite the fact that this platform has probably the strongest profile of all established biodiversity information platforms under discussion.

Discussion

In an era of data-driven research and open science (Krotoski 2012), biodiversity data platforms are facing a number of challenges. Perhaps the most important issue is the question of sustainability in data curation and software development. Data curation is a complex task that involves both primary data producers or providers and platforms which integrate such data. Although a primary responsibility for correctness lies with the primary data producers or providers, the platform has a responsibility to monitor the data quality and the frequency of updates from the data sources. A considerable part of quality control concerns the necessity of a data integration workflow, which typically exposes data quality issues, that were difficult to detect, while the data were curated in isolation. Beyond that, many platforms invest into purpose-built quality control tools, drawing on the development, computing, and data source integration power of the platform. Since the platform is often attracting a much larger number of users than the primary data source (should it be online), much feedback and annotation activity is likely to occur on the platform. Both, the platform workflow or tools-supplied and user-supplied feedback must be efficiently communicated to the primary data sources.

Amount and granularity of the primary data sources that are harvested or integrated into the platforms can range from huge databases to individual contributions both with elementary or rather detailed information. Although the various platforms have a different focus, in fact all have to support a wide spectrum of granularity from individuals to institutions. Because individuals typically have rather different means as well as motivations to curate a dataset than institutions, this further complicates quality control, annotation and feedback workflow. Presently, megascience platforms

rarely include the publishing level, which can be seen as a granularity gap between individual contributions (by direct editing) and data flow from private or institutional databases. New efforts (e.g., within the pro-iBiosphere project) explore the necessary collaboration infrastructure for a biodiversity 'Knowledge Organisation System' that bridges existing gaps between scientific publishing (journal articles as well as flora/fauna monographs) and megascience data platforms. To enable integration, structuring, quality control, feedback mechanism, attractive data retrieval and other sophisticated services (e.g., Hill et al. 2010), or even the realisation of virtual research environments, platforms need to invest into man person-years of software development work. A major problem with respect to the present dynamic world of a global information system is that software needs constant investment in maintenance and development simply to keep up with ongoing feature development and security fixes of the basic tools as well as software interfaces of partners.

Furthermore, the number of platforms with thematic but global focus in biology and environmental sciences is increasing. In the field of biodiversity they are often backboned by automatically generated template web pages filed according to taxon names. The temptation to fill these auto-generated pages with existing name lists and classification structures is evident and somehow understandable as it serves the desire to become globally relevant. The hope that such templates will be supplied with content by scientific community members, however, is rarely fulfilled.

The relation between megascience biodiversity information platforms and smaller, more focussed data providers is and will remain a complex one. Simplifying it by shifting all responsibility and ownership of data to a central institution or data node may, however, not be the right path into the future. While focussed central platforms can become a service to stakeholders, all-encompassing platforms are likely to satisfy only a limited number of use-cases. As a result, stakeholders still would require independent systems, leading in the end to lower total efficiency. We therefore believe that sharing responsibility and funding opportunities is the right path into the future. For the content partners of megascience biodiversity information platforms, it is most likely to be beneficial, if they operate their own original or primary databases under their own responsibility at an institution. In the long term that means – from the view of the megascience platforms – a decentralised approach should be realised. In that way, data sustainability and quality seems to be best ensured. The technical support for primary-content databases should be guaranteed by commitments of the institutions which hosts or own the databases. Also at that level of a decentralised biodiversity data network data architecture and IT infrastructure have to be continuously adapted to the changing requirements. At the same time, the infrastructure of the megascience platforms also depend on institutional or other reliable and permanent funding, as the technical and content data management of the platforms themselves will always remain a challenging task.

Due to the steadily increasing number of scientists from countries all over the world being involved in higher level biodiversity and environmental science projects, it is clear that certain architectures and mechanisms of data storage, transfer and provi-

sion will be recognized as obsolete. They are symptomatic of a past unilateral world. The megascience platforms discussed here, have to attract both, new primary-content partners by offering added values to them as well as new technical partners, e.g. as consortial members of equal rank. To be able to replicate information with primary-content partners, it will be necessary to implement technical interfaces that better support data exchange standards. In recent years with the rise of new user interface concepts, the mode of presentation needs to be adapted to changes in the device technologies (gestures and touch modes). Alleged limitations of database and data transfer technologies are sometimes used as an alibi to replace federated structures of distributed responsibility and ownership with central and often ‘monopolistic’ structures. However, centralised power always includes the temptation of abuse, be it to dictate prices (as seen in some major commercial scientific publishers), or be it to monopolize the use of data for research, trying to secure future research grants at the expense of excluding competing researchers (which may have a different research agenda, perspective, or insight).

Both single and distributed ownership of primary data can lead to monopolies or single-points of failure (for all or parts of the data). It is not uncommon that valuable data sources are either lost or that the owners decide to no longer share them. Long-term preservation and open access to scientific data is a prime value in science. Both a system of a single platform with a single data store, and a system where a large number of stakeholders could arbitrarily decide that it is no longer financially feasible or perhaps desirable to them to provide their data to the scientific community, does not fulfil this requirement. The solution would have to provide for a large number of duplicated storage of data, the use of which is at least as uninhibited as the use of books. Achieving this is (a) a technical problem in finding the right technologies to replicate large volumes of data, (b) a social problem in documenting and understanding the difference between primary holders that frequently update their data versus static copies that have been created for particular uses and which may become outdated, and (c) a legal problem, in providing sufficient rights over the copied data. Scientific knowledge becomes more valuable to society, the more it is shared. The scientific world must therefore take care that the principles of openness and sharing that have successfully governed science for centuries are not lost in the new age of digital scientific data. Sharing has to be open and permissive, following the principles of Open Science, Open Source and Open Data (Molloy 2011).

The megascience platforms discussed here already have to face complementary or alternative structures (e.g., EOL China, <http://www.eolchina.org/>; Species2000 China Node, <http://www.sp2000.cn/joaen/>; BHL China, <http://www.bhl-china.org/cms/>). Global platforms will probably still dominate in the near future and guide mainstream activities, but they will not be able to claim an exclusive status. They are driven by modern information technologies and have to support approaches for decentralized and ‘intelligent’ network structures with flexible data nodes. In this context, efforts of multilinguality and internationalisation should also be prioritized. Despite English being de facto the lingua franca of natural sciences, IT technologies will increasingly allow to (automatically) generate multilingual presentations to include users from countries outside the space of world-dominating languages.

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Internet resources

- Atlas of Living Australia (ALA) – <http://www.ala.org.au/>
- BioCASE Search Portal – <http://search.biocase.org/>
- Biodiversity Heritage Library (BHL) – <http://www.biodiversitylibrary.org/>; <http://biodiv-lib.wikispaces.com>
- Biodiversity Heritage Library China (BHL China) – <http://www.bhl-china.org>
- Bioexplorer – <http://www.bioexplorer.net>
- BioMed Central – <http://www.biomedcentral.com>
- Biowikifarm – <http://biowikifarm.net>
- BOLDSYSTEMS – <http://www.boldsystems.org/>; <http://www.barcodinglife.com>
- Catalogue of Life (COL) – <http://www.catalogueoflife.org/>; <http://www.catalogueoflife.org/colwebsite/content/contributors/>
- Cybertruffle – <http://www.cybertruffle.org.uk>
- Distributed Dynamic Diversity Databases for Life (4D4Life) – <http://www.4d4life.eu/>
- DNA Data Bank of Japan (DDBJ), Mishima, Japan – <http://www.ddbj.nig.ac.jp>
- EDIT Search Portal – <http://search.biocase.org/edit/>
- EMBL-Bank, European Nucleotide Archive, Cambridge, UK – <http://www.ebi.ac.uk/embl/>
- Encyclopedia of Life (EOL) – <http://eol.org>
- Encyclopedia of Life China (EOL China) – <http://eolchina.org>
- European Distributed Institute of Taxonomy (EDIT) – <http://www.e-taxonomy.eu/>
- FishBase – <http://www.fishbase.org/>
- Fungal Names Registration – <http://www.fungalinfo.net>
- Global Biodiversity Information Facility (GBIF) – <http://www.gbif.org>

Global Names Architecture (GNA) – <http://www.globalnames.org/>
GenBank, NCBI, Bethesda, MD, USA – <http://www.ncbi.nlm.nih.gov/genbank/>
Global Plants Initiative (GPI) – <http://gpi.myspecies.info/>; <http://plants.jstor.org/action/community/>
Index Fungorum – <http://www.indexfungorum.org>
International Barcode of Life (iBOL) – <http://www.barcodinglife.com>
International Nucleotide Sequence Database Collaboration (INSDC) – <http://www.insdc.org>
ITS2 Database – <http://its2.bioapps.biozentrum.uni-wuerzburg.de>
JSTOR – <http://www.jstor.org>
JSTOR Plant Science – <http://plants.jstor.org>
LIAS light – <http://liaslight.lias.net>
LIAS names – <http://liasnames.lias.net/>
LifeWatch – <http://www.lifewatch.eu>
Map of Life (MOL) – <http://www.mappinglife.org>
Mycobank – <http://www.mycobank.org/>
pro-iBiosphere – Coordination and policy development in preparation for a European Open Biodiversity Knowledge Management System, addressing Acquisition, Curation, Synthesis, Interoperability and Dissemination – <http://www.pro-ibiosphere.eu/>
Saccharomyces Genome Database (SGD) – <http://www.yeastgenome.org>
Scratchpads biodiversity online – <http://scratchpads.eu/>
SinBiota 2.0 – <http://sinbiota.biota.org.br>
Species Fungorum – <http://www.speciesfungorum.org/>
Species 2000 China Node – <http://www.sp2000.cn>
The Mycology Net – <http://www.mycology.net>
uBio Indexing & Organizing Biological Names – <http://names.ubio.org>
Virtual Biodiversity Research and Access Network for Taxonomy (ViBRANT) – <http://vbrant.eu/>
Wikimedia Toolserver – <https://toolserver.org>
Wikispecies – <https://species.wikimedia.org>
World Register of Marine Species (WoRMS) – <http://www.marinespecies.org/>

