WESTERDIJK FUNGAL BIO DIVERSITY INSTITUTE

New insights into the systematics of *Bactrodesmium* and its allies and introducing new genera, species and morphological patterns in the *Pleurotheciales* and *Savoryellales* (*Sordariomycetes*)

Martina Réblová[1*], Margarita Hernández-Restrepo[2], Jacques Fournier[3], and Jana Nekvindová[4]

[1]*The Czech Academy of Sciences, Institute of Botany, Department of Taxonomy, Průhonice, 252 43, Czech Republic;* [2]*Westerdijk Fungal Biodiversity Institute, Uppsalalaan 8, 3584 CT Utrecht, The Netherlands;* [3]*Las Muros, Rimont, 09420, France;* [4]*Institute of Clinical Biochemistry and Diagnostics, University Hospital and Faculty of Medicine, Charles University, Hradec Králové, 500 05, Czech Republic*

*Correspondence: Martina Réblová, martina.reblova@ibot.cas.cz

Abstract: The newly discovered systematic placement of *Bactrodesmium abruptum*, the lectotype species of the genus, prompted a re-evaluation of the traditionally broadly conceived genus *Bactrodesmium*. Fresh material, axenic cultures and new DNA sequence data of five gene regions of six species, i.e. *B. abruptum*, *B. diversum, B. leptopus*, *B. obovatum*, *B. pallidum* and *B. spilomeum*, were studied. *Bactrodesmium* is a strongly resolved lineage in the *Savoryellales* (*Sordariomycetes*), supported by Bayesian and Maximum Likelihood methods. The genus *Bactrodesmium* is emended and delimited to hyphomycetes characterised by sporodochial conidiomata, mononematous often fasciculate conidiophores, holoblastic conidiogenesis and acrogenous, solitary, dry, pigmented, transversely or rarely longitudinally septate conidia. The conidia are seceding rhexolytically, exhibiting multiple secession patterns. An identification key to 35 species accepted in *Bactrodesmium* is given, providing the most important diagnostic characters. Novel DNA sequence data of *B. longisporum* and *B. stilboideum* confirmed their placement in the *Sclerococcales* (*Eurotiomycetes*). For other *Bactrodesmium*, molecular data are available for *B. cubense* and *B. gabretae*, which position them in the *Dothideomycetes* and *Leotiomycetes*, respectively. All four species are excluded from *Bactrodesmium* and segregated into new genera, *Aphanodesmium*, *Gamsomyces* and *Kaseifertia*. Classification of 20 other species and varieties not recognised in the genus is discussed. Based on new collections of *Dematiosporium aquaticum*, the type species of *Dematiosporium*, the genus is emended to accommodate monodictys-like freshwater lignicolous fungi of the *Savoryellales* characterised by effuse colonies, holoblastic conidiogenous cells and dictyosporous, pigmented conidia with a pore in each cell. Study of additional new collections, cultures and DNA sequence data revealed several unknown species, which are proposed as taxonomic novelties in the *Savoryellales* and closely related *Pleurotheciales*. *Ascotaiwania latericolla*, *Helicoascotaiwania lacustris* and *Pleurotheciella erumpens* are described from terrestrial, lentic and lotic habitats from New Zealand and France, respectively. New combinations are proposed for *Helicoascotaiwania farinosa* and *Neoascotaiwania fusiformis*. Relationships and systematics of the *Savoryellales* are discussed in the light of recent phylogenies and morphological patterns newly linked with the order through cultural studies.

Key words: Conidial secession, Conidiogenesis, Molecular systematics, Sporodochium, Synnema, Wood-inhabiting fungi, 12 taxonomic novelties.

Taxonomic novelties: New genus: *Aphanodesmium* Réblová & Hern.-Restr., *Gamsomyces* Hern.-Restr. & Réblová, *Kaseifertia* Réblová, Hern.-Restr. & J. Fourn; **New species:** *Ascotaiwania latericolla* Réblová, Hern.-Restr. & J. Fourn., *Helicoascotaiwania lacustris* Réblová & J. Fourn., *Pleurotheciella erumpens* Réblová & J. Fourn; **New combination:** *Aphanodesmium gabretae* (Koukol & Kolářová) Réblová & Hern.-Restr., *Gamsomyces longisporus* (M.B. Ellis) Hern.-Restr. & Réblová, *Gamsomyces stilboideus* (R.F. Castañeda & G.R.W. Arnold) Hern.-Restr. & Réblová, *Helicoascotaiwania farinosa* (Linder) Réblová, Hern.-Restr. & J. Fourn., *Kaseifertia cubense* (R.F. Castañeda & G.R.W. Arnold) Réblová, Hern.-Restr. & J. Fourn., *Neoascotaiwania fusiformis* (Jing Yang, Bhat & K.D. Hyde) Réblová, Hern.-Restr. & J. Fourn.

Available online 3 March 2020; https://doi.org/10.1016/j.simyco.2020.02.002.

INTRODUCTION

Fungi classified in the *Pleurotheciales* and *Savoryellales* are non-lichenized perithecial ascomycetes and dematiaceous hyphomycetes with holoblastic conidiogenesis, some of which belong to the life cycle of known sexual morphs (Boonyuen *et al.* 2011, Réblová *et al.* 2016a). They are saprobes thriving on decaying wood or plant debris in aquatic and terrestrial habitats. Rarely, some species of the *Pleurotheciales* were identified as opportunistic human pathogens (*Phaeoisaria*, Guarro *et al.* 2000, Chew *et al.* 2010). Members of both orders share several sexual morphological traits such as the absence of stromatic tissue or clypeus, perithecial ascomata, similar anatomy of the ascomatal wall, thin-walled unitunicate asci with a non-amyloid apical annulus and symmetrical, transversely septate, hyaline or pigmented ascospores with hyaline end cells. However, the main variability between the two groups lies in conidial morphology and conidiogenous cell extension of the known asexual morphs and is characteristic of each order.

The *Savoryellales* are linked with asexual morphs characterised by sporodochial conidiomata or effuse colonies, mononematous conidiophores and thick-walled, dry, pigmented conidia with transverse and longitudinal septa. They are part of the life cycle of *Ascotaiwania*, *Canalisporium*, *Dematiosporium*, *Neoascotaiwania* and *Savoryella* (e.g. Sivichai *et al.* 1998, Chang 2001, Boonyuen *et al.* 2011, Réblová *et al.* 2016a, Yang *et al.* 2016, Hernández-Restrepo *et al.* 2017, Zhang *et al.* 2019). On the other hand, asexual morphs linked with the *Pleurotheciales* represent a diverse assemblage of fungi classified in 10 holomorphic or asexually reproducing genera. They produce effuse colonies or rarely sporodochial conidiomata, mononematous or synnematous conidiophores and usually thin-walled, hyaline or pigmented, straight or helicoid, septate, dry or slimy conidia formed mostly on short denticles or rachis on sympodially extending conidiogenous cells (e.g. Fallah

Peer review under responsibility of Westerdijk Fungal Biodiversity Institute.

Studies in Mycology

et al. 1999, Fernández et al. 1999, Réblová & Seifert 2011, Réblová et al. 2012, 2016a, b, Cheng et al. 2014, Hernández-Restrepo et al. 2017, Luo et al. 2018).

In this study, we focused on *Bactrodesmium*, an enigmatic and little understood hyphomycete genus whose representative species *B. pallidum* was linked with the *Savoryellales* by DNA sequence data (Hernández-Restrepo et al. 2017) and accepted in the broadly delimited *Ascotaiwania* (Dayarathne et al. 2019). The generic name *Bactrodesmium* was proposed by Cooke (1883) for dematiaceous hyphomycetes forming sporodochia in the substrate and clavate, transversely septate conidia to accommodate *Sporidesmium abruptum* (Berkeley & Broome 1865) and *Sporidesmium spilomeum* (Rabenhorst, Fungi europaei Exs. No. 1162. 1868), but the nomenclatural changes were not made. The designation of *B. abruptum* as the lectotype species of *Bactrodesmium* and new combinations were introduced by Hughes (1958). In 1886, Saccardo reduced *Bactrodesmium* to synonymy with *Clasterosporium* (Schweinitz 1832), but this treatment was not accepted by subsequent authors (e.g. Ellis 1959, Zhang et al. 2016). Some unusual elements such as distosepta and also oblique and longitudinal septa in conidia were accepted by Ellis (1976) and Sutton (1967, 1975, 1977) to expand the generic concept of *Bactrodesmium*.

So far, 57 species and varieties have been proposed in *Bactrodesmium* (Index Fungorum). The genus accommodates species that occur mostly on decaying wood and bark, although some species were also reported from leaves, living (*B. mastigophorum*) or fallen (e.g. *B. peruvianum*, *B. novaegeronense*), or other unusual substrates like paper (*B. papyricola*) (e.g. Sydow & Sydow 1920, Moreau & Moreau 1957, Ellis 1959, 1963, 1976, Holubová-Jechová 1972, Sutton 1977, Hughes 1983, 1984, Hughes & White 1983a–i, Castañeda-Ruiz 1985). Several morphological traits are highly characteristic for the genus. The sporodochial conidiomata are brown to black, visible as little shining spiky piles or little heaps easily overlooked on the substrate. Rarely, colonies of several species are effuse. Conidiophores of *Bactrodesmium* are macronematous or semi-macronematous, mononematous, seldom characterised as synnematous. Conidia are formed holoblastically on the conidiogenous cells; they are phragmosporous or dictyosporous, euseptate or distoseptate, sometimes with bands at the transverse septa, subhyaline or have various shades of golden, brown, olive brown to black colour, and some possess distinct pores at the septa. The conidial shape varies from subglobose, pyriform, clavate, obovoid, ellipsoidal, fusiform to cylindrical. The conidium secession of *Bactrodesmium* has been addressed several times and according to various authors it was considered either rhexolytic (e.g. Ellis 1963, 1976, Palm & Stewart 1982, Hughes 1983, Kirk 1985, 1986, Mercado et al. 1995, Hernández-Restrepo et al. 2013) or schizolytic (e.g. Palm & Stewart 1982, Révay 1993, Cooper 2005, Markovskaja 2006).

The broad delimitation of *Bactrodesmium* lacks phylogenetic support. In addition to *B. pallidum*, the published DNA sequence data confirmed the systematic placement of only two other species suggesting a polyphyletic nature of *Bactrodesmium*. They were assigned to distantly related groups pending nomenclatural changes, namely *B. cubense* (Castañeda-Ruiz & Arnold 1985) in the *Pleosporales* (*Dothideomycetes*) (Tanaka et al. 2015) and *B. gabretae* in the *Helotiales* (*Leotiomycetes*) (Koukol & Kolářová 2010). Hernández-Restrepo et al. (2017) placed several strains of *Trichocladium opacum*, a species confirmed by Ellis (1959) to be conspecific with *Sporidesmium fasciculare* (syn. *Bactrodesmium fasciculare sensu* Mason & Hughes 1953), in the *Pleosporales* and introduced a new genus *Pleotrichocladium*. In addition, Funk & Shoemaker (1983) confirmed by experimental studies that *B. obliquum* var. *suttonii* (Hughes & White 1983b) is the asexual morph of *Stuartella suttonii*, currently placed in the *Dothideomycetes* genera *incertae sedis*. The life history of other *Bactrodesmium* remains unknown.

Our extensive sampling in freshwater and terrestrial biotopes in the Czech Republic and France revealed several sporodochial *Bactrodesmium* species. They were identified with six known species, i.e. *B. abruptum*, *B. diversum, B. leptopus*, *B. obovatum*, *B. pallidum* and *B. spilomeum* (Ellis 1959, 1963, Saccardo 1881a, Hughes & White 1983a, c, Hernández-Restrepo et al. 2013), and isolated into the axenic culture. *Bactrodesmium stilboideum* (Castañeda-Ruiz & Arnold 1985), collected on a submerged twig in Puerto Rico and forming synnemata in culture and in the natural substrate, was compared with morphologically similar *B. longisporum* (Ellis 1976) from Japan and India, producing both sporodochia and synnemata in terrestrial habitats, while in culture only sporodochia were formed. Hughes (1978) transferred *B. longisporum* to *Stigmina* (*Mycosphaerellales*), but this treatment was not accepted by Rao & de Hoog (1986), who considered it conspecific with *B. stilboideum*. Mena-Portales & Mercado (1987) regarded *Stigmina* a correct genus and proposed *Stigmina longispora* var. *stilboidea*.

We also collected additional representatives of the *Pleurotheciales* and *Savoryellales* such as *Dematiosporium aquaticum* (Luo et al. 2019) and *Neoascotaiwania terrestris* (Hernández-Restrepo et al. 2017), which exist only in one exemplar, and three other unknown species. Examination of three collections of *D. aquaticum* and its axenic culture derived from conidia revealed that the fungus possesses dictyosporous conidia with a germ pore in each cell, diagnostic characters not described in the protologues of the genus and species (Luo et al. 2019). A collection of an undescribed fungus, which features the genus *Ascotaiwania* (Sivanesan & Chang 1992), was made on decaying wood in New Zealand. A monodictys-like asexual morph was observed in the juxtaposition to the ascomata; however, the axenic culture derived from the ascospores remained sterile. On wood submerged in small artificial lakes in gravel pits were collected specimens of a species highly reminiscent of *Helicoascotaiwania hughesii* (Fallah et al. 1999). Our samples can be distinguished from the latter species by different anatomy of the ascomatal wall, wider asci and presence of a shallow, refractive apical annulus obscured by a large pulvillus in the ascal apex. Numerous collections made on submerged wood in France belong to a species of *Pleurotheciella* (Réblová et al. 2012). *Pleurotheciella* has been experimentally linked with dactylaria-like asexual morphs, but the majority of its species reproduce only asexually. The axenic culture derived from the ascospore isolate yielded sterile mycelium only.

The motivation of this study was to assess the systematic placement of several *Bactrodesmium* species, including *B. abruptum*, and other undescribed species with affinity to the *Pleurotheciales* and *Savoryellales*. We based our study on morphological and cultivation studies and DNA sequence analyses. Evolutionary relationships of *Bactrodesmium* and related species were revealed in multigene-based phylogenies of five nuclear ribosomal and protein-coding loci of our isolates and members of four orders, the *Conioscyphales*, *Fuscosporellales*, *Pleurotheciales* and *Savoryellales*. These orders were recovered

Table 1. Isolates examined in this study.

Taxon	Source	Substrate and host	Locality
Ascotaiwania latericolla	ICMP 22739T	on decaying wood	Auckland, New Zealand
Bactrodesmium abruptum	CBS 145966	on submerged wood of *Robinia pseudoaccacia*	Ariège, France
B. abruptum	CBS 145968	on submerged wood	Ariège, France
B. abruptum	CBS 145967	on submerged wood	Ariège, France
B. abruptum	CBS 144404	on submerged wood of *Fraxinus excelsior*	Ariège, France
B. diversum	CBS 142448	on submerged wood of *Fraxinus excelsior*	Ariège, France
B. diversum	CBS 142450	on submerged wood of *Fraxinus excelsior*	Ariège, France
B. diversum	CBS 144079	on submerged wood of *Fraxinus excelsior*	Ariège, France
B. diversum	CBS 144401	on submerged wood of *Alnus glutinosa*	Ariège, France
B. diversum	CBS 144080	on submerged wood of *Alnus glutinosa*	Ariège, France
B. diversum	CBS 144081ET, IMI 506813ET	on submerged wood of *Fraxinus excelsior*	Ariège, France
B. diversum	CBS 144405	on submerged wood of *Robinia pseudoaccacia*	Ariège, France
B. diversum	CBS 145435	on submerged wood	Ariège, France
B. diversum	CBS 145965	on submerged wood of *Robinia pseudoaccacia*	Ariège, France
B. diversum	CBS 145970	on submerged wood	Ariège, France
B. diversum	CBS 145969	on submerged wood	Ariège, France
B. leptopus	CBS 144542	on decaying wood of *Acer campestre*	South Moravia, Czech Republic
B. obovatum	CBS 144078	on submerged wood of *Fraxinus excelsior*	Ariège, France
B. obovatum	CBS 144077	on submerged wood of *Corylus avellana*	Ariège, France
B. obovatum	CBS 145350	on submerged wood	Ariège, France
B. obovatum	CBS 144407	on decaying wood of *Fraxinus excelsior*	South Moravia, Czech Republic
B. pallidum	CBS 142449	on submerged wood of *Fraxinus excelsior*	Ariège, France
B. pallidum	CBS 145349	on submerged wood of *Robinia pseudoaccacia*	Ariège, France
B. spilomeum	CBS 146104	on submerged wood	Ariège, France
Dematiosporium aquaticum	CBS 144793	on submerged wood	Ariège, France
Gamsomyces longisporus	CBS 118.86	on decaying branch	Karnataka, India
G. longisporus	CBS 240.89	on decaying stem of bamboo	Kyoto, Japan
G. stilboideus	CBS 146494	on submerged twig	Puerto Rico
Helicoascotaiwania lacustris	CBS 145963T, MUCL 56486T	on submerged wood of *Populus* sp.	Haute-Garonne, France
H. lacustris	CBS 145964	on submerged wood of *Populus* sp.	Haute-Garonne, France
H. lacustris	CBS 146144	on submerged wood of *Salix atrocinerea*	Haute-Garonne, France
Neoascotaiwania terrestris	CBS 144402	submerged wood of *Fraxinus excelsior*	Ariège, France
Pleurotheciella erumpens	CBS 142447T	on submerged wood of a coniferous tree	Ariège, France

Remarks: T and ET denotes ex-type and ex-epitype strains.

as a robust monophylum within the *Hypocreomycetidae* and characterised by true, partially disintegrating paraphyses, while the rest of the subclass comprises several other types of hamathecial elements (Réblová *et al.* 2016a). The BLASTn search (Zhang *et al.* 2000) of nuclear ribosomal sequences of *B. longisporum* and *B. stilboideum* indicated that both species are not related to the rest of *Bactrodesmium* studied, but exhibit affinities with members of the *Sclerococcales* (*Eurotiomycetes*). In order to reveal their relationships, we based the phylogenetic analysis on four nuclear ribosomal and protein-coding loci of representatives of this order. In this study, we also investigated relationships of *B. gabretae* in a multigene phylogenetic analysis employing nuclear ribosomal, mitochondrial and protein-coding loci of seventeen families of the *Helotiales*.

MATERIALS AND METHODS

Fungal isolates and herbarium specimens

Herbarium specimens were obtained from Royal Botanical Gardens (K, IMI), Kew, United Kingdom, Fungarium of the University of Illinois (ILLS), Illinois Natural History Survey, Champaign, Illinois, USA and Westerdijk Fungal Biodiversity Institute (CBS), Utrecht, the Netherlands. Living cultures of *Bactrodesmium longisporum* were obtained from CBS. Additional material for this study was collected in the Czech Republic, France, New Zealand, USA and Spain.

Representative strains and ex-type strains are maintained at CBS, Facultat de Medicina de Reus (FMR), Tarragona, Spain,

BCCM/MUCL Agro-food & Environmental Fungal Collection (MUCL), Université catholique de Louvain, Louvain, Belgium, CABI-IMI Culture Collection (IMI), CABI Bioscience, Egham, United Kingdom, and International Collection of Microorganisms from Plants (ICMP), Auckland, New Zealand. Holotypes (as dried plant material) and other herbarium material are deposited in the New Zealand Fungarium (PDD), Auckland, New Zealand and the Herbarium of the Institute of Botany (PRA), Czech Academy of Sciences, Průhonice, Czech Republic.

Dead branches and decaying wood removed from trunks lying on the ground were collected in paper bags, transferred to the laboratory and air-dried. Twigs and branches submerged in streams were collected in plastic bags and transported to the laboratory. Sediments were washed off with tap water. Freshwater samples were air-dried, placed in the moist chambers and incubated at a temperature of 20–25 °C (Castañeda-Ruiz *et al.* 2016) and periodically checked for the development of sporodochia. Isolates examined in this study and their sources are listed in Table 1.

Morphological characterisation

Morphological characteristics were obtained from fungi growing on the natural substrate and growth media. Descriptions in the keys are based on fungi growing on the natural substrate unless otherwise indicated.

Dried herbarium material was rehydrated with water and examined with an Olympus SZX12 dissecting microscope (Olympus America, Inc., Melville, USA). The sections of the ascomatal wall and centrum material containing asci, ascospores and paraphyses were studied in Melzer's reagent, 90 % lactic acid, lactophenol with cotton blue, Congo red, toluidin blue or Waterman blue ink. Sporodochia, synnemata, conidiophores and conidia were studied in water and lactic acid, occasionally in Melzer's reagent. Measurements of asci, ascospores and paraphyses were made in Melzer's reagent, measurements of conidiophores, conidiogenous cells and conidia were made in water. Means ± standard deviation (SD) based on the minimum of 20–25 measurements are given for dimensions of asci, ascospores and conidia.

Single and multiple ascospore and conidial isolates were obtained from fresh material with the aid of a single-spore isolator (Meopta, Czech Republic). The ascospore and conidium isolates were incubated on water agar or Modified Leonian's agar (MLA) (Malloch 1981) at a temperature of 20–25 °C and periodically checked for the development of germinating tubes that appeared within 48 h, and later for growth of mycelium and sporulation. Because all strains developed more or less abundant aerial mycelium and all sporulated within the given temperature range, the morphological characterisation of the colonies was carried out at a temperature of 23 °C. Different growth media were selected to cover various sources of carbon, nitrogen and B vitamins for colony description and stimulation of sporulation (Guarro *et al.* 2012, Crous *et al.* 2019). Also, MLA was selected to stimulate sporulation and mycelium growth (Malloch 1981) and also for the ability to stimulate the production of pigments in mycelium or diffusing in agar (M. Réblová *et al.*, in preparation).

For comparative purposes and culture characteristics, strains were inoculated in triplicate on five different media: cornmeal dextrose agar (CMD) (17 g of cornmeal agar Oxoid Limited, Hampshire, United Kingdom, 2 g of dextrose, 1 L of distilled water, sterilised for 15 min at 121 °C), malt extract agar (MEA), oatmeal agar (CBSOA) and potato-carrot agar (PCA) (Crous *et al.* 2019), MLA and oatmeal agar (OA) (modified from Gooding & Lucas 1959; 30 g of oatmeal cooked in 1 L of distilled water for 15–30 min, filtered through the cheesecloth, the filtrate was brought back to volume with distilled water, 15 g of agar, sterilised for 60 min at 121 °C). Descriptions of colonies are based on 2-, 4- and 6-wk-old cultures grown in darkness at 23 °C.

Microscopic observations were made using an Olympus BX51 compound microscope with differential interference contrast (DIC) and phase contrast (PC) illumination. Images of microscopic structures were captured with an Olympus DP70 camera operated by Imaging Software CellD (Olympus). Colony photographs were taken using a copy stand and Canon EOS 77D digital camera with Canon EF 100 mm f/2.8L Macro IS USM objective (Canon Europe Ltd., Middlesex, United Kingdom) with daylight spectrum 5 500 K 16W LED lights. All images were processed with Adobe Photoshop CS6 (Adobe Systems, San Jose, USA).

DNA extraction and amplification

Total genomic DNA was extracted from mycelium removed from 3-wk-old cultures grown on MLA using the DNeasy® UltraClean® Microbial Kit (Qiagen GmbH, Germany) following the manufacturer's protocol for filamentous fungi. All PCR amplifications were carried out in 25 µL volume reactions using Q5 High Fidelity DNA polymerase system/ kit (New England Biolabs Inc., GB) according to manufacturer's protocol, including Q5 PCR enhancer. Primers used for the amplification of genes and gene regions included: 1) NSSU131/NS24 (Gargas & Taylor 1992, Kauff & Lutzoni 2002) and NS1/NS8 (White *et al.* 1990) for the nuclear small subunit (SSU) 18S ribosomal DNA gene, 2) V9G/LR8 (de Hoog & Gerrits van den Ende 1998, Vilgalys unpublished) for the internal transcribed spacer (ITS) of the nuclear rRNA cistron and a first half (approx. 1 900 bp of the 5′ end) of the nuclear large subunit (LSU) 28S ribosomal DNA gene, 3) fRPB2-5F/fRPB2-7cR (Liu *et al.* 1999) for segments 5–7 of the second largest subunit of RNA polymerase II (*rpb2*), and 4) EF1-983F/EF1-2218R (Rehner & Buckley 2005) for the intermediate section of the coding region of the translation elongation factor 1-alpha (*tef1-α*).

PCR was carried out in a BioRad C1000 thermal cycler (Bio-Rad Laboratories Inc., USA) as following: (SSU) 98 °C for 30 s; 45 cycles of denaturation (98 °C for 20 s), annealing (56 °C for 30 s) and elongation (72 °C for 90 s) and a final extension step at 72 °C for 5 min; (ITS-LSU) 98 °C for 30 s; 40 cycles of denaturation (98 °C for 10 s), annealing (62 °C for 30 s) and elongation (72 °C for 90 s) and a final extension step at 72 °C for 5 min; (*rpb2*) 98 °C for 30 s; 45 cycles of denaturation (98 °C for 10 s), annealing (58 °C for 15 s) and elongation (72 °C for 30 s) and a final extension step at 72 °C for 2 min, and (*tef1-α*) 98 °C for 30 s; 40 cycles of denaturation (98 °C for 10 s), annealing (57 °C for 10 s) and elongation (72 °C for 60 s) and a final extension step at 72 °C for 2 min.

Amplicons were purified from agarose gel using NucleoSpin® Gel and PCR Clean-up Kit (Macherey-Nagel GmbH & Co. KG, Germany) following the manufacturer's instructions, with an elution volume of 25 µL. The DNA concentration was assessed

Table 2. Taxa, isolate information and new sequences determined for this study (in bold) and additional sequences retrieved from GenBank.

Taxon	Source	GenBank accession numbers					Reference
		ITS	LSU	SSU	*rpb2*	*tef1-α*	
Adelosphaeria catenata	CBS 138679T	KT278721	KT278707	KT278692	KT278743	—	Réblová *et al.* (2016a)
Anapleurothecium botulisporum	CBS 132713T	KY853423	KY853483	—	—	—	Hernández-Restrepo *et al.* (2017)
Ascotaiwania latericolla	ICMP 22739T	**MN699390**	**MN699407**	—	**MN704312**	—	This study
A. lignicola	NIL 00005	HQ446341	HQ446364	HQ446284	HQ446419	HQ446307	Boonyuen *et al.* (2011)
A. lignicola	NIL 00006	HQ446342	HQ446365	HQ446285	—	HQ446308	Boonyuen *et al.* (2011)
A. mitriformis	HKUCC 3706	—	AF132324	—	—	—	Ranghoo *et al.* (1999)
A. sawadae	SS 00051	HQ446340	HQ446363	HQ446283	HQ446418	HQ446306	Boonyuen *et al.* (2011)
A. uniseptata	Sloan 5406	—	KT278718	–	–	—	Réblová *et al.* (2016a)
Aspergillus fumigatus	INFU/Jc/KF/6, F-A, Af293	—	FM179606	GU980961	XM_741647	—	Nierman et al. (2005), Kusari et al. (2009), SSU sequence unpublished
Bactrodesmiastrum obovatum	FMR 6482T	FR870264	FR870266	—	—	—	Hernández-Restrepo *et al.* (2013)
B. pyriforme	FMR 10747T	FR870263	FR870265	—	—	—	Hernández-Restrepo *et al.* (2013)
Bactrodesmium abruptum	CBS 144404	**MN699391**	**MN699408**	**MN699365**	**MN704288**	**MN704313**	This study
B. abruptum	CBS 145966	**MN699392**	**MN699409**	**MN699366**	**MN704289**	**MN704314**	This study
B. abruptum	CBS 145967	**MN699393**	**MN699410**	**MN699367**	**MN704290**	**MN704315**	This study
B. abruptum	CBS 145968	**MN699394**	**MN699411**	**MN699368**	**MN704291**	**MN704316**	This study
B. diversum	CBS 142448	**MN699352**	**MN699412**	**MN699369**	**MN704292**	**MN704317**	This study
B. diversum	CBS 142450	**MN699353**	**MN699413**	**MN699370**	**MN704293**	**MN704318**	This study
B. diversum	CBS 144079	**MN699354**	**MN699414**	—	—	—	This study
B. diversum	CBS 144080	**MN699355**	**MN699415**	**MN699371**	**MN704294**	**MN704319**	This study
B. diversum	CBS 144081ET, IMI 506813ET	**MN699356**	**MN699416**	**MN699372**	**MN704295**	**MN704320**	This study
B. diversum	CBS 144401	**MN699357**	**MN699417**	—	—	—	This study
B. diversum	CBS 144405	**MN699358**	**MN699418**	—	—	—	This study
B. diversum	CBS 145435	**MN699359**	**MN699419**	—	—	—	This study
B. diversum	CBS 145965	**MN699360**	**MN699420**	—	—	—	This study
B. diversum	CBS 145969	**MN699361**	**MN699421**	—	—	—	This study
B. diversum	CBS 145970	**MN699362**	**MN699422**	**MN699373**	**MN704296**	—	This study
B. leptopus	CBS 144542	**MN699388**	**MN699423**	**MN699374**	**MN704297**	**MN704321**	This study
B. obovatum	CBS 144077	**MN699395**	**MN699424**	**MN699375**	**MN704298**	**MN704322**	This study
B. obovatum	CBS 144078	**MN699396**	**MN699425**	**MN699376**	—	**MN704323**	This study
B. obovatum	CBS 144407	**MN699397**	**MN699426**	**MN699377**	**MN704299**	**MN704324**	This study
B. obovatum	CBS 145350	**MN699398**	**MN699427**	**MN699378**	**MN704300**	**MN704325**	This study

(*continued on next page*)

Table 2. (Continued).

Taxon	Source	GenBank accession numbers					Reference
		ITS	LSU	SSU	*rpb2*	*tef1-α*	
B. pallidum	CBS 130515	KY853425	KY853485	—	—	—	Hernández-Restrepo *et al.* (2017)
B. pallidum	CBS 142449	**MN699363**	**MN699428**	**MN699379**	**MN704301**	**MN704326**	This study
B. pallidum	CBS 145349	**MN699364**	**MN699429**	**MN699380**	**MN704302**	**MN704327**	This study
B. spilomeum	CBS 146104	—	—	**MN699381**	**MN704303**	**MN704328**	This study
Canalisporium caribense	SS 03683	—	GQ390269	GQ390254	—	—	Boonyuen *et al.* (2011)
C. elegans	SS 00895	—	GQ390271	GQ390256	HQ446425	HQ446311	Boonyuen *et al.* (2011)
C. exiguum	SS 00809	—	GQ390281	GQ390266	HQ446436	—	Boonyuen *et al.* (2011)
C. grenadoidia	BCC 20507T	GQ390267	GQ390252	HQ446420	—	HQ446309	Boonyuen *et al.* (2011)
C. pulchrum	SS 03982	—	GQ390277	GQ390262	HQ446431	HQ446319	Boonyuen *et al.* (2011)
Conioscypha hoehnelii	FMR 11592T	KY853437	KY853497	HF937348	—	—	Hernández-Restrepo *et al.* (2017)
C. japonica	CBS 387.84T	—	AY484514	JQ437438	JQ437438	—	Réblová & Seifert 2004, Réblová *et al.* (2012)
C. lignicola	CBS 335.93T	—	AY484513	JQ437439	JQ429260	—	Réblová & Seifert 2004, Réblová *et al.* (2012)
C. varia	CBS 113653	—	AY484512	AY484511	JQ429261	—	Réblová & Seifert 2004, Réblová *et al.* (2012)
Cylindroconidiis aquaticus	MFLUCC 11-0294T	MH236576	MH236579	MH236580	—	—	Yu *et al.* (2018)
Dematiosporium aquaticum	CBS 144793	**MN699402**	**MN699433**	**MN699385**	**MN704307**	**MN704330**	This study
D. aquaticum	MFLU 18-1641	—	MK835855	—	MN194029	MN200286	Luo *et al.* (2019)
Eupenicillium javanicum	AFTOL-ID 429	—	EF413621	EF413620	EF413622	—	Geiser *et al.* (2007)
Fuscosporella pyriformis	MFLUCC 16-0570T	MG388217	KX550896	KX550900	KX576872	—	Yang *et al.* (2016)
Fusichalara minuta	CBS 709.88	KX537754	KX537758	KX537773	KX537770	—	Réblová *et al.* (2016b)
Gamsomyces longisporus	CBS 118.86	**MT020865**	**MT020877**	**MT026565**	**MT023101**	—	This study
G. longisporus	CBS 240.89	**MT020866**	**MT020878**	**MT026566**	**MT023102**	—	This study
G. stilboideus	CBS 146494	**MT020867**	**MT020879**	**MT026567**	**MT023103**	—	This study
Helicoascotaiwania farinosa	DAOMC 241947	JQ429145	JQ429230	—	—	—	Réblová *et al.* (2012)
H. farinosa	ILLS 53605T	—	AY094189	—	—	—	Campbell & Shearer (2004)
H. lacustris	CBS 145963T, MUCL 56486T	**MN699399**	**MN699430**	**MN699382**	**MN704304**	**MN704329**	This study
H. lacustris	CBS 145964	**MN699400**	**MN699431**	**MN699383**	**MN704305**	—	This study
H. lacustris	CBS 146144	**MN699401**	**MN699432**	**MN699384**	**MN704306**	—	This study
Melanotrigonum ovale	CBS 138743T	KT278724	KT278709	KT278696	KT278745	—	Réblová *et al.* (2016a)
M. ovale	CBS 138815	KT278722	KT278711	KT278698	KT278747	—	Réblová *et al.* (2016a)
Monotosporella setosa	HKUCC 3713	—	AF132334	—	—	—	Ranghoo *et al.* (1999)
Mucispora obscuriseptata	MFLUCC 15-0618T	MG388218	KX550892	KX550897	—	—	Yang *et al.* (2016)
Neoascotaiwania fusiformis	MFLUCC 15-0621T	MG388215	KX550893	—	KX576871	—	Yang *et al.* (2016)

Table 2. (Continued).

Taxon	Source	GenBank accession numbers					Reference
		ITS	LSU	SSU	*rpb2*	*tef1-α*	
N. fusiformis	MFLUCC 15-0625	MG388216	KX550894	KX550898	—	—	Yang *et al.* 2016
N. limnetica	CBS 126576	KY853452	KY853513	KT278689	**MN704308**	**MN704331**	Réblová *et al.* (2016a), Hernández-Restrepo *et al.* (2017), This study
N. limnetica	CBS 126792	KY853453	KY853514	KT278690	**MN704309**	**MN704332**	Réblová *et al.* (2016a), Hernández-Restrepo *et al.* (2017), This study
N. terrestris	CBS 144402	**MN699405**	**MN699434**	**MN699386**	**MN704310**	**MN704333**	This study
N. terrestris	CBS 142291T	KY853454	KY853515	KY853547	—	—	Hernández-Restrepo *et al.* (2017), This study
Parafuscosporella moniliformis	MFLUCC 15-0626T	MG388219	KX550895	KX550899	—	—	Yang *et al.* (2016)
Phaeoisaria aquatica	MFLUCC 16-1298T	MF399237	MF399254	—	MF401406	—	Luo *et al.* (2018)
P. clematidis	DAOMC 226789	JQ429155	JQ429231	JQ429243	JQ429262	—	Réblová *et al.* (2012)
P. fasciculata	CBS 127885T	KT278719	KT278705	KT278693	KT278741	—	Réblová *et al.* (2016a)
P. pseudoclematidis	MFLUCC 11-0393T	KP744457	KP744501	KP753962	—	—	Liu *et al.* (2015)
Phragmocephala stemphylioides	DAOM 673211	KT278730	KT278717	—	—	—	Réblová *et al.* (2016a)
Plagiascoma frondosum	CBS 139031T	—	KT278713	KT278701	KT278749	—	Réblová *et al.* (2016a)
Pleurotheciella aquatica	MFLUCC 17-0464T	MF399236	MF399253	MF399220	MF401405	—	Luo *et al.* (2018)
P. centenaria	DAOMC 229631T	JQ429151	JQ429234	JQ429246	JQ429265	—	Réblová *et al.* (2016a)
P. erumpens	CBS 142447T	**MN699406**	**MN699435**	**MN699387**	**MN704311**	**MN704334**	This study
P. fusiformis	MFLUCC 17-0113T	MF399233	MF399250	MF399218	MF401403	—	Luo *et al.* (2018)
P. guttulata	KUMCC 15-0296T	MF399240	MF399257	MF399223	MF401409	—	Luo *et al.* (2018)
P. krabiensis	MFLUCC 16-0852T	MG837018	MG837013	MG837023	—	—	Hyde *et al.* (2018)
P. lunata	MFLUCC 17-0111T	MF399238	MF399255	MF399221	MF401407	—	Luo *et al.* (2018)
P. rivularia	CBS 125238T	JQ429160	JQ429232	JQ429244	JQ429263	—	Réblová *et al.* (2012)
P. saprophytica	MFLUCC 16-1251T	MF399241	MF399258	MF399224	MF401410	—	Luo *et al.* (2018)
P. submersa	MFLUCC 17-1709T	MF399243	MF399260	MF399226	MF401412	—	Luo *et al.* (2018)
P. tropica	MFLUCC 16-0867T	MG837020	MG837015	MG837025	—	—	Hyde *et al.* (2018)
P. uniseptata	DAOMC 673210T	KT278729	KT278716	—	—	—	Réblová *et al.* (2016a)
P. aquaticum	MFLUCC 17-1331T	MF399245	MF399263	—	—	—	Luo *et al.* (2018)
P. floriforme	MFLUCC 15-1163T	KY697281	KY697277	KY697279	—	—	Hyde *et al.* (2017)
P. pulneyense	MFLUCC 16-1293T	—	MF399262	MF399228	MF401414	—	Luo *et al.* (2018)
P. recurvatum	CBS 101581	JQ429148	AF261070	JQ429248	JQ429266	—	Réblová *et al.* (2012)

(*continued on next page*)

Table 2. (Continued).

Taxon	Source	GenBank accession numbers					Reference
		ITS	LSU	SSU	*rpb2*	*tef1-α*	
P. semifecundum	CBS 131271T	JQ429159	JQ429240	JQ429254	JQ429270	—	Réblová *et al.* (2012)
Pseudosclerococcum golindoi	CBS 143732T	MK759885	MK759890	MK759887	—	—	Olariaga *et al.* (2019)
Rhopalophora clavispora	CBS 129.74	KX537751	KX537755	—	KX537767	—	Réblová *et al.* (2016b)
R. clavispora	CBS 281.75	KX537752	KX537756	KX537771	KX537768	—	Réblová *et al.* (2016b)
R. clavispora	CBS 637.73T	KX537753	KX537757	KX537772	KX537769	—	Réblová *et al.* (2016b)
Savoryella aquatica	SS 03801	HQ446349	HQ446372	HQ446292	HQ446441	HQ446326	Boonyuen *et al.* (2011)
S. lignicola	NF 00204	HQ446357	HQ446378	HQ446300	—	HQ446334	Boonyuen *et al.* (2011)
S. longispora	SAT 00322	HQ446359	HQ446380	HQ446302	HQ446450	HQ446336	Boonyuen *et al.* (2011)
S. paucispora	SAT 00866	HQ446360	HQ446381	HQ446303	HQ446451	HQ446337	Boonyuen *et al.* (2011)
S. verrucosa	SS 00052	HQ446353	HQ446374	HQ446296	HQ446445	HQ446330	Boonyuen *et al.* (2011)
Sclerococcum ahtii	RP23	KY661630	KY661659	—	—	—	Pino-Bodas *et al.* (2017)
S. glaucomarioides	RP275	KY661632	KY661660	—	—	—	Pino-Bodas *et al.* (2017)
S. haliotrephum	ATCC:MYA-3590	—	FJ176855	FJ176802	FJ238344	—	Schoch *et al.* (2009)
S. lobariellum	ARAN-Fungi 10091	—	MK759891	—	—	—	Olariaga *et al.* (2019)
S. mangrovei	CBS 110444	—	FJ176890	FJ176836	FJ238375	—	Schoch *et al.* (2009)
S. parasiticum	ARAN-Fungi 02724	—	MK759892	MK759888	—	—	Olariaga *et al.* (2019)
S. sphaerale	Diederich 17279	—	JX081672	—	—	—	Diederich *et al.* (2013)
S. stygium	ARAN-Fungi 03395/823	MK759886	MK759896	MK759889	—	—	Olariaga *et al.* (2019)
S. vrijmoediae	NTOU 4002T	—	KC692153	KC692152	KC692154	—	Pang *et al.* (2014)
Sterigmatobotrys macrocarpa	PRM 915682, CBS 113468	JQ429153	GU017317	JQ429255	JQ429271	—	Réblová *et al.* (2012)
S. rudis	DAOMC 229838	JQ429152	JQ429241	JQ429256	JQ429272	—	Réblová *et al.* (2012)
S. uniseptata	FMR 11937	HF677178	—	—	—	—	Hernández-Restrepo *et al.* (2017)
Tolypocladium capitatum	OSC 71233	—	AY489721	AY489689	DQ522421	AY489615	Castlebury *et al.* (2004), Spatafora *et al.* (2007)
T. japonicum	OSC 110991	—	DQ518761	DQ522547	DQ522428	DQ522330	Spatafora *et al.* (2007)
Trichocoma paradoxa	CBS 788.83	—	FJ358290	FJ358354	JN121550	—	Gueidan *et al.* (2008), Houbraken & Samson (2011)
beetle-associated isolate	INBio 4503Q	KM242300	KM242300	—	—	—	Vargas-Asensio *et al.* (2014)
beetle-associated isolate	INBio 4513J	KM242356	KM242356	—	—	—	Vargas-Asensio *et al.* (2014)
beetle-associated isolate	INBio 4513L	KM242358	KM242358	—	—	—	Vargas-Asensio *et al.* (2014)

Remarks: T and ET denotes ex-type and ex-epitype strains.

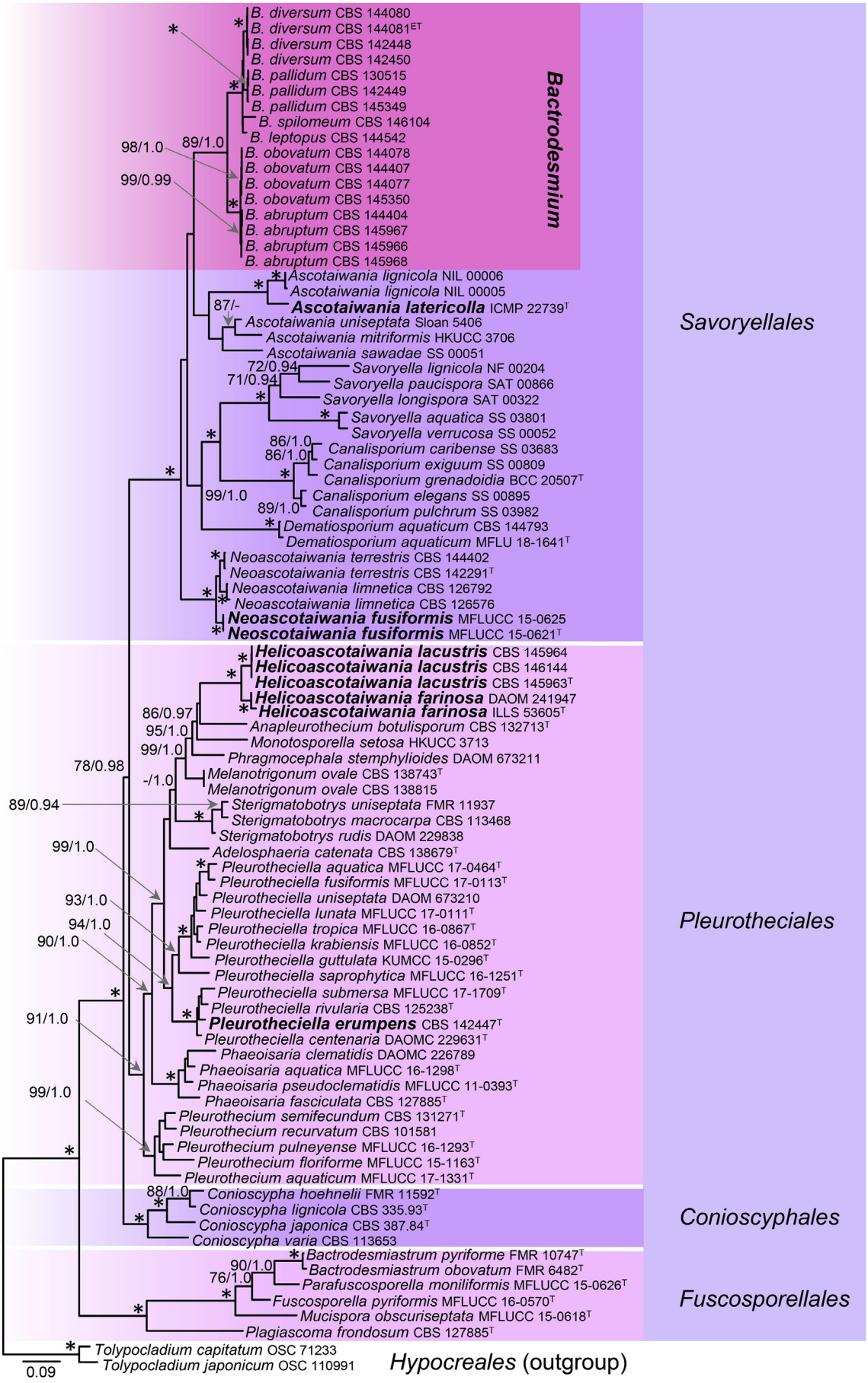

Fig. 1. Combined phylogeny using ITS, LSU SSU, *rpb2* and *tef1-α* of selected members of four orders of the *Hypocreomycetidae*. Species names given in bold are taxonomic novelties, T and ET indicates ex-type strains. An asterisk (*) indicates branches with ML BS = 100 %, PP values = 1.0. Branch support of nodes ≥70 % ML BS and ≥0.90 PP is indicated above or below branches.

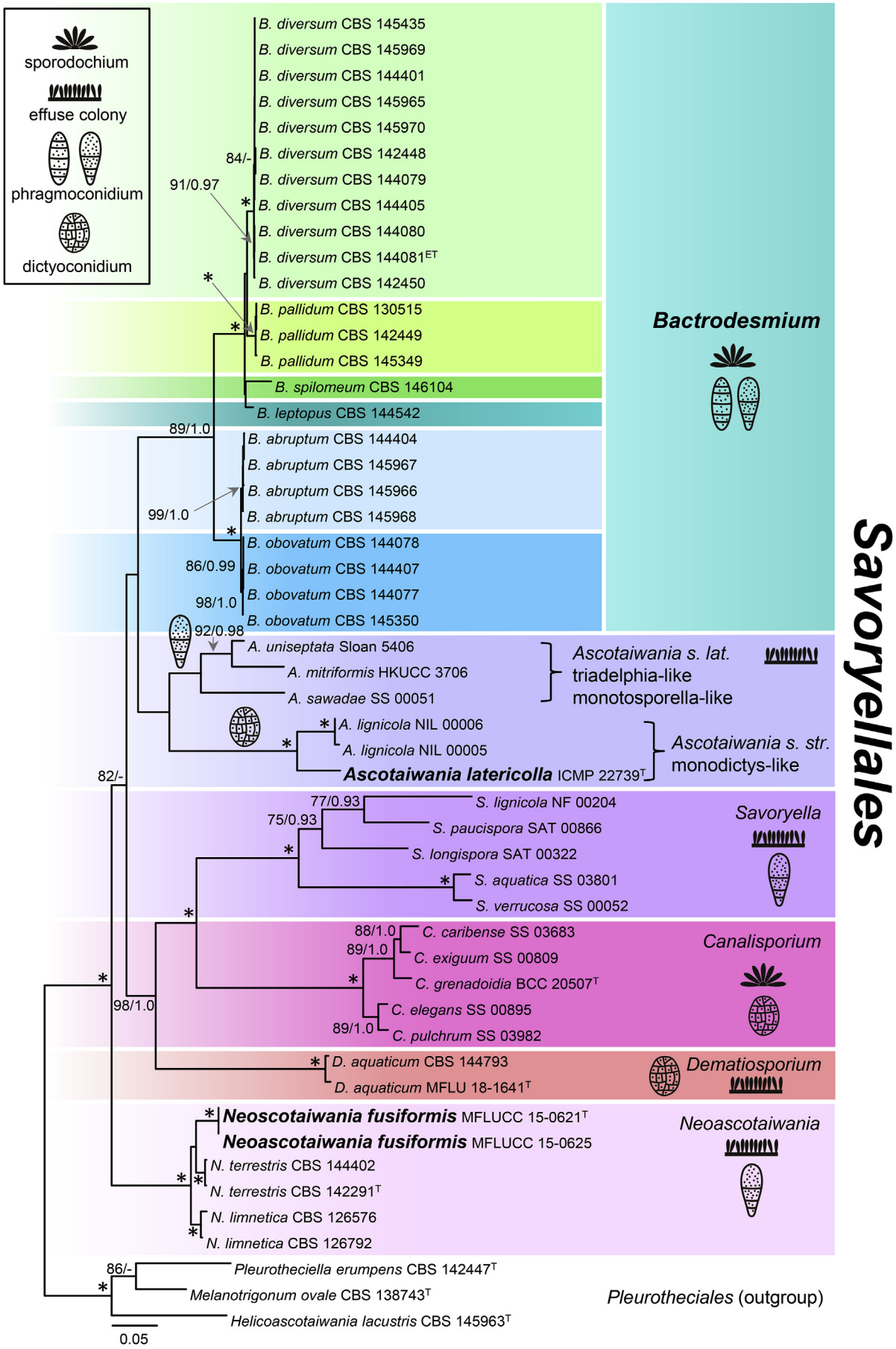

Fig. 2. Combined phylogeny using ITS, LSU, SSU, *rpb2* and *tef1-α* of members of the *Savoryellales*. Species names given in bold are taxonomic novelties, T and ET indicates ex-type strains. An asterisk (*) indicates branches with ML BS = 100 %, PP values = 1.0. Branch support of nodes ≥70 % ML BS and ≥0.90 PP is indicated above or below branches. Morphology of conidia and colonies for individual genera is indicated by icons for phragmoconidium/dictyoconidium and sporodochium/effuse colony.

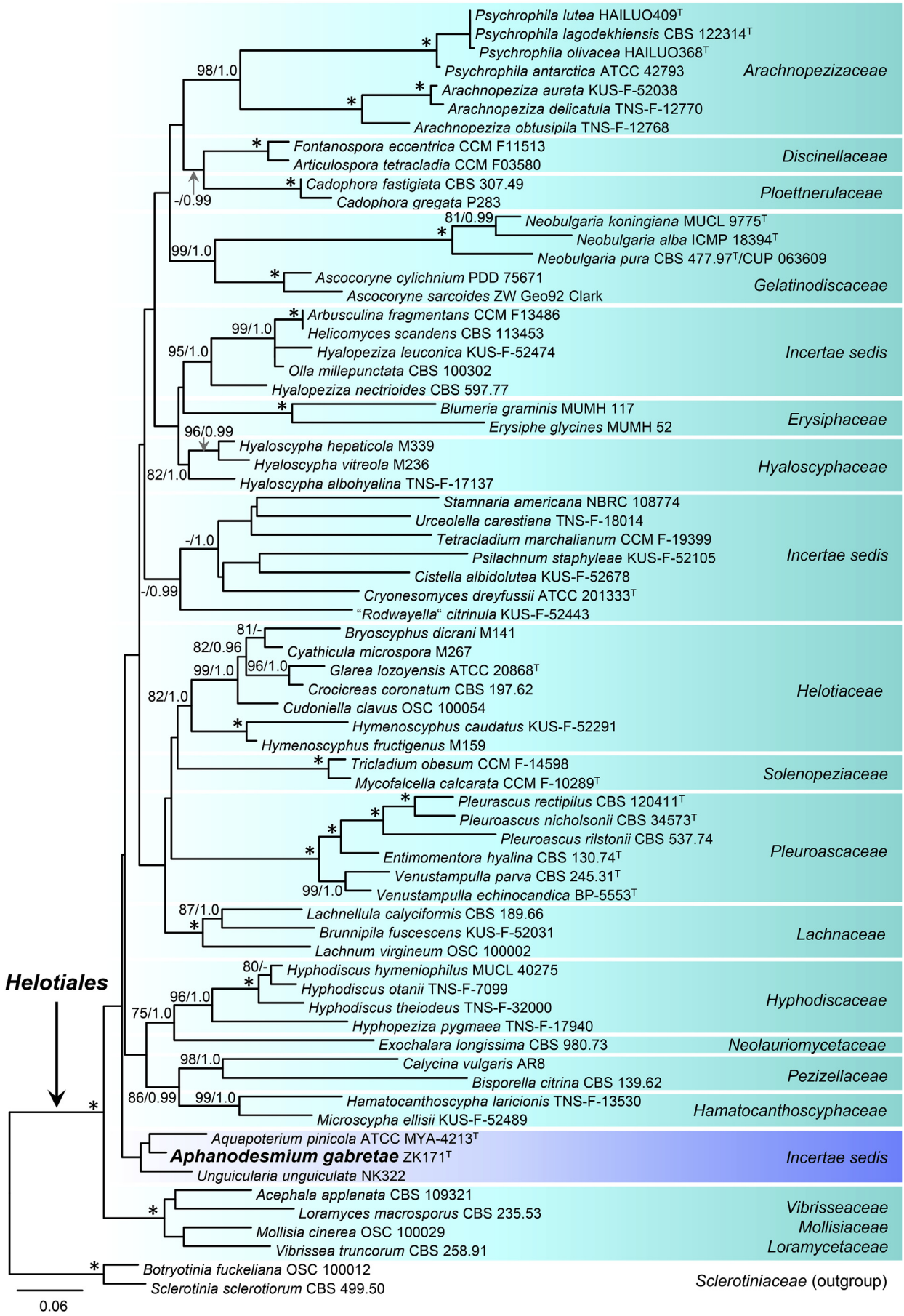

Fig. 3. Combined phylogeny using LSU, SSU, *rpb2* and mitSSU of representatives of the *Helotiales*. The species name given in bold is a taxonomic novelty, T indicates ex-type strains. An asterisk (*) indicates branches with ML BS = 100 %, PP values = 1.0. Branch support of nodes ≥70 % ML BS and ≥0.90 PP is indicated above or below branches.

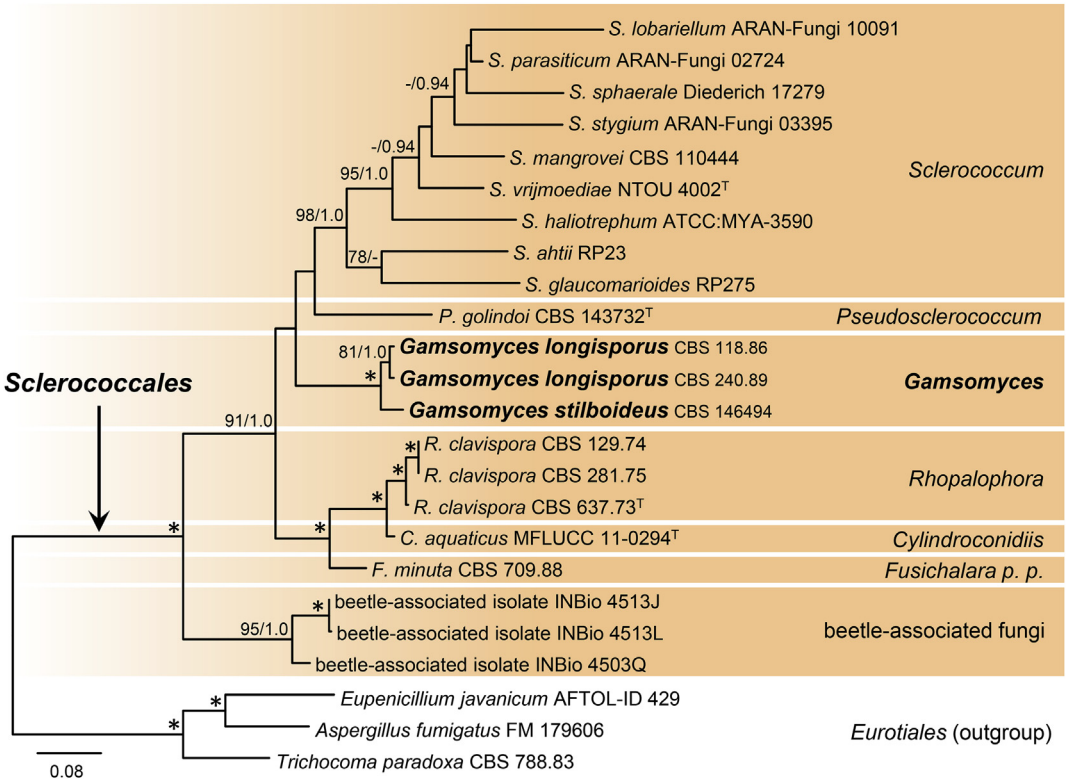

Fig. 4. Combined phylogeny using ITS, LSU, SSU and *rpb2* of representatives of the *Sclerococcales*. Species names given in bold are taxonomic novelties, T indicates ex-type strains. An asterisk (*) indicates branches with ML BS = 100 %, PP values = 1.0. Branch support of nodes ≥70 % ML BS and ≥0.90 PP is indicated above or below branches.

fluorimetrically using Quant-iT PicoGreen dsDNA Assay Kit and Qubit fluorometer (Invitrogen / Thermo Fisher Scientific, USA) to assure required sequencing concentrations adjusted for the length of amplicons/ number of reads required.

Each of the amplicons was sequenced in both directions using the PCR primers and nested primers: ITS5, ITS4, JS1, JS7, JS8, LR7 and LR8 for ITS-LSU (Vilgalys & Hester 1990, White *et al.* 1990, Landvik 1996, Vilgalys unpublished) and NS4, NS5, NSSU1088, NSSU1088R, NSSU897R, NS6 for SSU (White *et al.* 1990, Kauff & Lutzoni 2002). Automated sequencing was carried out by Eurofins GATC Biotech Sequencing Service (Cologne, Germany). Raw sequence data were assembled, examined and edited using Sequencher v. 5.4.6 (Gene Codes Corp., Ann Arbor, USA).

GenBank accession numbers for ITS, SSU, LSU, *rpb2* and *tef1-α* sequences generated in this study and previously published homologous sequences of members of the *Conioscyphales*, *Fuscosporellales*, *Pleurotheciales* and *Savoryellales* (*Hypocreomycetidae*) retrieved from GenBank (Sayers *et al.* 2019) are listed in Table 2. The LSU, SSU, the mitochondrial small subunit (mitSSU) 18S rRNA gene and *rpb2* sequences of representative species belonging to the *Helotiales* were obtained from our study (Untereiner *et al.* 2019) and selected according to Johnston *et al.* (2019). The closest relatives of *B. gabretae* (ex-type strain ZK171, LSU: FN561755, Koukol & Kolářová 2010), i.e. *Aquapoterium pinicola* (ex-type strain ATCC MYA-4213, LSU: EU183121, Raja *et al.* 2008) and *Unguicularia unguiculata* (strain NK322, SSU: HG326613, *rpb2*: HG326614, unpublished), were selected from the top-scoring matches using BLASTn and retrieved from GenBank.

Selected markers, alignments and phylogenetic analyses

Five gene markers (ITS, LSU, SSU, *rpb2* and *tef1-α*) were used in combinations to evaluate the evolutionary relationships of studied fungi with members of the four orders of the *Hypocreomycetidae* (*Sordariomycetes*) and *Sclerococcales* (*Eurotiomycetes*). The ITS gene has been sanctioned the universal DNA barcode for fungi (Schoch *et al.* 2012). The LSU, SSU, *rpb2* and *tef1-α* markers have been used in concatenated alignments to explore ordinal and supraordinal phylogenetic relationships of *Ascomycota* (Schoch *et al.* 2009) including *Sordariomycetes* (e.g. Zhang *et al.* 2007) and have a good representation in the *Hypocreomycetidae*. Besides, *rpb2* and *tef1-α* genes also provide subordinate taxon resolution and have high species resolving power (e.g. Rivera & Seifert 2011, Stielow *et al.* 2015, Wang *et al.* 2019). The mitSSU marker is an additional gene that has been used to resolve the relationships of members of the *Helotiales* (Han *et al.* 2014, Untereiner *et al.* 2019).

ITS, LSU, SSU, *rpb2* and *tef1-α* sequences were aligned manually in BioEdit v. 7.1.8 (Hall 1999); the alignment of mitSSU sequences was generated in MAFFT v. 7 (Katoh & Standley 2013) and corrected manually. Introns and ambiguous regions were excluded from the alignment. Single-locus data sets for members of four orders, including *Savoryellales*, of the *Hypocreomycetidae* (ITS: 70 sequences/709 characters including gaps, LSU: 90/1 920, SSU: 70/1 770, *rpb2*: 62/1 149, *tef1-α*: 33/1 014), *Helotiales* (*Leotiomycetes*) (LSU 69/1 232; SSU: 43/1 797; *rpb2*: 41/1 156; mitSSU 36/1 987) and *Sclerococcales* (ITS: 15/490; LSU 21/1 208; SSU: 13/1 727; *rpb2*: 10/1 137) were

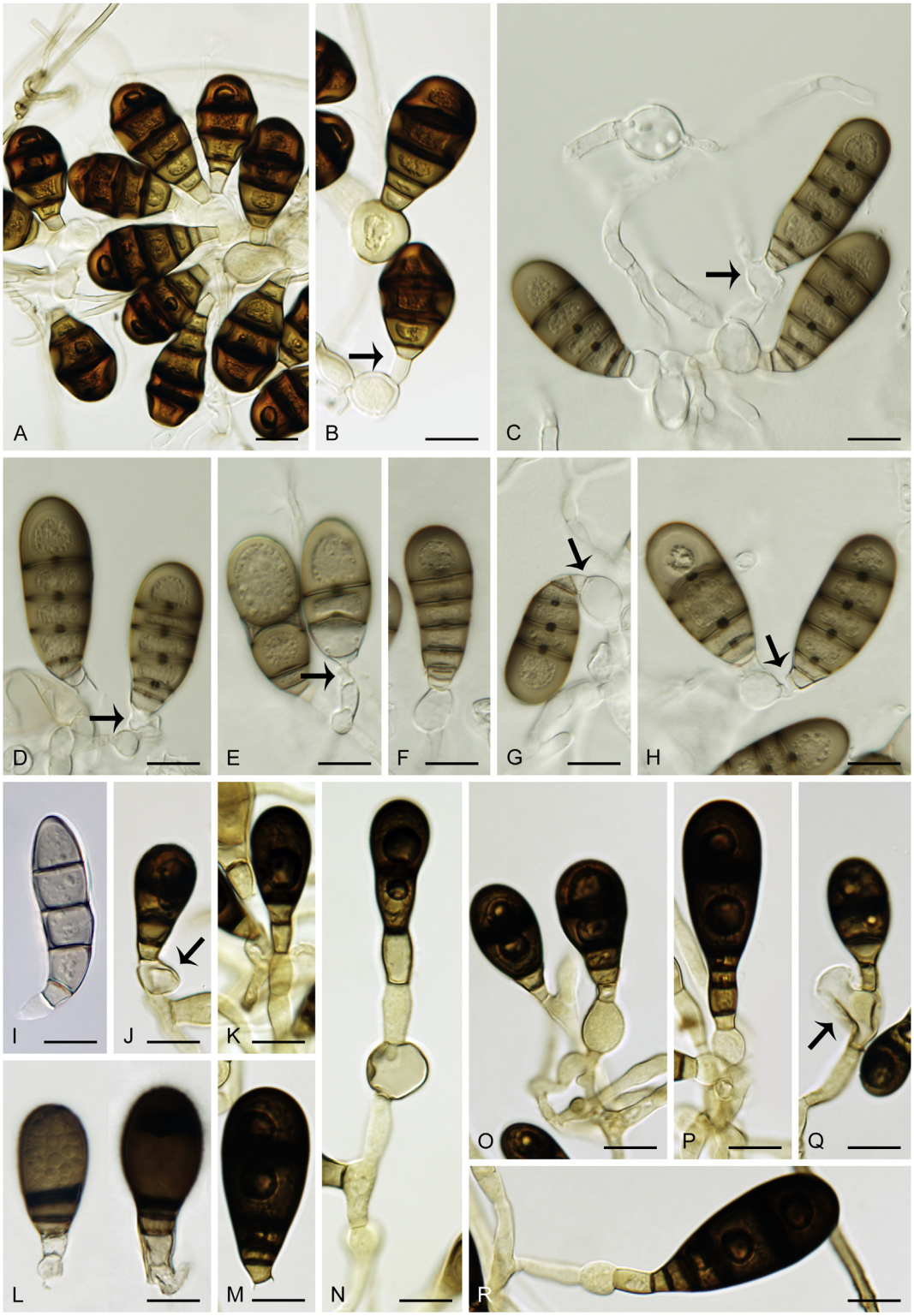

Fig. 5. Multiple secession patterns of rhexolytic detachment of conidia in *Bactrodesmium in vitro*. **A–H**. Conidia and conidiogenous cells of *B. diversum*. **I**. Conidium of *B. pallidum*. **J, K, M–R**. Conidia and conidiogenous cells of *B. obovatum*. **L**. Conidia of *B. abruptum*. Arrows indicate globose conidiogenous cells or subtending cells which collapse. Images: A, B CBS 144079, C–H CBS 145969, I CBS 145349, J CBS 144407, K–O CBS 144078, P, R CBS 144077, Q CBS 145967. Bars: A–R = 10 µm.

assessed for conflicts using the 70 % reciprocal bootstrap criterion (Mason-Gamer & Kellogg 1996). Conflict-free data sets were concatenated into two multi-locus alignments (deposited in TreeBASE 25367) that were subjected to subsequent phylogenetic analyses.

The combined datasets were partitioned into subsets of nucleotide sites, i.e. ITS, LSU, SSU, *rpb2*, *tef1-α* and mitSSU, for which we assumed rate heterogeneity. Bayesian Inference (BI) and Maximum Likelihood (ML) analyses were used to estimate phylogenetic relationships and were performed through the CIPRES Science Gateway v. 3.3 (Miller *et al.* 2010). BI analyses were performed in a likelihood framework as implemented in MrBayes v. 3.2.6 (Huelsenbeck & Ronquist 2001). For the BI approach, MrModeltest2 v. 2.3 (Nylander 2008) was used to infer the appropriate substitution model that would best fit the model of DNA evolution. According to the Akaike information criterion, the SYM+G model was selected for ITS, LSU, SSU and *rpb2* partitions, while the GTR model was chosen for the *tef1-α* partition

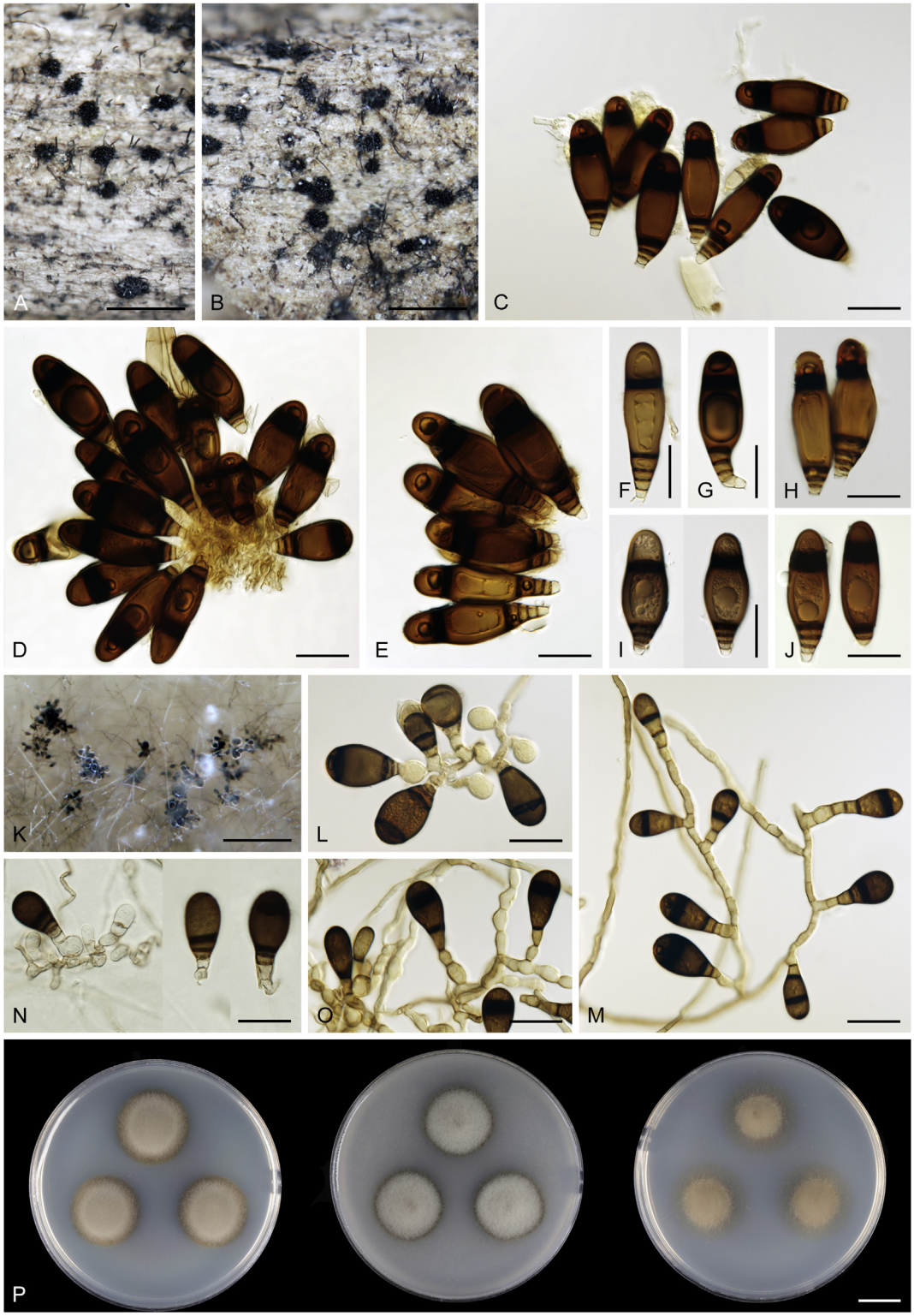

Fig. 6. *Bactrodesmium abruptum*. **A, B**. Sporodochial conidiomata on wood. **C–J**. Conidia and conidiophores. **K**. Clusters of conidia formed on submerged hyphae in the agar. **L–O**. Conidia and conidiophores. A–J. On natural substrate. **K–O**. On MLA. **P**. Colonies on MLA, OA and PCA after 4 wk. Images: A–D, J, O, M CBS 145966, E–G, I, K–N CBS 145967, H, P CBS 145968. Bars: A, B = 500 µm, C–J, L–M = 20 µm, K = 250 µm, P = 1 cm.

of the *Hypocreomycetidae* sequence data set. For all partitions of the *Helotiales* and *Sclerococcales* data sets, the GTR+I+G and SYM+G models, respectively, were selected. ML analyses were performed with RAxML-HPC v. 8.2.12 (Stamatakis 2014) with a GTRCAT approximation. Nodal support was determined by non-parametric bootstrapping (BS) with 1 000 replicates. Two Bayesian searches were performed using default parameters. The B-MCMCMC analyses lasted until the average standard deviation of split frequencies was below 0.01 with trees saved every 1 000 generations. The first 25 % of saved trees, representing the burn-in phase of the analysis, were discarded. The remaining trees were used for calculating posterior probabilities (PP) of recovered branches. Obtained trees were viewed in FigTree v. 1.3.1 (Rambaut 2009) and edited in MS PowerPoint.

RESULTS

Phylogenetic analyses

Phylogenetic relationships of *B. abruptum*, *B. diversum*, *B. leptopus*, *B. obovatum*, *B. pallidum* and *B. spilomeum*, and three undescribed species of *Ascotaiwania*, *Helicoascotaiwania* and *Pleurotheciella* were resolved by conducting two analyses of the combined ITS, SSU, LSU, *rpb2* and *tef1-α* sequences with homologous sequences of representatives of four orders (*Conioscyphales*, *Fuscosporellales*, *Pleurotheciales* and *Savoryellales*) of the *Hypocreomycetidae*. In total, 86 isolates were studied and divided into two subsets. Evolutionary relationships of *B. longisporum* and *B. stilboideum* were assessed in the analysis of the combined ITS, LSU, SSU and *rpb2* loci of members of the *Sclerococcales*. Phylogenetic relationships of *B. gabretae* were resolved by the study of the combined LSU, SSU, *rpb2*, and mitSSU sequences of representatives of the *Helotiales*. *Aspergillus fumigatus*, *Eupenicillium javanicum* and *Trichocoma paradoxa* (*Eurotiales*), *Tolypocladium capitatum* and *T. japonicum* (*Hypocreales*), *Botryotinia fuckeliana* and *Sclerotinia sclerotiorum* (*Sclerotiniales*) and the new species of *Helicoascotaiwania* and *Pleurotheciella* and *Melanotrigonum ovale* (*Pleurotheciales*), were used to root the trees and thus served as outgroups.

In order to evaluate identification markers that could serve as barcodes distinguishing among *Bactrodesmium* species (*Savoryellales*), ITS, LSU, SSU, *rpb2* and *tef1-α* single-gene sequence data sets of 24 *Bactrodesmium* strains were analysed by Maximum Likelihood method. The LSU and SSU data sets could not determine relationships of more than two species. The analyses of *rpb2* and *tef1-α* genes confirmed six well-supported species clades, compared to the ITS, which could not sufficiently resolve relationships between *B. abruptum* and *B. obovatum*. *Bactrodesmium spilomeum* was not included in the ITS and LSU analyses; despite several attempts, we could not amplify these genes.

The first phylogenetic analysis was based on the combined ITS-LSU-SSU-*rpb2*-*tef1-α* sequences of 86 isolates representing 66 species of four orders of the *Hypocreomycetidae*. The alignment had 6 562 characters including gaps and 2 986 unique character sites. The ML tree is shown in Fig. 1. Four robust terminal clades were identified as the *Conioscyphales* (100 % ML BS/1.0 BI PP), *Fuscosporellales* (100/1.0), *Pleurotheciales* (91/1.0) and *Savoryellales* (100/1.0). In the ML analysis, *Ascotaiwania* is shown monophyletic, but the clade is statistically unsupported; *Bactrodesmium* and *Neoascotaiwania* are inferred as strongly supported monophyletic genera. In the BI, the *Ascotaiwania* clade is paraphyletic. The *A. mitriformis* and *A. uniseptata* subclade (0.90) is shown as a sister to *Bactrodesmium*, while an unsupported lineage including *A. lignicola*, the new species and *A. sawadae* is a sister clade to the remaining genera of the *Savoryellales*. The unknown *Helicoascotaiwania* is positioned as a sister to *H. farinosa* in a strongly supported clade (100/1.0), and the unknown *Pleurotheciella* is nested in the *Pleurotheciella* lineage (94/1.0). Both fungi are described as new species in the *Pleurotheciales*.

The second analysis of the combined ITS-LSU-SSU-*rpb2*-*tef1-α* data set included a reduced set of 48 isolates of the *Savoryellales* representing 25 species in six genera. The concatenated alignment consisted of 6 435 characters including gaps and 2 294 unique character sites. The ML tree is shown in Fig. 2. The treatment of *Ascotaiwania* according to Dayarathne *et al.* (2019) was not confirmed in our analysis, and the genus is shown to be paraphyletic in the ML and BI analyses. *Bactrodesmium* (89/1.0), including all six species, and *Neoascotaiwania* (100/1.0) with three species, are resolved as monophyletic, well-supported clades. *Ascotaiwania fusiformis* is nested within *Neoascotaiwania,* and a new combination is proposed in the latter genus. The remaining *Ascotaiwania* form a statistically unsupported clade. The unknown *Ascotaiwania* with a monodictys-like asexual morph is closely related to *A. lignicola*. *Dematiosporium* is positioned in the *Savoryellales*, unrelated to *Ascotaiwania* with a monodictys-like asexual morphs; it resides on a single branch as a sister taxon to the strongly supported *Canalisporium* and *Savoryella* clade (100/1.0). The tree topologies of the *Savoryellales* recovered in the first and second analyses are highly similar; the differences lie in the position of *B. leptopus* and *B. spilomeum* and grouping of species within the *Ascotaiwania* clade.

The third phylogenetic analysis of the combined LSU-SSU-*rpb2*-mitSSU data set included 67 isolates of members of the *Helotiales*. The concatenated alignment consisted of 6 172 characters including gaps and 2 304 unique character sites. The ML tree is shown in Fig. 3. 17 families and three *incertae sedis* lineages were inferred using the four markers. The backbone of both trees from ML and BI analyses is statistically unsupported. *Bactrodesmium gabretae* is resolved in an *incertae sedis* lineage as a sister taxon to *Aquapoterium pinicola* ATCC MYA-4213 and *Unguicularia unguiculata* NK 322.

In the fourth analysis of the combined ITS-LSU-SSU-*rpb2* sequences, we assessed relationships of *B. longisporum* and *B. stilboideum* with 18 members of the *Sclerococcales*. The concatenated alignment consisted of 4 562 characters including gaps and 1 396 unique character sites. The ML and BI trees differed in the position of *Pseudosclerococcum golindoi*. The ML tree is shown in Fig. 4. The *Sclerococcales* encompass four genera, namely *Cylindroconidiis*, *Pseudosclerococcum*, *Rhopalophora*, *Sclerococcum*, and also *Fusichalara minuta* CBS 709.88 and three strains isolated from the digestive tracts of Neotropical wood-inhabiting beetles. Three strains of *B. longisporum* and *B. stilboideum* formed a strongly supported lineage (100/1.0), which was introduced as a new genus below.

TAXONOMY

Bactrodesmium Cooke, Grevillea 12(61): 35. 1883. Emend. Réblová, Hern.-Restr. & J. Fourn.

Type species: *Bactrodesmium abruptum* (Berk. & Broome) E.W. Mason & S. Hughes, Can. J. Bot. 36: 738. 1958.

Emended description: *Asexual morph*: *Conidiomata* sporodochial, superficial, brown to black, scattered or clustered, shining, punctiform, pulvinate, ellipsoidal, elongate or irregular in outline, sometimes confluent. Mycelium mostly immersed, composed of septate, subhyaline to pale brown, compacted hyphae forming partly immersed or superficial pseudostromata. *Conidiophores* mononematous, macronematous to semi-macronematous, simple or sparsely or penicillately branched, sometimes monilioid composed of inflated cells, often fasciculate, growing from the basal hyphae, hyaline and thin-walled, sometimes brown to dark

brown or reddish-brown and thick-walled. *Conidiogenous cells* terminal, integrated, often intercalary *in vitro*, holoblastic, mono- or polyblastic, rarely sympodially elongating, hyaline to subhyaline, conidial secession rhexolytic. *Conidia* acrogenous, solitary, dry, subglobose, clavate, pyriform, ellipsoidal, obovoid, fusiform or cylindrical, euseptate, sometimes with longitudinal or oblique septa, transverse septa sometimes banded, thickly or faintly, usually smooth-walled, pale to dark brown, olivaceous brown, golden-brown, reddish-brown or nearly black, often with a conspicuous thickening at each septum. *Sexual morph*: unknown.

Habitat and distribution: Saprobes on decaying wood and bark of deciduous and coniferous trees, rarely on fallen leaves or dead palm rachis in terrestrial and freshwater habitats in temperate, subtropical and tropical regions of Southern and Northern Hemispheres (e.g. Ellis 1959, 1963, Holubová-Jechová 1972, Sutton 1977, Hughes 1983, Hughes & White 1983a–h, Rao 1983, Castañeda-Ruiz 1985, Kirk 1985, Matsushima & Matsushima 1995, Mercado *et al.* 1995, Cooper 2005).

Notes: Six species of *Bactrodesmium*, including *B. abruptum*, form a well-resolved monophylum nested in the *Savoryellales* in the combined five-gene phylogenies (Figs 1, 2). The present taxonomic treatment of *Bactrodesmium* emphasises the formation of sporodochial conidiomata *vs* effuse colonies on the natural substrate, mononematous *vs* synnematous conidiophores and euseptate *vs* distoseptate conidia following the evidence provided by DNA sequence data (Koukol & Kolářová 2010, Tanaka *et al.* 2015, this study). Based on the morphological comparison of our isolates with other *Bactrodesmium*, we accepted 35 species, although some of them possess unusual characters such as oblique or longitudinal septa, a mucilaginous cap at the conidial apex or conidiophores branched in a penicillate fashion, and thus their placement may be only temporary and in need of verification by DNA sequence data. The accepted species are distinctive in conidium morphology and to some extent also in conidiogenous cell morphology.

Based on *in vitro* studies and examination of herbarium material, the mode of conidial secession of *Bactrodesmium* is referred to as rhexolytic, exhibiting multiple secession patterns (Fig. 5). The conidial secession of some species is unknown or has been reported as schizolytic and should be re-evaluated *in vitro*. In the axenic culture of *B. diversum* (MLA, 6 wk), we regularly observed conidia that undergo a rhexolytic separation. *In vitro*, conidiogenous cells are terminal or intercalary, often globose to subglobose and monoblastic or polyblastic, usually in a chain to form monilioid conidiophores or similar vegetative hyphae or they are cylindrical to subcylindrical cells and appear monoblastic. Sometimes between the conidium and the conidiogenous cell is a smaller cell. We observed that the periclinal wall of the smaller subtending cell and sometimes also that of the globose conidiogenous cell of *B. diversum* began to degenerate or rupture (Fig. 5C–F, H). In the culture of *B. pallidum* (Fig. 5I) and *B. spilomeum* (MLA, 4–7 wk), conidia remained attached on the conidiophores or rarely were seen liberated, sometimes still connected to the slightly inflated conidiogenous cell. In the axenic culture of *B. obovatum* (MLA, 5–8 wk), we observed globose to subglobose or cylindrical conidiogenous cells, sometimes accompanied by a smaller subhyaline cell below the conidium (Fig. 5J, K, M–R). Eventually, they collapsed or ruptured to release the conidium which bears a basal frill. Given the intercalary position of the globose cells of *B. obovatum* and their various size, it is possible that one of the originally cylindrical cells of the conidiophore (near conidium) become inflated during conidium maturation and collapses to release the conidium still attached to the conidiogenous cell. A similar pattern of conidium secession was observed in cultures of *B. abruptum* (Figs 5L, 6L, N).

Conidia of *Bactrodesmium* characterised in this study have a conspicuous thickening at the centrum of each septum surrounding the pore. This feature is well visible especially in species with more or less evenly spaced septa such as *B. diversum*, *B. leptopus*, *B. pallidum* and *B. spilomeum*. In the side view, it is barrel-shaped but in surface view, the thickening has a circular outline. These structures resemble a dolipore septum occurring in basidiomycete hyphae. Similar structures were reported in several other hyphomycetes and coelomycetes, for example in *Canalisporium* spp. (Nawawi & Kuthubutheen 1989), *Cancellidium applanatum* (Tubaki 1975), or *Sarcostroma grevilleae* and *S. hakeae* (Nag Raj 1993). In *Bactrodesmium*, the barrel-shaped thickening in septal pores was noticed by Hughes & White (1983c) in *B. spilomeum* and described as a "conspicuous central pore".

We believe that the present generic concept is the first step towards recognition of this little-understood genus and that the provided key containing important diagnostic characters will facilitate species identification and will help to bring forward new specimens and collection data so much needed to understand *Bactrodesmium*.

Key to species accepted in *Bactrodesmium*

1a. Conidia with longitudinal and/or oblique septa……..2
1b. Conidia with only transverse septa……..4

2a. Apical and basal cells paler than the middle cells, subhyaline to pale brown……...3
2b. Apical cell not paler than the middle cells, conidia 2–3-septate, apical cell sometimes with an oblique septum, 14–20 × 11.5–13.5 µm, pyriform to obovoid, brown, frequently curved dorsiventrally……*B. peruvianum*

3a. Conidia 4(–6)-septate, longitudinal septa in three apical cells, 22.5–29.5 × 11.5–14.5 µm, obovoid to cask-shaped, often bent……*B. pithoideum*
3b. Conidia 4-septate, up to 3 longitudinal or oblique septa in apical and basal cells, (25–)29–32.5(–36) × (18–)20–23.5(–25.2) µm, broadly ellipsoidal, formed obliquely or laterally on the conidiogenous cell…....*B. obliquum*

4a. Apical and basal cells paler than the middle cells, hyaline or subhyaline to pale brown……5
4b. Apical cell not paler than the middle cells……12

5a. Conidia with black bands at the septa, (1–)4–5(–6)-septate, 20–35 × 9–18 µm, ellipsoidal, cylindrical or clavate, brown to dark brown……..*B. cedricola*
5b. Conidia without black bands at the septa……6

6a. Conidia not or slightly to scarcely constricted at the septa……...7
6b. Conidia not constricted at the septa……9

7a. Conidiophores penicillately branched, dense, conidia not or slightly constricted at the septa, 3–13-septate,

20–62.5 × 5.5–8 µm, cylindrical-fusiform, pale to mid brown (*in vitro*)……*B. guamense*

7b. Conidiophores simple or sparsely branched, conidia slightly to scarcely constricted at the septa……8

8a. Conidia (3–)5–8(–10)-septate, (18–)23–40 × 7–9.4 µm, ellipsoidal to clavate, brown……*B. biformatum*

8b. Conidia (4–)5(–6)–septate, (18–)20–23(–25) × 6.5–7.5 µm, elongate ellipsoidal to clavate, pale brown……..*B. pusillum*

9a. Conidia 4-septate, central cell is the longest, 26–40 × 9–15 µm, ellipsoidal or cylindrical, brown to dark brown, apical and basal cells subhyaline to pale brown……*B. betulicola*

9b. Conidia with more septa, cells of approximately the same size……...10

10a. Conidiophores simple, conidia 6–9-septate, 30–44 × 11–14 µm, ellipsoidal or cylindrical, middle cells pale brown……*B. pluriseptatum*

10b. Conidiophores penicillately branched, dense, conidia narrower……11

11a. Conidia (2–)4–6(–8)-septate, (18–)30–55 × 5–6.5 µm, cylindrical, middle cells brown (*in vitro*)…...*B. fruticosum*

11b. Conidia 8–12-septate, 40–64 × 5–7 µm, fusiform, middle cells pale olivaceous grey, with a mucilaginous cap at the apex (*in vitro*)……*B. ramosius*

12a. Most cells equally pigmented with the basal cell sometimes paler, or apical and penultimate cells slightly darker than other cells and colour becoming paler towards the basal cell……13

12b. Apical cell darkest of all cells, occupying half or more than a half of the conidium……29

13a. Conidia with black bands at the septa……14

13b. Conidia without black bands at the septa……17

14a. Conidia narrowly banded, apical cell prominent, 3–4-septate, (30–)33–55(–58) µm long, of two morphological types: obovoid to pyriform, light brown, (14–)17–26 µm wide or subglobose to lacrymoid, dark brown, (20–)26–40 µm wide……*B. moenitum*

14b. Conidia with a broad band at the septum near the apex……15

15a. Conidia (1–)2-septate, 14–26 × 3.5–7.5 µm, cylindrical, ellipsoid to obovoid, slightly curved, brown…*B. xerophilum*

15b. Conidia with more septa, septum near the apex obscured by a broad black band, the bands over other septa are progressively narrower towards the base…16

16a. Black band at the septum near the apex 5.5–7(–8.5) µm wide, the penultimate cell is the largest of all cells, conidia (3–)4–6(–7)-septate, (36.5–)42–65.5(–70) × (12.5–)14–18(–19) µm, clavate to oblong-clavate, brown or reddish-brown…*B. abruptum*

16b. Black band at the septum near the apex 3.5–5 µm wide, apical and penultimate cells are approximately of the same size and larger than other cells, (3–)4–5-septate, (27.5–)35–46(–48) × 15.5–20 µm, clavate to obovoid, brown to dark brown……*B. obovatum*

17a. Conidia 1–2-septate……18

17b. Conidia with more septa……..21

18a. Conidia 1-septate……..19

18b. Conidia 2-septate……..20

19a. Conidia 3–13 × 7–10 µm, obovoid to subglobose, brown……..…*B. novageronense*

19b. Conidia 19–24 × 12–16 µm, pyriform, obovoid to globose, golden brown to pale olivaceous brown……*B. simile*

20a. Conidia (21–)26–30 × (12.5–)13–16(–17.5) µm, obovoid to pyriform, brown to dark brown…*B. pyriforme*

20b. Conidia 10.5–15 × 5.5–7.5 µm, ellipsoidal to obovoid, brown……...*B. esheri*

21a. Conidia slightly constricted at the septa, 8–11-septate, 36–54 × 11–15 µm, ellipsoidal to fusiform, brown to dark olivaceous brown……*B. hebridense*

21b. Conidia not constricted at the septa……22

22a. Conidia up to 14 µm wide……23

22b. Conidia wider than 14 µm……27

23a. Conidia up to 47 µm long……24

23b. Conidia longer than 47 µm……..26

24a. Conidia with apical cells dark to mid-brown, colour becoming paler towards the base, 3–5(–6)-septate, 20–37 × 8–12 µm, clavate to ellipsoidal ……*B. traversoanum*

24b. Conidia with most cells equally pigmented, basal cell subhyaline……..25

25a. Conidia subhyaline to yellowish-brown, 5–6-septate, 30–42 × 9–12, ellipsoidal to oval, narrowed towards the apex……*B. ellipsoideum*

25b. Conidia pale to mid-brown, 3–5-septate, 24–43 × 8.5–11 µm, elongated ellipsoidal to ellipsoidal-clavate, rounded at the apex……*B. spilomeum*

26a. Conidia yellowish to golden brown, 4–5-septate, 35–52 × 7–11 µm, clavate to cylindrical, rounded at the apex……..*B. indicum*

26b. Conidia pale brown, (4–)5–6-septate, 29–54(–57) × 9–13 µm, elongated ellipsoidal or ellipsoidal-clavate, narrowed towards the apex……*B. pallidum*

27a. Conidia 5–8-septate, 47–55 × 18–25 µm, obovoid to pyriform, brown……*B. nothofagi*

27b. Conidia narrower, up to 18 µm wide……..28

28a. Conidia 3–5(–6)-septate, (27–)30–48(–52.5) × (14–)15–19.5(–20.5) µm, clavate to ellipsoidal-clavate, occasionally pyriform or obovoid, or sigmoid, brown, apical cell(s) slightly darker, colour becoming paler towards the base……*B. diversum*

28b. Conidia 3–5-septate, (21–)24–42(–44) × 11.5–15.5 µm, clavate to ellipsoidal-clavate, brown, becoming paler towards the base……*B. leptopus*

29a. Conidia with up to three septa……30

29b. Conidia with more than three septa……33

30a. Conidia abruptly curved at the base, 3-septate, 24–32 × 14–20 µm, subglobose to broadly

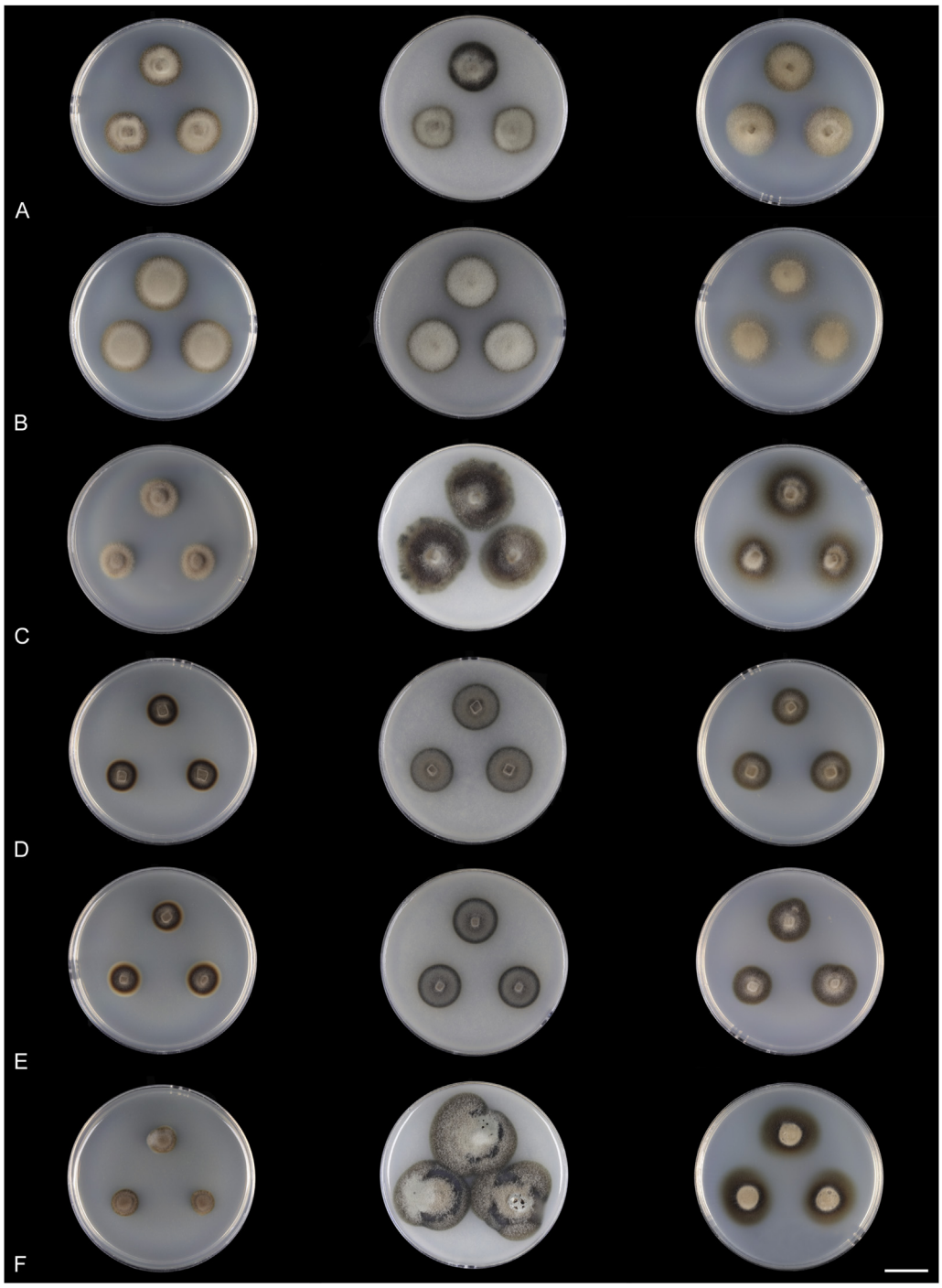

Fig. 7. Diversity of colony morphology in *B. abruptum* (**A–C**) and *B. obovatum* (**D–F**). From left to right on MLA, OA and PCA after 4 wk. Images: A CBS 145966, B CBS 145968, C CBS 145967, D CBS 144078, E CBS 144077, F CBS 145350. Bar = 1 cm.

pyriform, apical cell black-brown, basal cell pale brown……*B. curvatum*

30b. Conidia straight, apical cell(s) dark brown to black, basal cell hyaline to pale brown……31

31a. Conidia 2–3-septate, 30–47.5 × (17.5–)20–23.7 µm, obovoid or broadly clavate……*B. globosum*

31b. Conidia with less than three septa, narrower, up to 20.5 µm wide……32

32a. Conidia (0–)1–2-septate, 20–33.6 × 14.5–20.5 µm, subglobose to pyriform……*B. linderi*

32b. Conidia 1–2-septate, 15–25 × 10–15 µm, broadly pyriform……*B. aquaticum*

33a. Conidia verrucose, 3–4-septate, 22–44 × 15.2–22 µm, obovoid, clavate or ellipsoidal, apical cell black, other cells pale brown……*B. palmicola*

33b. Conidia smooth, 3–5-septate……34

34a. Conidia with apical cell almost black, opaque, conidia obovoid, 43–72 × 22–38 µm……*B. atrum*

34b. Conidia with apical cell brown, translucent in transmitted light, conidia clavate, 35–60 × 20–30 µm (*in vitro*) ……*B. mucosum*

Bactrodesmium abruptum (Berk. & Broome) E.W. Mason & S. Hughes, Can. J. Bot. 36: 738. 1958. Fig. 6.

Fig. 8. *Bactrodesmium diversum*. **A, B.** Sporodochial conidiomata on wood. **C–F.** Conidia and conidiophores. **G**. Sporodochial conidiomata. **H**. Conidia formed on hyphae submerged in the agar. **I–M**. Conidia and conidiophores (I–K in Melzer reagent, L, M in water). **A–F**. On natural substrate. **G–M**. On MLA. **N**. Colonies on MLA, OA and PCA after 4 wk. Images: A–D, G, J CBS 142448, E CBS 144405, F CBS 144081, H CBS 145965, I, K CBS 144079, L CBS 145969, M, N CBS 145970. Bars: A, B = 500 µm, C–F, I–M = 20 µm, G = 1 000 µm, H = 200 µm, N = 1 cm.

Basionym: *Sporidesmium abruptum* Berk. & Broome, Ann. Mag. nat. Hist., Ser. 3. 15: 401. 1865.
Synonyms: *Clasterosporium abruptum* (Berk. & Broome) Sacc., Syll. fung. 4: 389. 1886.
Bactrodesmium abruptum (Berk. & Broome) E.W. Mason & S. Hughes, in Walsh & Rimington, Nat. Hist. Scarborough Distr. 1: 159. 1953. (Nom. inval., Art. 41.5)

Description on the natural substrate: *Asexual morph*: *Conidiomata* sporodochial, scattered, superficial, black, shining, punctiform, pulvinate, sometimes confluent and irregular in outline, 150–500 µm diam. Mycelium mostly immersed, composed of septate, pale brown hyphae 2.5–4.5 µm wide. *Conidiophores* semi-macronematous, fasciculate, arising from basal hyphae, subhyaline to pale brown, simple, seldom branched, up to 45 µm long, 2.5–3 µm wide, septate.

Conidiogenous cells terminal, integrated, monoblastic, 3–5.5 µm wide, oblong to short-cylindrical, often broadening towards the apex, hyaline, thin-walled. *Conidia* (36.5–)42–65.5(–70) × (12.5–)14–18(–19) µm (mean ± SD = 53.5 ± 6.2 × 16.5 ± 1.3 µm), 36.5–45 × (12.5–)17–19 µm (3-septate), (39–)42–52 × 13.5–19 µm (4-septate), 46.5–60(–62) × (14–)15–18(–19) µm (5-septate), (40–)58–65.5(–69) × 16–17.5 µm (6-septate), 63–70 × 14.5–17 µm (7-septate), 3–5 µm wide at the base, clavate to oblong-clavate, usually straight or slightly flexuous in the basal part, rounded at the apex, truncate at the base, (3–)4–6(–7)-septate, mostly 5-septate, smooth, with a large globule at each cell, brown to reddish-brown, darker in the upper part, the colour becoming progressively paler towards the basal cell which is hyaline to subhyaline to very pale brown and bears a short frill of wall. The penultimate cell is the largest of all cells; the septum near the apex is obscured by a broad black band 5.5–7(–8.5) µm wide, the black bands are progressively narrower toward the base. *Sexual morph*: unknown.

Description on MLA: Vegetative hyphae hyaline to subhyaline, 2–3 µm wide, septate, often monilioid. *Conidiomata* sporodochium-like, usually developed as clusters of fasciculate conidiophores. *Conidiophores* macronematous, semi-macronematous, mostly simple or sparsely branched, or micronematous often reduced to conidiogenous cells, hyaline, arising from aerial or submerged hyphae. *Conidiogenous cells* terminal, intercalary, integrated, monoblastic, 3.5–10 µm wide, hyaline, subglobose to globose or cylindrical to subcylindrical often broadening towards the apex. *Conidia* (19.5–)24.5–33.5 × (9–)10.5–17.5 µm (mean ± SD = 29.5 ± 2.9 × 13.3 ± 2.7 µm), (2.5–)3–4.5 µm wide at the base, clavate to oblong-clavate, rounded at the apex, truncate at the base, (2–)3–4(–5)-septate, the septum near the apex with a black band 4–5.5 µm wide, other septa narrowly banded, smooth, brown to reddish-brown, paler towards the basal cell, which is subhyaline to pale brown and bears a short frill of wall.

Culture characteristics: Colonies on MLA 11–12(–16) mm after 4 wk, circular, flat, convex centrally, margin entire, lanose, floccose becoming cobwebby towards the margin, beige to pale brown with a mid-brown outer zone of melanised submerged mycelium; reverse dark brown. Colonies on OA 11–16(–25) mm after 4 wk, circular, flat becoming slightly convex centrally, margin entire to weakly fimbriate, lanose, floccose towards the margin, olivaceous grey to grey-brown with a dark grey to dark olivaceous grey outer zone; reverse olivaceous brown. Colonies on PCA 16–20 mm after 4 wk, circular, flat, convex, margin entire to weakly fimbriate, lanose, floccose, beige with a mid-brown outer zone of submerged growth; reverse dark brown. Sporulation on all media after 6–8 wk or after prolonged incubation.

Habitat and distribution: *Bactrodesmium abruptum* occurs on decaying wood and bark of various deciduous trees in terrestrial and freshwater habitats; it has been collected so far on *Acer pseudoplatanus*, *Beilschmiedia tawa*, *Fraxinus excelsior*, *Quercus* sp., *Robinia pseudoaccacia* and on other unidentified substrates. The species is known in Europe in France and United Kingdom and New Zealand (Ellis 1959, Hughes 1978, this study).

Specimens examined: **France**, Ariège, Rimont, La Maille brook, 550 m a.s.l., on submerged wood, 28 May 2018 (incubated in moist chamber for 1 wk), J. Fournier M.R. 3953 (PRA-00016129, culture CBS 145968); *ibid.*, J. Fournier M.R. 3957 (PRA-00016130, culture CBS 145967); *ibid.*, on submerged wood of *Fraxinus excelsior*, 18 Oct. 2017, J. Fournier J.F. 17068 (culture CBS 144404); *ibid.*, Ariège, Las Muros, Peyrau brook, 400 m a.s.l., on submerged wood of *Robinia pseudoacacia*, 9 Aug. 2018 (incubated in moist chamber for 1 wk), J. Fournier J.F. 18064 (PRA-00016128, culture CBS 145966). **United Kingdom**, England, Bodelwyddan, on decaying wood, Mar. 1864, Bloxam (**holotype** IMI 6833); *ibid.*, St. Catherines, Batheaston, Apr. 1867, C.E. Broome, in Rabenhorst, Fungi europaei Exs. No. 1163 (IMI 6835).

Notes: *Bactrodesmium abruptum* is well distinguishable among other species of the genus by clavate to oblong-clavate, brown to reddish-brown, septate conidia with a conspicuous dark band over the septum near the apex and the penultimate cell, which is the largest of all cells. Conidia of *B. abruptum* in material from France were slightly shorter (36.5–)42.5–59(–61.5) × (12.5–)14–18(–19) µm than those from material originating from United Kingdom (40.5–)47.5–65.5(–70) × (13–)15–18 µm.

In the present phylogenetic analyses, *B. abruptum* is resolved as a sister to *B. obovatum* (Figs 1, 2). The difference between both species lies in two motifs in the ITS region corresponding to 99.25 % sequence identity, *rpb2* corresponding to 99.19 % identity and *tef1-α* corresponding to 99.28 % identity. Additional minor intraspecific variability occurs in the ITS and *rpb2* genes. Despite high sequence similarity in the studied loci between them, they are morphologically well distinguishable and therefore treated as two separate species. The diagnostic phenotypic traits that characterise each species are consistent among collections of *B. abruptum* and *B. obovatum in vitro* and *in vivo*. However, all four strains of *B. abruptum* originate in a small area, in two brooks approximately 5 km apart. More collections of both species from various regions are needed to study their genetic variability.

Bactrodesmium obovatum differs from *B. abruptum* in having brown to dark brown, clavate to obovoid, shorter and broader, (3–)4–5-septate conidia, four septa being most common. Both species also differ by the length ratio between the apical and penultimate cells; in *B. abruptum* the penultimate cell is the largest of all cells, while in *B. obovatum* the apical and penultimate cells have approximately the same size and are always larger than the other cells. Both species share several morphological traits. Their conidia are narrowing towards the base to form a kind of a stipe, the upper cells are darkest becoming progressively paler towards the base, and the septum near the apex is thickly banded, though the band is wider in *B. abruptum* [5.5–7(–8.5) µm wide] than in *B. obovatum* (3.5–5 µm wide).

A comparison of the six strains (three per each species) on three media showed specific variability among them and also within each species. *Bactrodesmium abruptum* (Fig. 7A–C) generally forms more aerial mycelium on MLA, OA and PCA compared to *B. obovatum* (Fig. 7D–F) which is slower-growing with less developed aerial mycelium, which is abundant only at the centre of the colony. In the studied strains, hyphae at the margin of the colony are submerged, well-developed, melanised, usually visible as a distinct dark ring not yet overgrown by aerial mycelium, or the zone of submerged growth is wider and more prominent correlating with less developed aerial mycelium. On MLA, two strains of *B. abruptum* (CBS 145966, CBS 145968) grow slightly faster (13–16 mm) than the third strain CBS 145967 (11–12 mm), while the growth of all three *B. obovatum* strains on the same medium is comparable. On OA, strains of both species tend to produce olivaceous grey to olivaceous brown colonies, but their appearance varies within the species. Strains CBS 145967 of *B. abruptum* and CBS 145350 of *B. obovatum* grow slightly faster (21–26 mm) on OA than other strains of the same species (*B. a.*: 13–16 mm, *B. o.*: 13–14 mm). The appearance of the darker

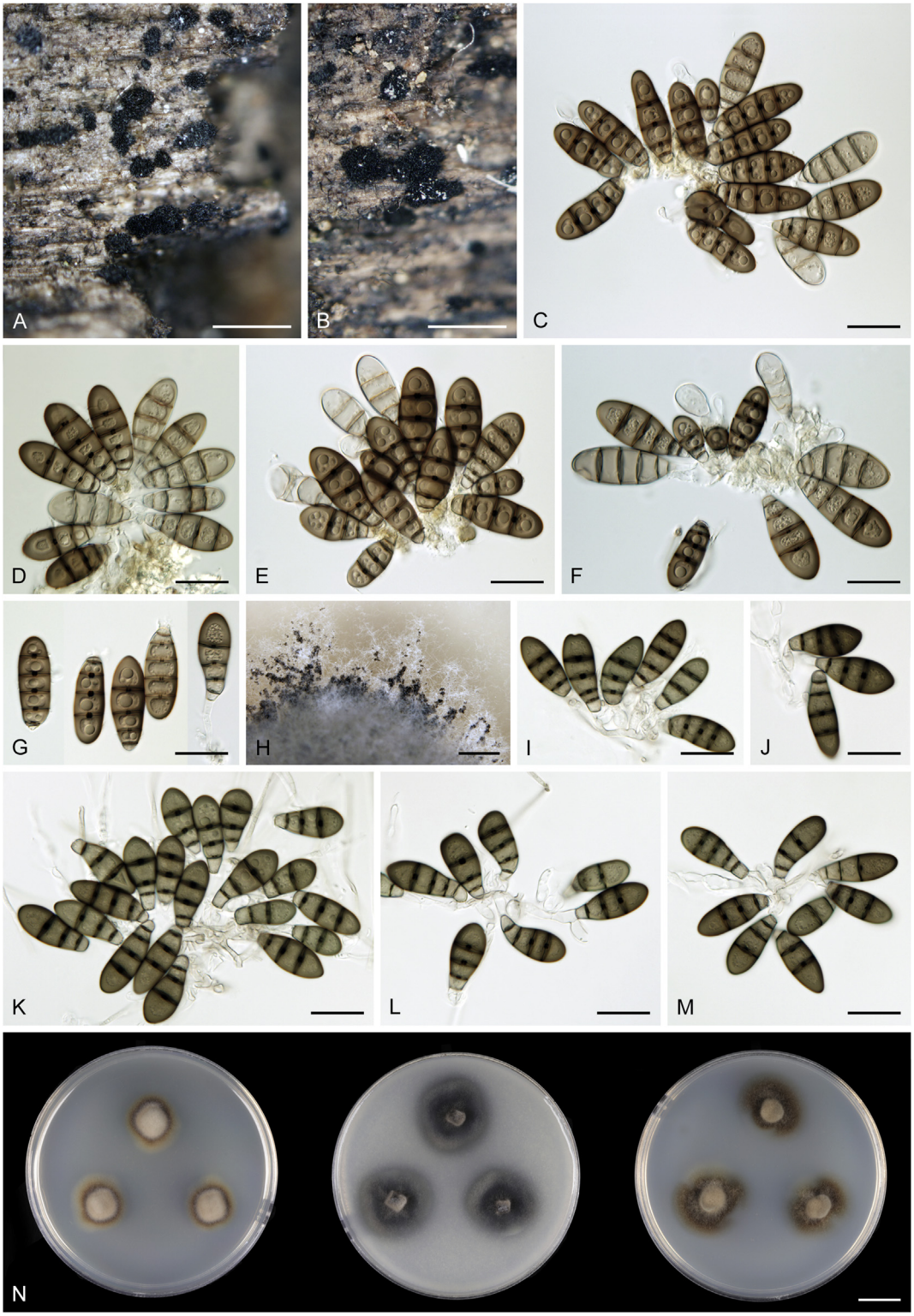

Fig. 9. *Bactrodesmium leptopus* (CBS 144542). **A, B**. Sporodochial conidiomata on wood. **C–G**. Conidia and conidiophores. **H**. Clusters of sporodochial conidiomata and conidia. **I–M**. Conidia and conidiophores. **A–G**. On natural substrate. **H–M**. On MLA. **N**. Colonies on MLA, OA and PCA after 4 wk. Bars: A, B = 500 µm, C–G, I–M = 20 µm, H = 1 000 µm, N = 1 cm.

outer zones of submerged growth varies on OA; it is visible as a dark olivaceous grey to almost black ring (*B.a.*: CBS 145966 and CBS 145968, *B.o.*: CBS 144077 and CBS 144078) or as an irregular outer zone expanding radially (*B.a.*: CBS 145967) or the zone of submerged growth is partly obscured by abundant aerial mycelium at the margin of the colony while creating areas of sparse growth near the centre (*B. o.*: CBS 145350).

Bactrodesmium diversum Hern.-Restr., J. Mena, Gené & Guarro, Mycologia 105: 177. 2013. Fig. 8.

Description on the natural substrate: *Asexual morph*: *Conidiomata* sporodochial, scattered, superficial, black, shining, punctiform, pulvinate, 150–300 µm diam, sometimes confluent up to 500 µm diam. Mycelium mostly immersed in the substrate, composed of septate, subhyaline to pale brown hyphae 2–4 µm wide. *Conidiophores* macronematous to semi-macronematous, fasciculate, arising from basal hyphae, septate, subhyaline to pale brown, simple or sparsely branched, up to 65 µm long, 2.5–4 µm wide near the base. *Conidiogenous cells* terminal, integrated,

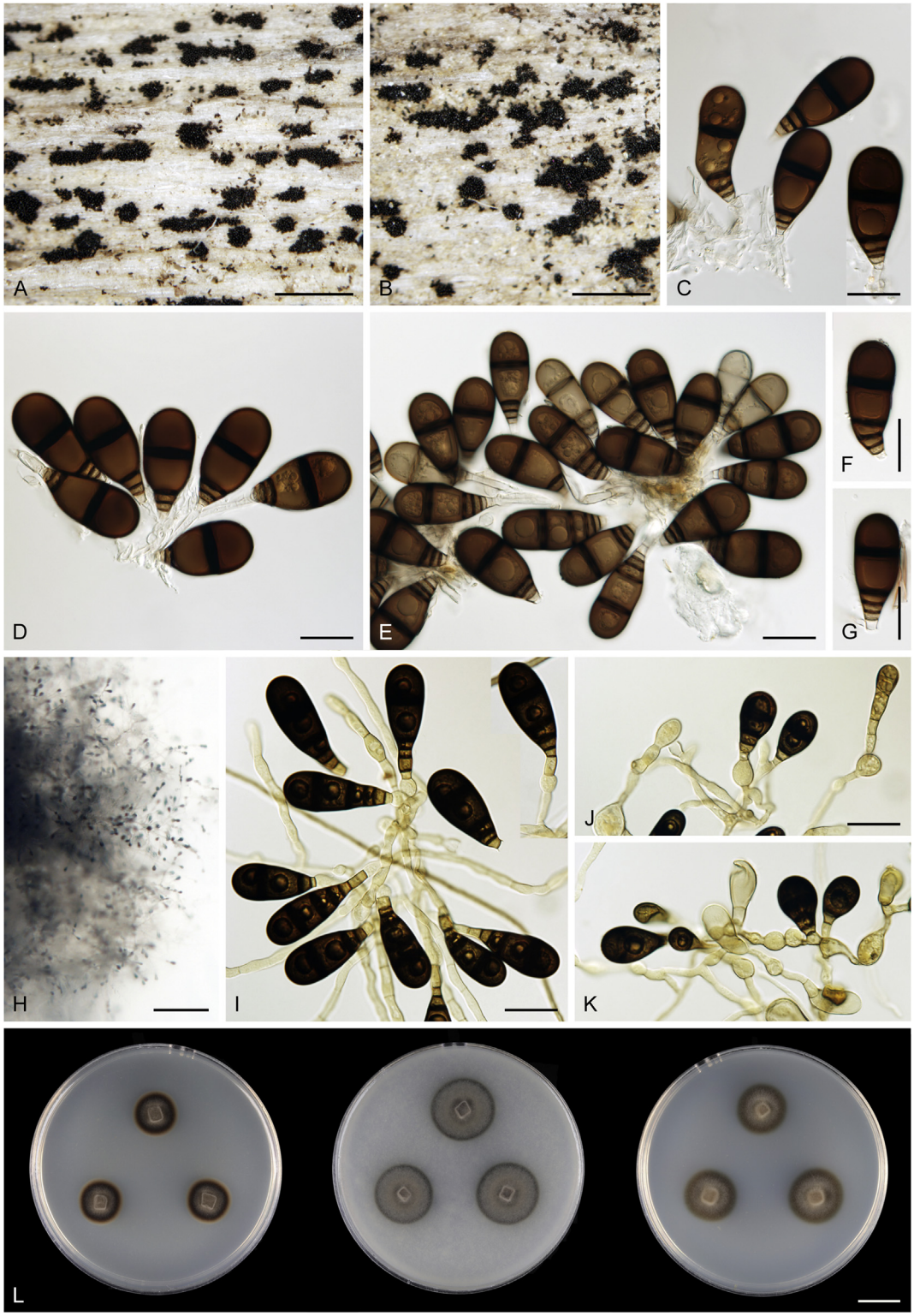

Fig. 10. *Bactrodesmium obovatum*. **A, B**. Sporodochial conidiomata on wood. **C–G**. Conidia and conidiophores. **H**. Conidia formed on hyphae submerged in the agar. **I–K**. Conidia and conidiophores. **A–G**. On natural substrate. **H–K**. On MLA. **L**. Colonies on MLA, OA and PCA after 4 wk. Images: A–D CBS 145350, E, F, H, J–L CBS 144078, G, I CBS 144077. Bars: A, B = 500 µm, C–G, I–K = 20 µm, H = 200 µm, L = 1 cm.

polyblastic, 3–4.5 µm wide, oblong to cylindrical, often broadening towards the apex, thin-walled. *Conidia* (27–)30–48(–52.5) × (14–)15–19.5(–20.5) µm (mean ± SD = 42.3 ± 4.7 × 15.9 ± 1.4 µm), 28.5–31 × 12.5–15(–18) µm (3-septate), (27–)33–40(–42) × 15–17.5(–19) µm (4-septate), (33–)40–48(–52.5) × 15–19.5(–20.5) µm (5-septate), 44.5–50 × 17–20 µm (6-septate), 3–4(–4.5) µm wide at the base, clavate to ellipsoidal-clavate, occasionally pyriform or obovoid, sometimes curved at the base or slightly sigmoid, rounded at the apex, truncate at the base, 3–5(–6)-septate, smooth, with a conspicuous central pore at the septa and a large guttule at each cell, brown, the colour becoming paler towards the basal cell which is subhyaline to pale brown and often bears a short frill of wall. *Sexual morph*: unknown.

Description on MLA: Vegetative hyphae hyaline to subhyaline, 1.5–3 µm wide, septate, sometimes monilioid. *Conidiomata* sporodochium-like clusters, superficial or partly immersed in the

agar, 150–250 µm diam, confluent, pulvinate, brown. *Conidiophores* semi-macronematous, septate, simple or sparsely branched, sometimes moniliform, or micronematous often reduced to conidiogenous cells, hyaline, thin-walled. *Conidiogenous cells* terminal, intercalary, integrated, polyblastic, 4–10 µm wide, hyaline, globose to subglobose or cylindrical to subcylindrical. *Conidia* 29–42 × (12–) 13.5–15.5(–17) µm (mean ± SD = 33.9 ± 3.4 × 14.4 ± 1.1 µm), 3–3.5(–4) µm wide at the base, clavate to ellipsoidal-clavate, straight or curved at the base, 3–6-septate, smooth, with a conspicuous central pore at the septa and a large guttule at each cell, brown, the colour becoming paler towards the basal cell which is subhyaline to pale brown, sometimes with a short frill of wall.

Culture characteristics: Colonies on MLA 9–10 mm after 4 wk, circular, flat, slightly convex at the centre, margin entire, lanose, somewhat floccose at the periphery, beige becoming pale brown with a dark brown outer zone; reverse brown. Colonies on OA 11–12 mm after 4 wk, circular, flat, margin entire, velvety-lanose becoming floccose towards the margin, aerial mycelium bearing small, colourless droplets of exudate, ivory becoming beige with ca. 1–2 mm dark olivaceous brown outer zone; reverse olivaceous brown. Colonies on PCA 10–11 mm after 4 wk, circular, flat, slightly convex at the centre, margin fimbriate, lanose becoming floccose towards the margin, aerial mycelium bearing small, colourless droplets of exudate, beige to pale brown with a dark brown outer zone; reverse dark brown. Sporulation on all media after 6–8 wk or after prolonged incubation.

Specimens examined: **France**, Ariège, Rimont, La Maille brook, 560 m a.s.l., on submerged wood of *Fraxinus excelsior*, 19 Jun. 2017, J. Fournier J.F. 17033, MBT390462 (**epitype designated here**, PRA-00016136, culture ex-epitype CBS 144081 = IMI 506813); *ibid*., on submerged wood of a branch of *Fraxinus excelsior*, 4 Jul. 2016, J. Fournier J.F. 16051 (PRA-00016131, culture CBS 142448); *ibid*., on submerged wood of *Robinia pseudoaccacia*, 18 Oct. 2017, J. Fournier J.F. 17069 (PRA-00016137, culture CBS 144405); *ibid*., on submerged wood of *Robinia pseudoaccacia*, 9 Aug. 2018, J. Fournier J.F. 18066 (PRA-00016139, culture CBS 145965); *ibid*., on submerged wood, 28 May 2018 (incubated in moist chamber for 1 wk), J. Fournier M.R. 3954 (PRA-00016140, culture CBS 145970); *ibid*., J. Fournier M.R. 3955A (PRA-00016141, culture CBS 145969); Ariège, Rimont, Peyrau brook, ca. 400 m a.s.l., on submerged wood of *Fraxinus excelsior*, 15 Sep. 2016, J. Fournier J.F. 16056 (PRA-00016132, culture CBS 142450); *ibid*., on submerged wood of *Fraxinus exclesior*, 17 Jun. 2017, J. Fournier J.F. 17018 (PRA-00016133, culture CBS 144079); *ibid*., on submerged wood of *Alnus glutinosa*, associated with *Bactrodesmium obovatum*, 17 Jun. 2017, J. Fournier J.F. 17024 (PRA-00016134, culture CBS 144401); *ibid*., on submerged wood of *Alnus glutinosa*, associated with *Bactrodesmium obovatum* and *Varicosporella aquatica*, 17 Jun. 2017, J. Fournier J.F. 17025A (PRA-00016135, culture CBS 144080); *ibid*., on submerged wood, 7 Apr. 2018 (incubated in moist chamber for 1 wk), J. Fournier J.F. 18007 (PRA-00016138, culture CBS 145435).

Habitat and distribution: *Bactrodesmium diversum* occurs on decaying wood of deciduous trees in terrestrial and freshwater habitats; it has been collected so far on *Alnus glutinosa*, *Fraxinus excelsior*, *Robinia pseudoaccacia* and other undetermined substrates. The species is known in Europe in France and Spain (Hernández-Restrepo *et al.* 2013, this study).

Notes: *Bactrodesmium diversum* is characterised by clavate to ellipsoidal-clavate, 3–5(–6)-septate conidia, sometimes slightly curved at the base, brown becoming paler towards the basal cell. The present species is reminiscent of *B. spilomeum,* which is distinguished by subtler, brown, often elongated sporodochia and conidia which are elongated ellipsoidal to ellipsoidal-clavate, narrower and pale brown with most cells equally pigmented and a subhyaline to pale brown basal cell. *Bactrodesmium leptopus* (Saccardo 1881a, 1886) is highly similar to *B. diversum* in the conidial size and shape but differs by paler brown, 3–5-septate conidia (see also Hughes & White 1983c). *Bactrodesmium traversoanum* (Ellis 1959) resembles *B. diversum* in clavate to ellipsoidal, brown conidia which become paler towards the basal cell, but is distinguished by shorter and narrower conidia (20–37 × 8–12 µm). Among our specimens, *B. diversum* was one of the most commonly encountered species in the freshwater habitat.

Bactrodesmium leptopus (Sacc.) S. Hughes, Can. J. Bot. 36: 739. 1958. Fig. 9.
Basionym: *Clasterosporium clavaeforme* (Preuss) Sacc. var. *leptopus* Sacc., Fungi italici autogr. del. 17–28. Tab. 749. 1881; Syll. Fung. 4: 391. 1886.
Synonym: *Clasterosporium leptopus* (Sacc.) Mussat, Syll. fung. 15: 90. 1901.

Description on the natural substrate: *Asexual morph*: *Conidiomata* sporodochial, scattered, superficial, black, punctiform, pulvinate, 150–300 µm diam, often confluent up to 500 µm diam. Mycelium mostly immersed in the substrate, composed of septate, subhyaline to pale brown hyphae 2–3.5 µm wide. *Conidiophores* macronematous to semi-macronematous, fasciculate, arising from basal hyphae, septate, hyaline to subhyaline, sparsely branched, up to 70 µm long, 2–3.5 µm wide near the base. *Conidiogenous cells* terminal, integrated, monoblastic, 2.5–3.5 µm wide, oblong to cylindrical, sometimes slightly broadening towards the apex, hyaline, thin-walled. *Conidia* (21–) 24–42(–44) × 11.5–15.5 µm (mean ± SD = 34.4 ± 4.8 × 12.5 ± 1.3 µm), (21–)24–29 × 11.5–15.5 µm (3-septate), (29–)31–37 × 12–14.5(–15) µm (4-septate), 35–42(–44) × 11.5–15.5 µm (5-septate), 2.5–3.5 µm wide at the base, clavate to ellipsoidal-clavate, rounded to slightly narrowed at the apex, truncate at the base, 3–5-septate, predominantly 5-septate, smooth, with a conspicuous central pore at the septa and a large guttule at each cell, brown becoming paler towards the base, basal cell subhyaline to pale brown with a short frill of wall. *Sexual morph*: unknown.

Description on OA: Vegetative hyphae hyaline to subhyaline, 1.5–2.5 µm wide, septate. *Conidiomata* sporodochium-like clusters, confluent. *Conidiophores* semi-macronematous or micronematous often reduced to conidiogenous cells, sparsely branched, hyaline, composed of cylindrical or slightly inflated cells, arising from aerial and submerged hyphae. *Conidiogenous cells* terminal, intercalary, integrated, monoblastic, 3.5–4.5(–5) µm wide, hyaline, subcylindrical to oblong, sometimes slightly expanding apically. *Conidia* 25.5–34(–36) × 9–12.5 µm (mean ± SD = 29.4 ± 2.8 × 11.2 ± 1.0 µm), 3–4.5 µm wide at the base, clavate or pyriform or ellipsoidal-clavate, rounded or slightly narrowed at the apex, truncate at the base, 3–4-septate, brown to olivaceous brown, paler towards the basal cell, which is subhyaline to pale brown and bears a short frill of wall.

Culture characteristics: Colonies on MLA 11–13 mm after 4 wk, circular, slightly convex, margin fimbriate, lanose, floccose becoming cobwebby towards the margin, colony centre beige becoming beige-brown with a dark brown outer zone, brown pigment diffusing from the colony margin to 1–1.5 mm into the surrounding agar; reverse brown. Colonies on OA 11–14 mm after 4 wk, circular, flat, raised margin, margin fimbriate, velvety-lanose, floccose to cobwebby towards the

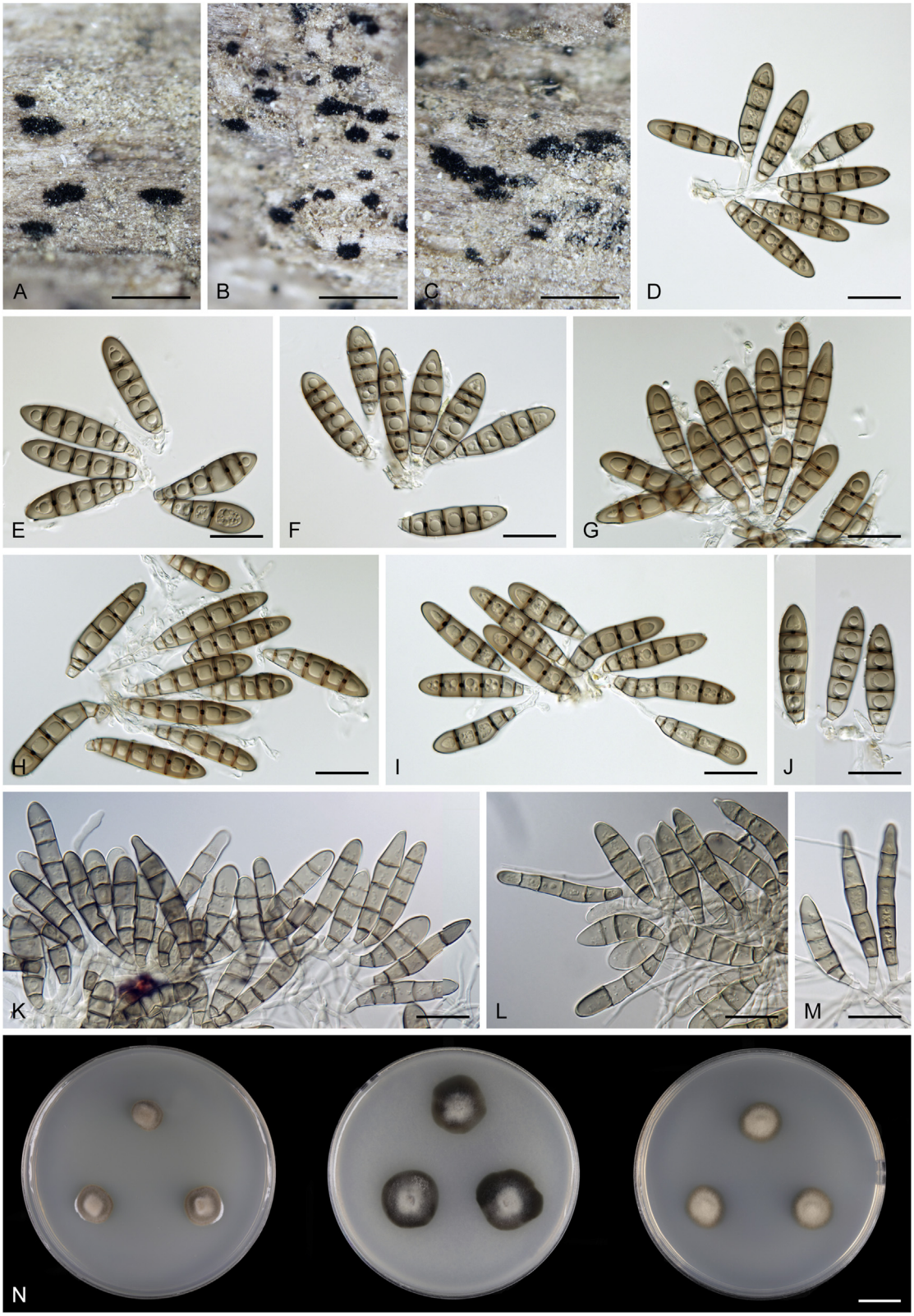

Fig. 11. *Bactrodesmium pallidum*. Sporodochial conidiomata on wood. **D–J**. Conidia and conidiophores. **K–M**. Conidia and conidiophores. **A–J**. On natural substrate. **K–M**. On MLA. **N**. Colonies on MLA, OA and PCA after 4 wk. Images: A–C, E, F, J–N CBS 145349, D, I PRA-00016148, G, H CBS 142449. Bars: A–C = 500 µm, D–M = 20 µm, N = 1 cm.

margin, beige-grey becoming paler towards the periphery with irregular whitish floccose patches of aerial mycelium at the margin, grey to olivaceous grey pigment diffusing from the colony margin to 2–2.5 mm into the surrounding agar; reverse dark olivaceous grey. Colonies on PCA 15–17 mm after 4 wk, circular to irregular, flat, margin fimbriate, lanose, floccose becoming cobwebby towards the margin, locally smooth corresponding to irregular spots of sparse growth, beige to pale brown becoming dark brown towards the periphery, beige to pale brown pigment diffusing from the colony margin to ca. 1 mm into the surrounding agar; reverse brown. Sporulation on OA after 4 wk, on MLA and PCA after 6–8 wk or after prolonged incubation.

Specimen examined: **Czech Republic**, South Moravia, Hodonín distr., Mikulčice oppidum, Mikulčický luh Nature Park, Malá Pinuška, on decaying wood of *Acer campestre*, 7 Nov. 2017, M. Réblová M.R. 3933 (PRA-00016150, culture CBS 144542).

Habitat and distribution: *Bactrodesmium leptopus* occurs on decaying wood of *Acer campestre* and *Ficus carica* (Saccardo 1881a, this study). This species is known in Europe in the Czech Republic and Italy.

Notes: *Bactrodesmium leptopus* was illustrated (Saccardo 1881a) and described (Saccardo 1881b, 1886) with sporodochium-like conidiomata and 3–6-septate, fusiform to ovoid-clavate, brown conidia, 30–40 × 15–20 µm. The type material was not available to us, but it was examined earlier by Hughes & White (1983c). These authors observed that conidia in the holotype were scattered rather than aggregated, mostly clavate, 3–5-septate, straight or irregularly bent and gave the following measurements: 23.4–29.7 × 11.7–16.2 µm (3-septate), 23.4–41.5 × (10.8–) 12.6–18 µm (4-septate) and 32–47 × 11.7–16.2 µm (5-septate). However, the scattered conidia could be a result of disruption of fragile conidiomata in old herbarium material, a feature that we often observed in our material from freshwater when fine sand and detritus disrupted conidiomata. Our specimen matches well *B. leptopus* based on measurements of the holotype given by Hughes & White (1983c), though, the maximum of the width of conidia being slightly smaller.

Bactrodesmium spilomeum closely resembles *B. leptopus* but differs by narrower (8.5–11 µm wide in *B. s. vs* 11.5–15.5 µm wide in *B. l.*) and more ellipsoidal conidia. Hughes & White (1983c), who studied holotypes of both species, concluded to keep them separate until further variation in the conidia of *B. spilomeum* (see below) is established from European collections. Based on the examination of our specimens of *B. leptopus* and *B. spilomeum* and its type material, supported by the present phylogenetic analyses, we follow this conclusion and *B. leptopus* and *B. spilomeum* are treated as separate species in this study.

Bactrodesmium obovatum (Oudem.) M.B. Ellis, Mycol. Pap. 87: 42. 1963. Fig. 10.
Basionym: *Cryptocoryneum obovatum* Oudem., Ned. kruidk. Archf, 3 sér. 2: 313. 1901.
Synonym: *Bactrodesmium arnaudii* Hughes, Can. J. Bot., 36: 738. 1958.

Description on the natural substrate: *Asexual morph*: *Conidiomata* sporodochial, scattered, superficial, black, shining, punctiform, pulvinate, sometimes confluent and irregular in outline, 200–500 µm diam. Mycelium mostly immersed, composed of septate, subhyaline to pale brown hyphae 2.5–4.5 µm wide. *Conidiophores* semi-macronematous, fasciculate, arising from basal hyphae, subhyaline to pale brown, simple or branched, up to 60 µm long, 2.5–4 µm wide, septate, cells sometimes slightly inflated. *Conidiogenous cells* terminal, integrated, monoblastic, 3–5 µm wide, oblong to short-cylindrical, often broadening towards the apex, hyaline, thin-walled. *Conidia* (27.5–) 35–46(–48) × 15.5–20 µm (mean ± SD = 42.6 ± 3.4 × 17.7 ± 1.3 µm), (27.5–)38.5–40 × 15.5–18 µm (3-septate), (30–) 35–46(–48) × 15.5–20 µm (4-septate), 38–47(–48 × 16.5–20 µm (5-septate), 3–5 µm wide at the base, clavate to obovoid, rounded at the apex, truncate at the base, (3–)4–5-septate, mostly 4-septate, smooth, with a large globule at each cell, brown to dark brown, darker in the upper part, the colour becoming progressively paler towards the basal cell which is hyaline to subhyaline to very pale brown and bears a short frill of wall. The apical and penultimate cells are approximately the same size and larger than other cells; the septum near the apex is obscured by a broad black band 3.5–5 µm wide, the black bands are progressively narrower toward the base. *Sexual morph*: unknown.

Description on MLA: Vegetative hyphae hyaline to subhyaline, 2–3.5 µm wide, septate. *Conidiomata* sporodochium-like clusters. *Conidiophores* semi-macronematous, mostly simple or sparsely branched, or micronematous often reduced to conidiogenous cells, hyaline, arising from aerial or submerged hyphae. *Conidiogenous cells* terminal, intercalary, integrated, monoblastic, 4.5–12 µm wide, hyaline, subglobose to globose or cylindrical to subcylindrical and often broadening towards the apex. *Conidia* (27–)29.5–34.5(–47) × 10–13.5(–16.5) µm (mean ± SD = 31.2 ± 3.7 × 11.6 ± 1.0 µm), 3–4 µm wide at the base, clavate to obovoid, rounded at the apex, truncate at the base, (2–)3–4(–5)-septate, the septum near the apex with a black band 3–3.5 µm wide, other septa narrowly banded, smooth, brown to dark brown, paler towards the basal cell, which is subhyaline to pale brown and bears a short frill of wall.

Culture characteristics: Colonies on MLA 8–11 mm after 4 wk, circular, flat, slightly convex centrally, margin entire, velvety, pale brown becoming dark brown towards the margin; reverse dark brown. Colonies on OA 13–14(–26) mm after 4 wk, circular, flat, margin entire to weakly fimbriate, velvety to velvety-lanose, floccose towards the margin, olivaceous grey to olivaceous brown with a dark olivaceous grey to almost black outer zone; reverse olivaceous brown. Colonies on PCA 10–13 mm after 4 wk, circular, flat, margin entire to weakly fimbriate, velvety to velvety-lanose, beige becoming brown towards the periphery; reverse dark brown. Sporulation after 4 wk only on PCA in CBS 145350; sporulation of other strains on different media after 6–8 wk or after prolonged incubation.

Habitat and distribution: *Bactrodesmium obovatum* occurs on decaying wood and bark of various deciduous trees in terrestrial and freshwater habitats; it has been collected so far on *Alnus glutinosa*, *Betula* sp., *Carpinus betulus*, *Carya ovata*, *Corylus avellana*, *Fagus crenata*, *Fagus sylvatica*, *Fraxinus excelsior*, *Fraxinus angustifolia*, *Populus* sp., *Quercus* sp. and *Ulmus* sp. The species is known in Europe in the Czech Republic, France, the Netherlands, United Kingdom, and Spain, in Asia in Japan and also in North America in the U.S.A. and Canada (Hughes 1958, Ellis 1959, 1963, Holubová-Jechová 1972, Matsushima 1975, Hughes & White 1983a, Mena-Portales *et al.* 2000, this study).

Specimens examined: **Czech Republic**, South Moravia, Hodonín distr., Mikulčice oppidum, Mikulčický luh Nature Park, Malá Pinuška, on decaying wood of *Fraxinus excelsior*, associated with *Bactrodesmium* cf. *diversum*, 7 Nov. 2017, M. Réblová M.R. 3938 (PRA-00016145, culture CBS 144407). **France**, Ariège, Rimont, La Maille brook, 550 m a.s.l., on submerged wood of *Corylus avellana*, 19 Jun. 2017, J. Fournier J.F. 17031 (PRA-00016143, culture CBS 144077); *ibid*., Las Muros, Peyrau brook, 400 m a.s.l., on submerged wood of *Fraxinus excelsior*, 17 Jun. 2017, J. Fournier J.F. 17026 (PRA-00016142, culture CBS 144078); *ibid*., on submerged wood, 14 Mar. 2018 (incubated in moist chamber until 7 Apr. 2018), J. Fournier J.F. 18006A (PRA-00016144, culture CBS 145350).

Notes: *Bactrodesmium obovatum* is based on *Cryptocoryneum obovatum* introduced by Oudemans (1901). Ellis (1963) studied

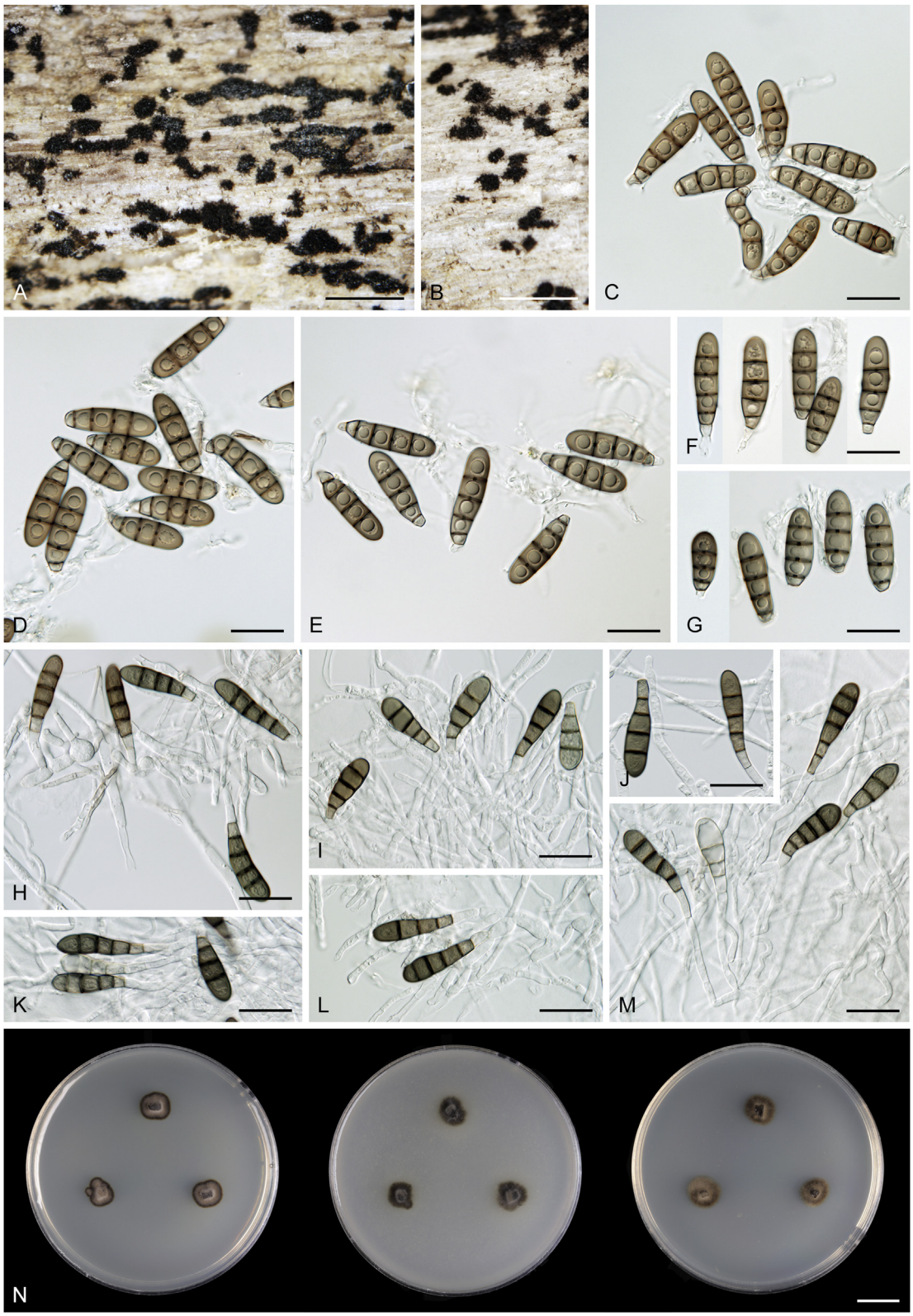

Fig. 12. *Bactrodesmium spilomeum* (CBS 146104). **A, B**. Sporodochial conidiomata on wood. **C–G**. Conidia and conidiophores. **H–M**. Conidia and conidiophores. **A–G**. On natural substrate. **H–M**. On MLA. **N**. Colonies on MLA, OA and PCA after 4 wk. Bars: A, B = 500 µm, C–M = 20 µm, N = 1 cm.

three collections of this species from Ouedeman's herbarium and concluded that *C. obovatum* is conspecific with *Bactrodesmium arnaudii* (Hughes 1958), which he earlier illustrated and described from numerous collections from England (Ellis 1959). *Bactrodesmium arnaudii* was introduced based on erroneously used name *Bactrodesmium fasciculare sensu* Mason & Hughes (1953) (Nom. inval., Art. 41.5) after examining a portion of Fuckel's material of "*Sporidesmium*" *fasciculare*. Ellis (1959) examined the type collection of *S. fasciculare* and confirmed that it is a different fungus conspecific with *Trichocladium opacum* (Hughes 1952) (= *Pleotrichocladium opacum*, Hernández-Restrepo *et al.* 2017). We have not examined Ouedeman's material now deposited in the National Herbarium of the Netherlands (L) in Leiden because it was not available to us, but we accept Ellis's synonymy. Our material matches well the fungus described and illustrated by Ellis (1959) under the name

B. arnaudii and Hughes & White (1983a) under the name *B. obovatum*.

Bactrodesmium obovatum is morphologically similar to *B. abruptum,* but the latter species differs in having brown to reddish-brown, clavate to oblong-clavate, longer [(36.5–) 42–65.5(–70) µm] and usually slightly narrower [(12.5–) 14–18(–19) µm], (3–)4–6(–7)-septate conidia, five septa being most common, the penultimate cell is the largest of all cells and the band at the septum near the apex is wider. The *in vitro* variability among selected strains of *B. abruptum* and *B. obovatum* is depicted in Fig. 7 and discussed above.

Bactrodesmium pallidum M.B. Ellis, Mycol. Pap. 72: 11. 1959. Fig. 11.

Description on the natural substrate: *Asexual morph*: *Conidiomata* sporodochial, scattered, superficial, brown to dark brown, punctiform, pulvinate, 120–300 µm diam, often elongated or confluent up to 500 µm diam. Mycelium mostly immersed in the substrate, composed of septate, subhyaline to pale brown hyphae 2–4 µm wide. *Conidiophores* macronematous to semi-macronematous, fasciculate, arising from basal hyphae, hyaline to subhyaline, sparsely branched, up to 75 µm long, 2–3.5 µm wide near the base, septate. *Conidiogenous cells* terminal, integrated, monoblastic, 2.5–3.5(–5) µm wide, sympodially elongating, oblong to cylindrical, often broadening towards the apex, hyaline, thin-walled. *Conidia* 29–54(–57) × 9–13 µm (mean ± SD = 43.3 ± 5.9 × 10.9 ± 1.0 µm), 29–33(–37) × 9–10(–11) µm (4-septate), (32–)35–47(–55) × 9.5–13 µm (5-septate), 42–54(–57) × 9–12.5 µm (6-septate), 1.5–3.5 µm wide at the base, elongated ellipsoidal or ellipsoidal-clavate, narrowed towards the apex, truncate at the base, (4–)5–6-septate, predominantly 5-septate, smooth, with a conspicuous central pore at the septa and a large guttule at each cell, pale brown, cells equally pigmented except the basal cell which is sometimes very pale brown to subhyaline and often bears a short frill of wall. *Sexual morph*: unknown.

Description on MLA: Vegetative hyphae hyaline to subhyaline, 1.5–3 µm wide. *Colonies* effuse, conidiomata not observed. *Conidiophores* micronematous often reduced to conidiogenous cells, hyaline. *Conidiogenous cells* terminal, intercalary, integrated, monoblastic, 2.5–4 µm wide, hyaline, subcylindrical to oblong, broadening towards the apex, sometimes slightly inflated. *Conidia* 28.5–47(–50) × 7.5–10 µm (mean ± SD = 39.4 ± 7.4 × 8.9 ± 0.9 µm), (2.5–)3–4 µm wide at the base, elongated ellipsoidal to ellipsoidal-clavate, rounded or narrowed at the apex, sometimes with a short protuberance at the top of the apical cell, truncate at the base, 4–6-septate, central pore at the septa indistinct, with one to several small guttules in each cell, pale brown, cells equally pigmented, basal cell of the same colour or very pale brown to subhyaline, basal frill of the wall indistinct (conidia remained mostly attached).

Culture characteristics: Colonies on MLA 7–9 mm after 4 wk, circular, slightly convex, margin entire, lanose, zonate, beige becoming grey-brown towards the margin with a beige ring and outer cinnamon-brown zone; reverse brown. Colonies on OA 12–15 mm after 4 wk, circular, flat, margin entire, lanose, floccose becoming cobwebby towards the margin, creamy, olivaceous brown towards the periphery due to conspicuous submerged growth; reverse dark olivaceous brown. Colonies on PCA 9–10 mm after 4 wk, circular, flat, margin entire, lanose, floccose, beige with a cinnamon-brown outer zone; reverse brown. Sporulation on all media after 6–8 wk or after prolonged incubation.

Specimens examined: **France**, Ariège, Rimont, La Maille brook, 550 m a.s.l., on submerged wood of *Fraxinus excelsior*, 19 Jun. 2017, J. Fournier J.F. 17030 (PRA-00016148); *ibid.*, Las Muros, Peyrau brook, 400 m a.s.l., on submerged wood of *Fraxinus excelsior*, 15 Sep. 2016, J. Fournier J.F. 16057 (PRA-00016146, culture CBS 142449); *ibid.*, on submerged wood of *Robinia pseudoaccacia*, 17 Jun. 2017, J. Fournier J.F. 17020 (PRA-00016147, culture CBS 145349). **Spain**, Cantabria, Saja-Besaya Natural park, on decaying wood of a twig, Jul. 2010, M. Hernández-Restrepo, J. Mena & J. Guarro (culture CBS 130515 = FMR 11345). **United Kingdom**, England, Yorkshire, Kingthorpe Woods, on bark of *Fraxinus excelsior*, Nov. 1945, E.W. Mason & S.J. Hughes (**holotype** of *B. pallidum* IMI 1355b).

Habitat and distribution: *Bactrodesmium pallidum* occurs on decaying wood and bark of various deciduous trees in terrestrial and freshwater habitats; it has been collected so far on *Fagus sylvatica*, *Fraxinus excelsior*, *Quercus* sp., and *Robinia pseudoaccacia* and other unidentified hosts. It is known from Europe in the Czech Republic, United Kingdom, France and Spain (Ellis 1959, Holubová-Jechová 1972, this study)

Notes: The conidia of *B. pallidum* are usually narrowed towards the apex; sometimes conidia form a short protrusion on the apical cell in culture. *Bactrodesmium spilomeum* is similar to *B. pallidum*, but differs by shorter (24–43 µm) and slightly darker brown, 3–5-septate, predominantly 4-septate conidia; the 6-septate conidia are uncommon and occur only in some collections (Holubová-Jechová 1972, Hughes & White 1983c). Holubová-Jechová (1972) questioned the distinction between *B. pallidum* and *B. spilomeum* and suggested that the former species is most likely a variety of *B. spilomeum* and transferred the name to its synonymy. Hughes & White (1983c) suggested that the elongation in conidia of *B. pallidum* is accompanied by narrowing to form the longer 4–6-septate conidia. In the phylogenetic trees (Figs 1, 2), *B. pallidum* and *B. spilomeum* are resolved as separate, though closely related species.

Bactrodesmium ellipsoideum and *B. indicum*, described by Rao (1983) from decaying bark in India, resemble *B. pallidum* in conidial morphology. *Bactrodesmium indicum* is distinguished from *B. pallidum* by narrower (7–11 µm), 4–5-septate, yellowish to golden brown conidia rounded at the apex, while *B. ellipsoideum* differs from it by shorter (30–42 µm), ellipsoidal conidia which are illustrated as somehow narrowed at the apex. *Bactrodesmium diversum, B. ellipsoideum*, *B. indicum*, *B. leptopus*, *B. pallidum* and *B. spilomeum* compose a group of morphologically highly similar species with pale brown to golden brown, thin-walled, transversely septate, cylindrical, elongated ellipsoidal to ellipsoidal-clavate conidia without bands at the septa. The morphological and molecular phylogenetic study is necessary to resolve the taxonomy of this species complex.

Bactrodesmium spilomeum (Berk. & Broome) E.W. Mason & S. Hughes, Can. J. Bot. 31: 616. 1953. Fig. 12.
Basionym: *Sporidesmium spilomeum* Berk. & Broome, in Rabenhorst, Fungi europaei Exs. No. 1162. 1868.

Description on the natural substrate: *Asexual morph*: *Conidiomata* sporodochial, scattered, superficial, brown, punctiform, pulvinate, 120–300 µm diam, often elongated or confluent up to 480 µm diam. Mycelium mostly immersed in the substrate, composed of septate, subhyaline to pale brown hyphae 2–3.5 µm wide. *Conidiophores* macronematous to semi-macronematous, fasciculate,

arising from basal hyphae, septate, hyaline to subhyaline, sparsely branched, up to 90 µm long, 2–3.5 µm wide near the base. *Conidiogenous cells* terminal, integrated, monoblastic, 2.5–4.5 µm wide, oblong to subcylindrical, often broadening towards the apex, hyaline, thin-walled. *Conidia* 24–43 × 8.5–11 µm (mean ± SD = 33 ± 4.3 × 9.9 ± 0.7 µm), 24–28 × 9–10.5 µm (3-septate), (28–)30–38 × 9–10 µm (4-septate), 37–43 × 10–11 µm (5-septate), 2.5–3.5 µm wide at the base, elongated ellipsoidal or ellipsoidal-clavate, rounded at the apex, truncate at the base, 3–5-septate, predominantly 4-septate, smooth, with a conspicuous central pore at the septa and a large guttule at each cell, pale brown to pale golden brown, cells equally pigmented except the basal cell which is paler, very pale brown to subhyaline and often bears a short frill of wall. *Sexual morph*: unknown.

Description on OA: Vegetative hyphae hyaline 2–3.5 µm, sometimes monilioid 5–9.5 µm wide. Colonies effuse, conidiomata not observed. *Conidiophores* semi-macronematous, sometimes sparsely fasciculate, or micronematous, hyaline, occasionally monilioid and formed by inflated cells. *Conidiogenous cells* terminal, integrated, rarely intercalary, monoblastic, 3.5–4.5 µm wide, hyaline, subcylindrical to oblong, broadening towards the apex. *Conidia* 23–39(–43) × (6–)6.5–9 µm (mean ± SD = 32.2 ± 4.2 × 7.8 ± 0.7 µm), 23–29.5 × 7.5–9 µm (3-septate), 28.5–39 × 6–9 µm (4-septate), 33.5–43 × 7.5–8.5 µm (5-septate), 2.5–4 µm wide at the base, elongated ellipsoidal to ellipsoidal-clavate, rounded at the apex, truncate at the base, 3–5-septate, predominantly 4-septate, smooth, with a central pore at each cell, mid-brown, basal cell pale brown to subhyaline.

Culture characteristics: On MLA colonies 7–8 mm diam after 4 wk, circular, flat, slightly convex centrally, margin fimbriate, velvety-lanose, floccose, grey-brown, dark brown at the margin due to melanised submerged hyphae; reverse dark brown to nearly black. On OA colonies 6–8 mm diam after 4 wk, circular, flat, margin fimbriate, sparsely lanose, floccose becoming cobwebby, dark olivaceous grey becoming dark grey-brown towards the periphery with an indistinct pale olivaceous beige outer zone of submerged growth; reverse dark olivaceous brown. On PCA colonies 7–8 mm diam after 4 wk, circular, flat, margin fimbriate, colonies similar to those on MLA, velvety-lanose, floccose, grey-brown, dark brown at the margin; reverse dark brown. Sporulation abundant on OA after 4 wk, sparse on MLA and PCA after 8 wk.

Specimens examined: **France**, Ariège, Rimont, Las Muros, Peyrau brook, 400 m a.s.l., on submerged wood, 14 Mar. 2018 (incubated in moist chamber until 7 Apr. 2018), J. Fournier J.F. 18006B (PRA-00016149, culture CBS 146104). **United Kingdom**, England, Batheaston, on decaying wood of a trunk of *Ulmus campestris*, Apr. 1867, C.E. Broome, in Rabenhorst, Fungi europaei Exs. No. 1162 (**holotype** IMI 45899).

Habitat and distribution: *Bactrodesmium spilomeum* occurs on decaying wood and bark of various deciduous trees in terrestrial and freshwater habitats; it has been collected so far on *Acer pseudoplatanus*, *Acer saccharum*, *Betula lutea*, *Betula* sp., *Fagus grandifolia*, *Fagus sylvatica*, *Fraxinus angustifolia*, *Fraxinus excelsior*, *Populus tremuloides*, *Tilia cordata*, and *Ulmus campestris* and on other unidentified hosts. The species is known in Europe in the Czech Republic, France and United Kingdom and in North America in Canada (Ellis 1959, Holubová-Jechová 1972, Hughes & White 1983c, this study).

Notes: Although the width of conidia of *B. spilomeum* has been reported consistently around (8–)9–12.5 µm (Ellis 1959, Holubová-Jechová 1972, this study), conidia in some European and Canadian collections examined by Hughes & White (1983c) were wider and thus resembling those of *B. leptopus*.

Bactrodesmium leptopus is reminiscent of *B. spilomeum* in the morphology of pale brown, ellipsoidal to clavate, 3–5-septate conidia but differs by broader (11.5–15.5 µm) conidia. *Bactrodesmium pallidum* closely resembles *B. spilomeum* but differs in having longer [29–54(–57) µm], paler, ellipsoidal to ellipsoidal-clavate conidia narrowed towards the apex with (4–)5–6 septa, 5-septate being the most common. *Bactrodesmium traversoanum* (Peyronel 1916, Ellis 1959, Hughes & White 1983d) is similar to *B. spilomeum* but differs in having ellipsoidal to clavate and darker brown conidia becoming paler towards the base. For morphological comparison among *B. spilomeum* and other morphologically similar species see notes under *B. pallidum*.

Genera segregated from *Bactrodesmium* and additional species of the *Pleurotheciales* and *Savoryellales* characterised in this study

Aphanodesmium Réblová & Hern.-Restr., **gen. nov.** MycoBank MB832922

Etymology: Aphanés (Gk) inconspicuous, unseen, referring to the "hidden" endophytic life style of the fungus; desmós (Gk) = bond, link, referring to the aggregated conidia in sporodochium-like conidiomata.

Type species: *Aphanodesmium gabretae* (Koukol & Kolářová) Réblová & Hern.-Restr.

Description: *Asexual morph*: *Colonies* effuse with sporodochium-like clusters *in vitro*. *Conidiophores* semi-macronematous or micronematous, loosely fasciculate, branched, sometimes swollen, hyaline. *Conidiogenous cell* monoblastic, integrated, terminal. *Conidia* dry, solitary, ellipsoidal to obovoid, distoseptate with transverse and oblique septa, pigmented, basal cell hyaline to pale brown. Conidia secede rhexolytically. *Sexual morph*: unknown.

Aphanodesmium gabretae (Koukol & Kolářová) Réblová & Hern.-Restr., **comb. nov.** MycoBank MB832923
Basionym: *Bactrodesmium gabretae* Koukol & Kolářová, Nova Hedwigia 91: 244. 2010.

Description: For description and illustration refer to Koukol & Kolářová (2010).

Habitat and distribution: *Aphanodesmium gabretae* exhibit an endophytic life style and occurs in needles of *Picea abies*. The species is so far known in Europe in the Czech Republic (Koukol & Kolářová 2010).

Notes: Given the morphology of sporodochia, fasciculate conidiophores, monoblastic conidiogenous cells and pigmented, distoseptate and dictyoseptate conidia seceding rhexolytically, this fungus was originally assigned to *Bactrodesmium* with affinity to the *Helotiales* based on the Blast search of ITS and LSU sequences (Koukol & Kolářová 2010). In our phylogeny, the ex-type strain ZK171 of *B. gabretae* is nested in the *Helotiales*; it resides in an *incertae sedis* lineage as a sister taxon to two apothecial species with unknown sexual-asexual connections, i.e. *Aquapoterium pinicola* (strain ATCC MYA-4213, Raja *et al.* 2008) and

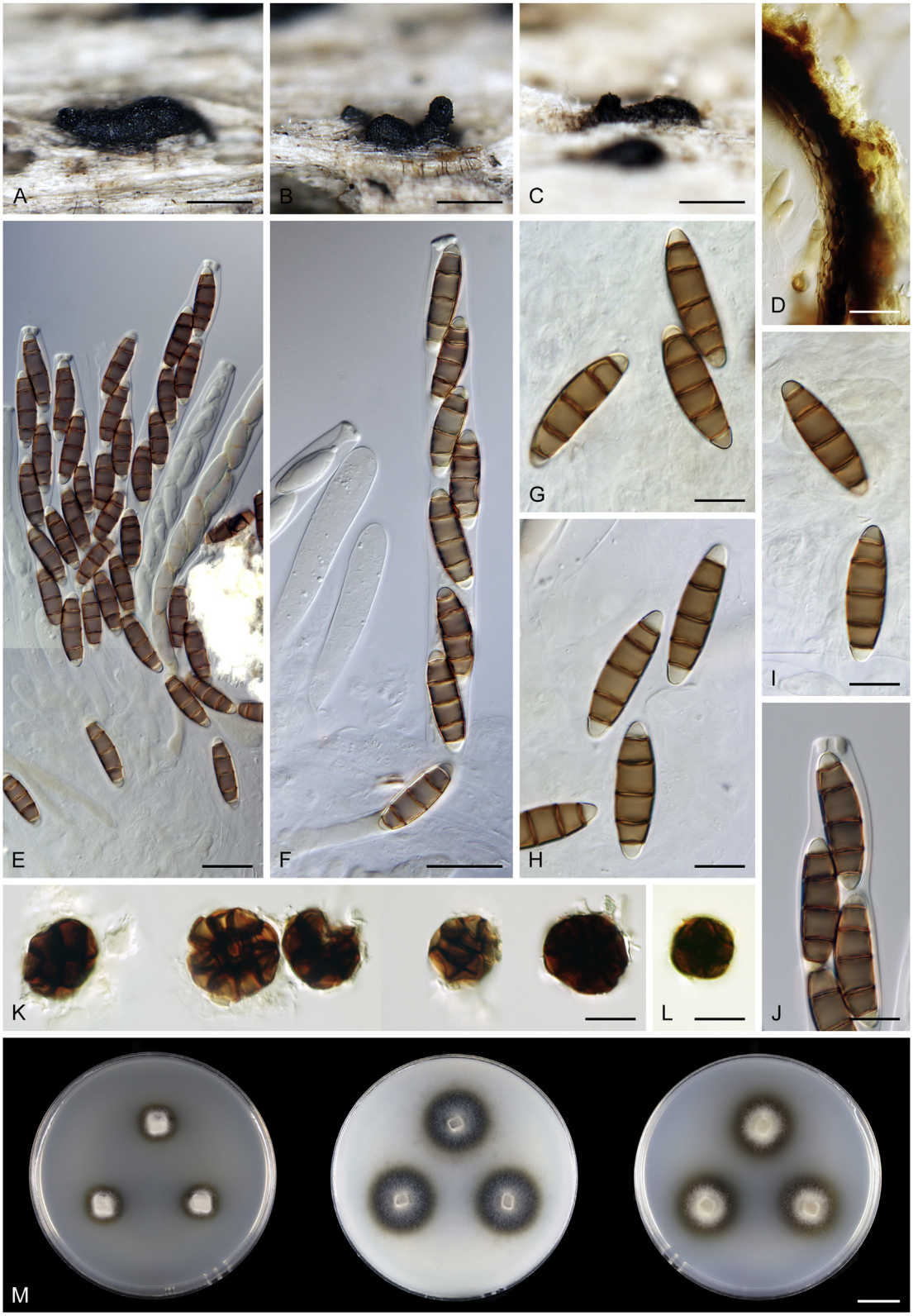

Fig. 13. *Ascotaiwania latericolla* (ICMP MB22739). **A–C**. Ascomata. **D**. Vertical section of the ascomal wall. **E, F**. Asci containing ascospores. **G–I**. Ascospores. **J**. Ascal apex with the apical ring. **K, L**. Monodictys-like asexual morph on the natural substrate. **A–L**. On natural substrate. **M**. Colonies on MLA, OA and PCA after 4 wk. Bars: A–C = 500 µm, D–F = 20 µm, G–L = 10 µm, M = 1 cm.

Unguicularia unguiculata (strain NK 322). Therefore, *B. gabretae* is excluded from *Bactrodesmium* and segregated into a new genus *Aphanodesmium* and a new combination is proposed.

Aphanodesmium gabretae was isolated from green needles of *Picea abies* incubated on agar plates. *In vitro*, the fungus forms effuse colonies (on 2 % malt extract) with abundant whitish, aerial mycelium and sporodochium-like clusters at the margin of the colony.

Ascotaiwania Sivan. & H.S. Chang, Mycol. Res. 96: 481. 1992.

Type species: *Ascotaiwania lignicola* Sivan. & H.S. Chang, Mycol. Res. 96: 481. 1992.

Notes: The genus *Ascotaiwania* was introduced by Sivanesan & Chang (1992) for saprobic lignicolous fungi resembling *Savoryella* (Jones & Eaton 1969) and characterised by non-stromatic ascomata with a lateral neck lying horizontally or obliquely on the host, transversely septate ascospores with brown middle cells and hyaline end cells, stipitate asci with a prominent non-amyloid apical ring and rapidly disintegrating paraphyses. The distinction between the two genera has always been challenging and was based predominantly on ascospore septation and the morphologies of the ascal apex and also paraphyses to some extent. A survey of these diagnostic characters and their interpretation by various authors was summarised in Réblová *et al.* (2016a). The monodictys-like asexual morph of *A. lignicola*, the generic type, was experimentally verified by Chang (2001). Up to date, 15 binomials were introduced in *Ascotaiwania* (Index Fungorum), some of which were reassigned to different genera based on the evidence of DNA molecular data, i.e. *Helicoascotaiwania* (Dayarathne *et al.* 2019), *Neoascotaiwania* (Hernández-Restrepo *et al.* 2017) and *Pseudoascotaiwania* (Yang *et al.* 2016). Nonetheless, the remaining species represent a heterogeneous assemblage, of which only six (*A. hsilio*, *A. latericolla*, *A. lignicola*, *A. mitriformis*, *A. sawadae*, *A. wulai*) conform to the sexual diagnostic morphological traits of *Ascotaiwania* and only two of them, *A. latericolla* and *A. lignicola*, produce dictyoconidia. Despite morphological similarity, the monophyly of *Ascotaiwania* is not statistically supported (Figs 1, 2).

A key to species of *Ascotaiwania sensu lato*

1a. Sexual morph known, ascospores transversely septate……..2
1b. Sexual morph unknown, asexual morph triadelphia-like; conidiogenous cells ampulliform, conidia 1-septate, obovoid, upper cell dark brown, lower cell brown 12.5–16 × 6.5–10.5 µm……*A. uniseptata*

2a. Ascomata lying horizontally or obliquely towards the surface of the substrate, neck erect, lateral, on decaying wood……3
2b. Ascomata upright with a central ostiole, on decaying wood, grass, or palm glade……9

3a. Ascospores versicolorous, middle cells brown, end cells hyaline to subhyaline……..4
3b. Ascospores uniformly pale brown, 5–7-septate, 19–30 × 6–8 µm……*A. mauritiana*

4a. Ascospores 7-septate……5
4b. Ascospores with less than seven septa……7

5a. Ascospores 62 µm or longer, 62.5–72.5 × 12.5–17.5 µm, monotosporella-like asexual morph……*A. mitriformis*
5b. Ascospores 62 µm or shorter……6

6a. Ascospores 14 µm or wider, 53–62 × 14–16 µm…*A. wulai*
6b. Ascospores narrower than 14 µm, 42–55 × 8–13 µm, monodictys-like asexual morph……*A. lignicola*

7a. Ascospores 3-septate, 25.2–44.6 × 7.1–10.3 µm, monotosporella-like asexual morph……..*A. sawadae*
7b. Ascospores 5-septate, 25–35 × 7–9 µm……8

8a. Asci up to 140 µm long, 120–140 × 12.3–13.4 µm, trichocladium-like asexual morph……*A. hsilio*
8b. Asci longer than 140 µm, 190–237 × 14–17.5 µm, monodictys-like asexual morph……*A. latericolla*

9a. Ascospores versicolorous……10
9b. Ascospores uniformly yellow or light brown, (2–)3(–5)-septate, 16–25 × 5–7 µm……*A. pallida*

10a. Ascospores 3-septate……...11
10b. Ascospores 7-septate, 28.5–37.5 × 6–7.8 µm…*A. licualae*

11a. Ascospores 5 µm or wider, 17.5–20 × 5–6.5 µm, asci 150 µm or longer……*A. palmicola*
11b. Ascospores narrower than 5 µm, 18–22 × 3.5–4 µm, asci shorter than 150 µm……*A. pennisetorum*

Ascotaiwania latericolla Réblová, Hern.-Restr. & J. Fourn. **sp. nov.** MycoBank MB833391. Fig. 13.

Typification: **New Zealand**, Auckland Region, Waitakere Ranges Nature Reserve, ca. 30 km SW from Auckland, Anawhata Road, on decaying wood, 24 Apr. 2005, M. Réblová M.R. 3530/NZ 824 (**holotype** PDD 117342, culture ex-type ICMP 22739).

Etymology: Collum (L) neck, lateralis (L) lateral, referring to the lateral position of the neck on ascomata.

Description on the natural substrate: *Sexual morph*: *Ascomata* perithecial, non-stromatic, solitary to aggregated, immersed to semi-immersed becoming erumpent, black, flask-shaped, glabrous with sparse dark brown hyphae at the base, lying horizontally or obliquely towards the surface of the substrate, with a lateral, erect, rostrate or beak-like neck. Venter 450–750 µm high, 200–320 µm diam, ellipsoidal, often laterally flattened. *Neck* 200–450 µm high, 100–120 µm diam, cylindrical. *Ostiole* periphysate. *Ascomatal wall* leathery, 20–27 µm thick, two-layered; outer layer consisting of 3–4 rows of thick-walled, brown, polyhedral cells of textura angularis to prismatica, inner layer consisting of several rows of subhyaline to hyaline, thin-walled, elongated cells of textura prismatica. *Paraphyses* hyaline, septate, 4–8 µm wide, tapering to 2–2.5 µm, deliquescing early and observed only as fragments in ascomata containing mature ascospores. *Asci* 190–237 × 14–17.5 µm (mean ± SD = 208.7 ± 20.7 × 15.2 ± 1.5 µm), in the sporiferous part 157–168(–183) µm long (mean ± SD = 169 ± 10.1), cylindrical, long-stipitate. Ascal apex obtuse with a non-amyloid ring 7–7.5 µm wide and 3–3.5 µm high. *Ascospores* (24.5–) 25.5–32.5(–35) × 7.5–8.5(–9) µm (mean ± SD = 29 ± 2.5 × 8 ± 0.4 µm), fusiform, inequilateral, straight to slightly curved in the side view, transversely 5-septate, smooth-walled, versicolorous, the middle cells brown, end cells hyaline, shorter and obtusely to narrowly rounded; ascospores obliquely uniseriate or biseriate to partially overlapping biseriate in the ascus, no appendages or mucilaginous sheath observed. *Asexual morph*: *Colonies* effuse, with irregular outline, blackish brown, composed of individual conidia. Mycelium scant, mostly immersed, hyaline to subhyaline, composed of septate hyphae ca. 1.5–2.5 µm wide. *Conidiophores* micronematous, reduced to undifferentiated hyphal branches; conidial secession probably schizolytic. *Conidiogenous cells* not preserved. *Conidia* dry, terminal, blastic, globose, subglobose to ellipsoidal, (12.5–)13.5–22 × (9.5–)10.5–17.5(–18.5) µm (mean ± SD = 16.6 ± 2.6 × 14.0 ± 2.3 µm), reddish brown to dark brown, dictyosporous, slightly constricted at the septa.

Culture characteristics: On MLA colonies 8–9 mm diam after 4 wk, circular, flat, margin fimbriate, velvety-lanose, whitish-beige

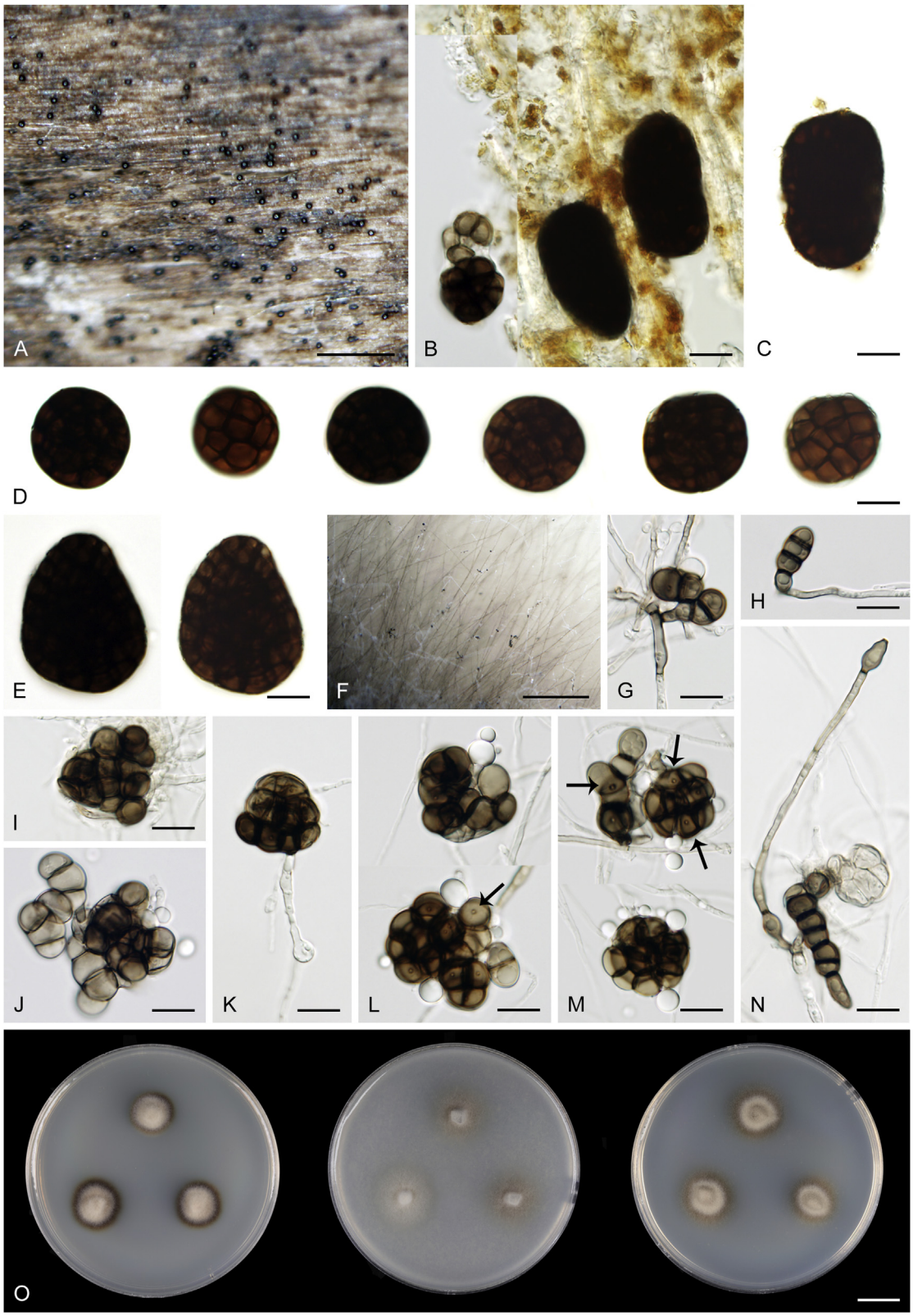

Fig. 14. *Dematiosporium aquaticum* (CBS 144793). **A**. Effuse colony with visible single conidia. **B–E**. Conidia. **F**. Conidia formed on submerged hyphae in agar. **G, H**. Conidial initials. **I–N**. Conidia and conidiophores (pores indicated by arrows). **A–E**. On natural substrate. **F–N**. On MLA. **O**. Colonies on MLA, OA and PCA after 4 wk. Bars: A = 250 µm, B–E, G–N = 10 µm, F = 500 µm, O = 1 cm.

with a dark olivaceous brown outer zone of submerged growth; reverse dark olivaceous brown. On OA colonies 16–18 mm diam after 4 wk, circular, flat, margin fimbriate, lanose, floccose, cobwebby at the margin, pale beige becoming olivaceous brown towards the margin with a prominent zone of submerged growth; reverse dark olivaceous brown. On PCA colonies 12–13 mm diam after 4 wk, circular, flat, slightly convex centrally, margin fimbriate, lanose, floccose, cobwebby at the margin, beige with a dark brown outer zone of submerged growth; reverse dark brown. On OA and PCA, pale olivaceous brown pigment diffusing from the colony margin into the surrounding agar. Sporulation absent on all media, even after prolonged incubation (>3 mo).

Habitat and distribution: *Ascotaiwania latericolla* occurs on decaying wood in terrestrial habitats. The species is so far known in New Zealand.

Notes: Based on morphology of ascospores, asci, ascomata and DNA sequence data, the present species is attributed to *Ascotaiwania* and introduced as the new species *A. latericolla*. Although the axenic culture derived from ascospores remained sterile, a monodictys-like fungus forming effuse colonies around ascomata on the host likely represents the asexual morph of *A. latericolla*. Conidiogenous cells were not preserved on the natural substrate. *Ascotaiwania lignicola* differs from the present species by larger (42–55 × 8–13 µm) 7-septate ascospores, and larger (234–290 × 13–19 µm) asci and (29.5–42.75 × 17.25–44.5 µm) conidia (Sivanesan & Chang 1992, Chang 2001). *Ascotaiwania hsilio* (Chang *et al.* 1998) resembles *A. latericolla* in size and septation of ascospores but differs by shorter and narrower (120–140 × 12.3–13.4 µm) asci and a trichocladium-like asexual morph.

Dematiosporium Z.L. Luo, K.D. Hyde & H.Y. Su, Fung. Diver. 99: 573. 2019. Emend. Réblová, Hern.-Restr. & J. Fourn.

Type species: *Dematiosporium aquaticum* Z.L. Luo, K.D. Hyde & H.Y. Su

Emended description: *Asexual morph*: *Colonies* effuse, black-brown, composed of individual conidia. Mycelium scant, mostly immersed, hyaline to subhyaline. *Conidiophores* micronematous, reduced to undifferentiated hyphal branches; conidial secession probably schizolytic. *Conidiogenous cells* terminal, integrated, monoblastic *in vitro*. *Conidia* dry, single, terminal, blastic, globose, subglobose, ellipsoidal or pyriform, pigmented, dictyosporous. *Sexual morph*: unknown.

Notes: *Dematiosporium* was introduced by Luo *et al.* (2019) for a hyphomycete with dry, dark brown to black, mostly globose to subglobose, smooth conidia. The type species, *D. aquaticum*, was recollected on submerged wood in France and successfully obtained in axenic culture. Based on our observations *in vitro* and *in vivo*, the generic description *sensu* Luo *et al.* (2019) is inaccurate because it does not contain diagnostic characters of conidia, i.e. the conidia are dictyosporous with a pore at each cell (Fig. 14L, M). The photographs accompanying the protologue of *D. aquaticum* do not have sufficient quality to recognize the septation and presence of pores inside conidia. Although difficult to see, some figures (Luo *et al.* 2019: fig. 45c–e, j) show traces of septa in conidia, but these are not interpreted or described. The generic and species descriptions are therefore emended to include diagnostic characters of conidia. Although the conidiogenous cells were not preserved on the natural substrate, they are described and illustrated based on *in vitro* observations.

The comparison of *Dematiosporium* to *Conioscypha* (Höhnel 1904) by Luo *et al.* (2019) is misleading, and these genera are not morphologically similar. *Conioscypha* (*Conioscyphales*) is characterised by aseptate, dark brown conidia and a unique mode of blastic conidiogenesis, when conidia are born in cyathiform to doliiform blastic conidiogenous cells surrounded by hyaline, cup-like collarettes with a multilamellar structure (Shearer & Motta 1973).

The monodictys-like genus *Dematiosporium* is placed in the *Savoryellales* as a sister to a clade containing *Canalisporium* and *Savoryella* (Figs 1, 2). Based on available ITS and LSU sequence data of *Monodictys putredinis* (Hughes 1958) (strain CBS 127855, Vu *et al.* 2019), the type species of *Monodictys* (Hughes 1958), this genus is nested in the *Pleosporales*. Although *Dematiosporium* and *Monodictys* form effuse colonies and share similar conidia, conidiogenous cells and conidiophores, however, such morphology is rather nondescript; these characters do not facilitate identification of morphologically similar genera and attest to the polyphyletic nature of *Monodictys* (see Discussion).

Dematiosporium aquaticum Z.L. Luo, K.D. Hyde & H.Y. Su, Fung. Diver. 99: 573. 2019. Emend. Réblová, Hern.-Restr. & J. Fourn. Fig. 14.

Description on the natural substrate: *Asexual morph*: *Colonies* effuse, with irregular outline, blackish brown, composed of individual conidia, which are scattered or aggregated, positioned vertically, superficial. Mycelium scant, mostly immersed, hyaline to subhyaline, composed of septate, unbranched or simply branched hyphae 3.5–5 µm wide. *Conidiophores* micronematous, reduced to undifferentiated hyphal branches from which conidia arise; conidial secession probably schizolytic. *Conidiogenous cells* not preserved. *Conidia* dry, terminal, blastic, mostly globose, subglobose to ellipsoidal, 24–28(–31) × (18–)19.5–26(–30) µm (mean ± SD = 26.2 ± 2.5 × 23.1 ± 2.7 µm), sometimes obpyriform, 33.5–38 × (18–)19–25(–29.5) µm (mean ± SD = 35.6 ± 2.1 × 23.2 ± 4.6 µm), chestnut brown to dark brown to nearly black, dictyosporous, slightly constricted at the septa, with a pore in each cell. *Sexual morph*: unknown.

Description on MLA: Vegetative hyphae hyaline to pale brown, unbranched or simply branched, sometimes anastomosing, 1.5–3.5 µm, septate. *Colonies* effuse. *Conidiophores* semi-macronematous or micronematous, often reduced to undifferentiated hyphal branches. *Conidiogenous cells* terminal, integrated, monoblastic, either indistinguishable from other cells, hyaline, oblong to subcylindrical or pale brown and lageniform, 9–9.5 × 4 µm. *Conidia* dry, terminal, intercalary, subspherical to ellipsoidal, 18–25 × 15–20.5 µm (mean ± SD = 20.8 ± 2.8 × 19.1 ± 2.4 µm), rarely almost triangular, 20.5–22 µm long, 20.5–24 µm wide at the base (mean ± SD = 21.3 ± 1.2 × 22.3 ± 2.4 µm), brown, dictyosporous, constricted at the septa, with a pore in each cell.

Culture characteristics: On MLA colonies 10–11 mm diam after 4 wk, circular, flat, slightly convex centrally, margin fimbriate, lanose, floccose becoming cobwebby towards the margin, beige with a brown outer zone of melanised submerged hyphae; reverse brown. On OA colonies 12–14 mm diam after 4 wk, circular, flat, margin fimbriate, sparsely lanose becoming cobwebby at the margin, beige, pale brown towards the periphery with an indistinct pale beige outer zone of submerged growth; reverse pale brown. On PCA colonies 13–14 mm diam after 4 wk, circular, flat, margin fimbriate, similar to colonies on MLA, lanose, floccose, cobwebby at the margin, beige with a brown outer zone of melanised submerged hyphae; reverse brown. Sporulation on MLA after 8 wk, absent on OA and PCA.

Habitat and distribution: *Dematiosporium aquaticum* occurs on decaying submerged wood of *Alnus glutinosa* and other unidentified substrates. The species is so far known in Europe in France and in Asia in China (Luo *et al.* 2019, this study).

Specimens examined: **France**, Ariège, Rimont, Las Muros, Peyrau brook, 400 m a.s.l., on submerged wood of *Alnus glutinosa*, 14 Mar. 2018, J. Fournier J.F. 18009 (PRA-00016156, culture CBS 144793); *ibid.*, M. Fournier J.F. 18012 (PRA-

Fig. 15. *Gamsomyces longisporus*. **A–C**. Synnemata (A, viewed from the top). **D**. Sporodochium-like conidioma (indicated by arrow). **E, L**. Upper part of the synnema with conidiogenous cells and conidia. **F, H**. Conidia and conidiogenous cells. **G**. Conidiogenous cells (arrows indicate percurrently elongating conidiogenous cells. **I–K**. Conidia. **A–L**. On natural substrate. Images: A, K, L CBS H-3931, B–J CBS H-3972. Bars: A–D = 100 µm, E, L = 50 µm, F–K = 10 µm.

00016157); *ibid*., La Maille brook, 550 m a.s.l., on submerged wood, 28 May 2018 (incubated in moist chamber for 1 wk), J. Fournier M.R. 4081 (PRA-00016158).

Notes: The ontogeny of conidia *in vitro* on MLA is depicted in Fig. 14G–M. The conidial initials are pigmented, straight, transversely septate becoming cheiroid and coiled and result in dictyosporous conidia at maturity.

Monodictys paradoxa (*incertae sedis*) is similar to *D. aquaticum* in having brown dictyoconidia of a comparable size, but differs in conidia with one or more of the basal cells paler than the others and monilioid conidiophores (Ellis 1971, Prasher & Verma 2016). *Monodictys putredinis* resembles *D. aquaticum* in subglobose, ellipsoidal to pyriform conidia and absence of inflated cells in conidiophores (Hughes 1958, Ellis 1971), but differs by slightly larger (20–30 × 15–25 µm *fide* Ellis 1971) conidia and the systematic placement in the *Pleosporales*. *Dematiosporium aquaticum* can also be compared to the monodictys-like asexual morphs of two *Ascotaiwania*; *A. lignicola* differs by larger (29.5–42.75 × 17.25–44.5 µm), dark reddish-brown dictyoconidia (Chang 2001), while *A. latericolla*

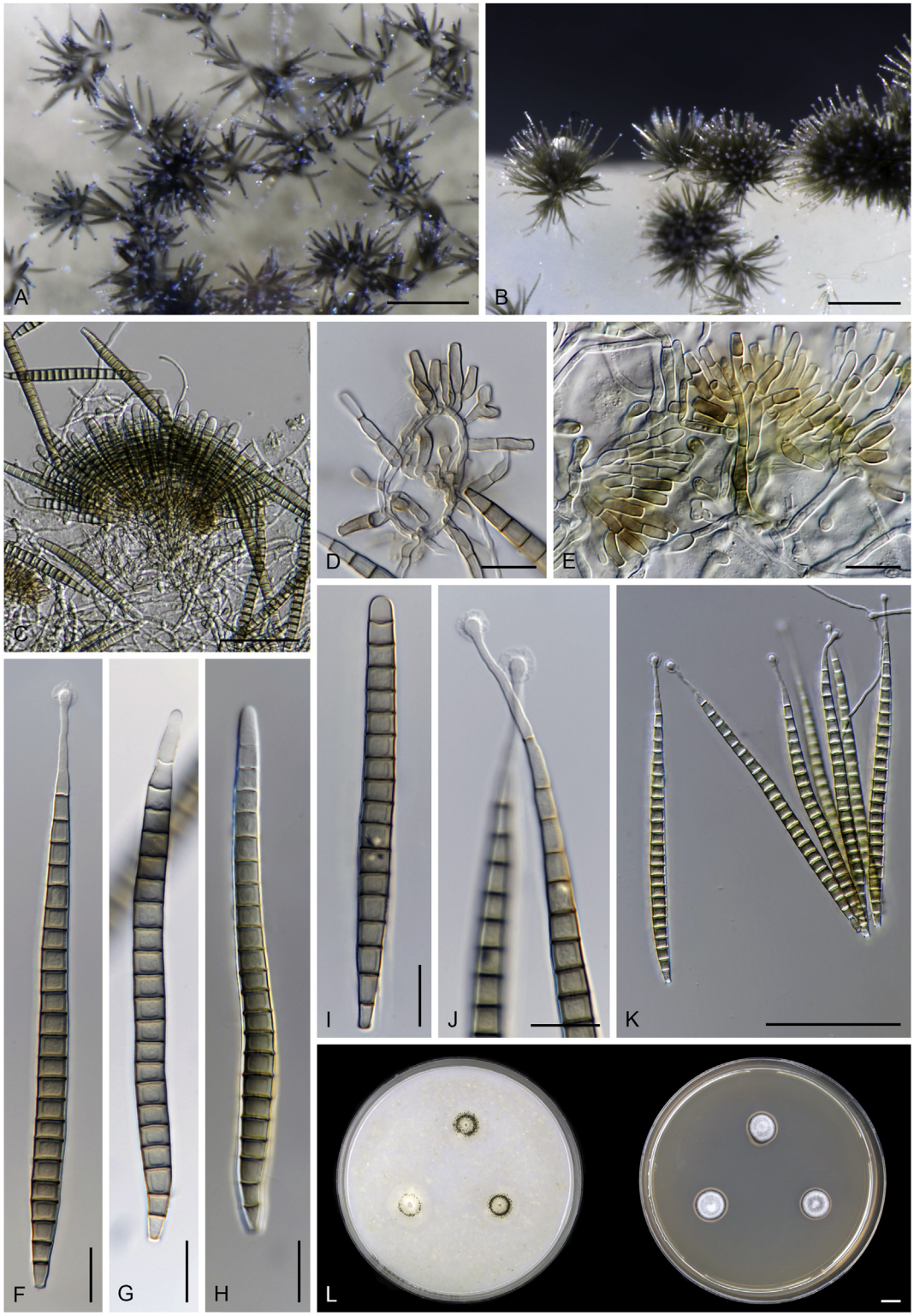

Fig. 16. *Gamsomyces longisporus*. **A–C**. Sporodochia. **D, E**. Conidiophores with conidiogenous cells. **F–K**. Conidia. **A–K**. On CBSOA. **L**. Colonies on CBSOA and MEA after 4 wk. Images: A, C, E CBS 240.89, B, D, F–L CBS 118.86. Bars: A, B = 200 µm, C, K = 50 µm, D–J = 10 µm, L = 1 cm.

has smaller [(12.5–)13.5–22 × (9.5–)10.5–17.5(–18.5) µm], dark reddish-brown to brown conidia (this study).

Gamsomyces Hern.-Restr. & Réblová, **gen. nov.** MycoBank MB834446

Etymology: This genus is named in honour of the late Walter Gams, our colleague and friend, for his contribution to mycology.

Type species: Gamsomyces longisporus (M.B. Ellis) Hern.-Restr. & Réblová

Description: *Asexual morph*: *Colonies* with sporodochial or synnematous conidiomata. *Conidiophores* semi-macronematous or macronematous, fasciculate, simple or penicillately branched, subhyaline to brown. *Conidiogenous cells* monoblastic, integrated, terminal, elongating percurrently. *Conidia* dry, solitary, curved, fusiform, pigmented, transversely euseptate, with a mucilaginous cap at the apex. Conidia secede schizolytically. *Sexual morph*: unknown.

Notes: Multigene phylogenetic analysis of three strains of *Bactrodesmium longisporum* and *B. stilboideum* revealed they were unrelated to *Bactrodesmium*; they formed a strongly supported lineage in the *Sclerococcales* (*Eurotiomycetes*), which is introduced as the new genus *Gamsomyces* (Fig. 4). Two species are accepted in the genus, and new combinations are proposed. *Gamsomyces* differs from *Bactrodesmium* in having inconspicuous, brown to olivaceous brown conidiomata, both sporodochia and synnemata, presence of a mucilaginous cap at the apex of conidia, absence of dark bands over the transverse septa and morphology of the conidiogenous cells. The percurrently elongating conidiogenous cells on the natural substrate, first mentioned by Hughes (1978) in *G. longisporus*, are in agreement with our observations (Fig. 15G). The same mode of the conidiogenous cell elongation is also present in *G. stilboideus* (Fig. 17E).

Key to species of *Gamsomyces*

1a. Sporodochia and synnemata on the natural substrate, synnemata 74–305 µm long, conidia 11–16-septate, 48.5–74 × 6–8 µm, or longer up to 80 µm *fide* (Ellis 1976) and 95 µm *fide* (Hughes 1978) with up to 21 septa; *in vitro* only sporodochia formed, conidia 41–163.5 × 5.5–8 µm, (6–)14–25-septate……*G. longisporus*

1b. Only synnemata 380–455 µm long on the natural substrate, conidia 10–13-septate, 46–69 × 7–9 µm, or shorter 30–55 × 7–8 µm (*fide* Castañeda-Ruiz & Arnold 1985); *in vitro* synnemata 325–633 µm long, conidia 42–90 × 6.5–10 µm, (5–)14–16-septate…*G. stilboideus*

Gamsomyces longisporus (M.B. Ellis) Hern.-Restr. & Réblová, **comb. nov.** MycoBank MB834448. Figs 15, 16.
Basionym: *Bactrodesmium longisporum* M.B. Ellis, More dematiaceous Hyphomycetes: 68. 1976.
Synonym: Stigmina longispora (M.B. Ellis) S. Hughes, New Zealand Journal of Botany 16: 353. 1978.

Description on the natural substrate: *Asexual morph*: Co-nidiomata sporodochial or synnematous, scattered, superficial, dark brown, synnemata 74–305 µm long and 18.5–35 µm wide. *Conidiophores* macronematous, fasciculate, unbranched or branched, subhyaline or pale brown, septate. *Conidiogenous cells* terminal, integrated, monoblastic, 4.5–13 × 2–4 µm, subcylindrical, brown, elongating percurrently. *Conidia* 48.5–74 × 6–8 µm (mean ± SD = 62.4 ± 7.5 × 7.3 ± 0.7 µm), fusiform, usually straight or slightly flexuous, truncate at the base, rounded to subulate or capitate at the apex with a mucilaginous cap, 11–16-septate, smooth, brown, paler towards both ends, apical cell hyaline to subhyaline, collapsing, secession schizolytic. *Sexual morph*: unknown.

Description on OA: Conidiomata sporodochial, scattered, superficial, punctiform, black, 50–170 µm diam. Mycelium mostly immersed, composed of septate, pale brown hyphae, 1.5–2.5 µm wide. *Conidiophores* semi-macronematous to macronematous, fasciculate, unbranched or densely branched, subhyaline or pale brown, septate, up to 50 µm long, 2–4 µm wide. *Conidiogenous cells* terminal, integrated, monoblastic, 4.5–12.45 × 2.5–4 µm, subcylindrical, pale brown. *Conidia* 41–163.5 × 5.5–8 µm (mean ± SD = 130.1 ± 22.6 × 6.8 ± 0.5 µm), 2–2.5 µm wide at the base, fusiform, usually straight or slightly flexuous, truncate at the base, rounded to subulate or capitate at the apex with a mucilaginous cap 5–7.5 diam, (6–)14–25-septate, smooth, pale brown to brown to olivaceous brown, paler towards both ends, apical cell hyaline, secession schizolytic.

Culture characteristics: Colonies on CBSOA 7–10 mm after 4 wk, circular, flat becoming slightly convex centrally, margin entire, lanose, powdery towards the margin, colony centre lavender grey to olivaceous grey with an olivaceous outer zone; reverse olivaceous buff. Colonies on MEA 12–15 mm after 4 wk, circular, convex, margin entire, lanose, floccose, pale olivaceous grey to olivaceous black; reverse pale mouse grey to olivaceous grey. Sporulation on CBSOA after 4 wk or after prolonged incubation.

Specimens examined: **India**, Karnataka, Shimoga, Agumbe, on rotten branches, Oct. 1985, V. Rao (CBS H-3848, culture CBS 118.86); *ibid.*, Karnataka, Jog Falls, on rotten twigs, Oct. 1985 V. Rao (CBS H-3931); *ibid.*, Tirupati, Andhra Pradesh, on rotten twig, Sep. 1983, V. Rao (CBS H-3972). **Japan**, Arashiyama near Kyoto, on decaying stem of bamboo, Sep. 1988, W. Gams (CBS H-9344 as dried culture, culture CBS 240.89).

Habitat and distribution: *Gamsomyces longisporus* occurs on decaying wood, timber and bamboo stems; it has been collected so far on *Alnus* sp., *Beilschmiedia tarairi*, *Olearia rani*, bamboo and other unidentified hosts. The species is known in Africa in South Africa, Australia, Asia in Hong Kong, India, Japan, Philippines and Taiwan, Europe in United Kingdom, Middle America in Guatemala and Mexico, New Zealand and South America in Brazil, Peru and Venezuela (Ellis 1976, Hughes 1978, Rao & de Hoog 1986, Matsushima 1993, Chang 1997, Wong & Hyde 2001, Cai *et al.* 2003, Vijaykrishna & Hyde 2006, Castañeda-Ruiz *et al.* 2009, Barbosa & Gusmão 2011, Figueroa *et al.* 2016, Santa Izabel & Gusmão 2016, Heredia *et al.* 2018).

Notes: *Gamsomyces longisporus* was described with sporodochial conidiomata from timber in mines in United Kingdom (Ellis 1976) and originally placed in the genus *Bactrodesmium*. Hughes (1978) transferred the species to *Stigmina* (*Mycosphaerellales*) based on percurrently elongating conidiogenous cells occurring in older specimens. Rao & de Hoog (1986) studied material from India and encountered variability in conidioma morphology; sporodochia and sometimes both synnemata and sporodochia were formed on the natural substrate. Rao & de Hoog (1986) questioned the taxonomic value of synnema *vs* sporodochium (see Discussion). They did not follow Hughes's taxonomic treatment, instead, they proposed *B. longisporum* conspecific with morphologically similar but synnematous *B. stilboideum* and accepted the species in *Bactrodesmium*.

Based on molecular DNA evidence, both species were transferred from *Bactrodesmium* to the new genus *Gamsomyces* and treated as separate taxa. In the three examined collections from India, conidiomata were sporodochial in CBS H-3848, sporodochium-like or short synnemata up to 74 µm long were formed in CBS H-3931, or conidiomata were mostly synnematous up to 305 µm long and also sporodochium-like in CBS H-3972 (Fig. 15A–D); cultures of the two latter specimens are not available. Strains of *G. longisporus* CBS 118.86 (ex CBS-H 3848) and CBS 240.89 (ex CBS H-9344 as dried culture, Japan) formed exclusively sporodochia *in vitro* (Fig. 16A, B).

Because *G. longisporus* and *G. stilboideus* were considered conspecific, the given geographical distribution of the

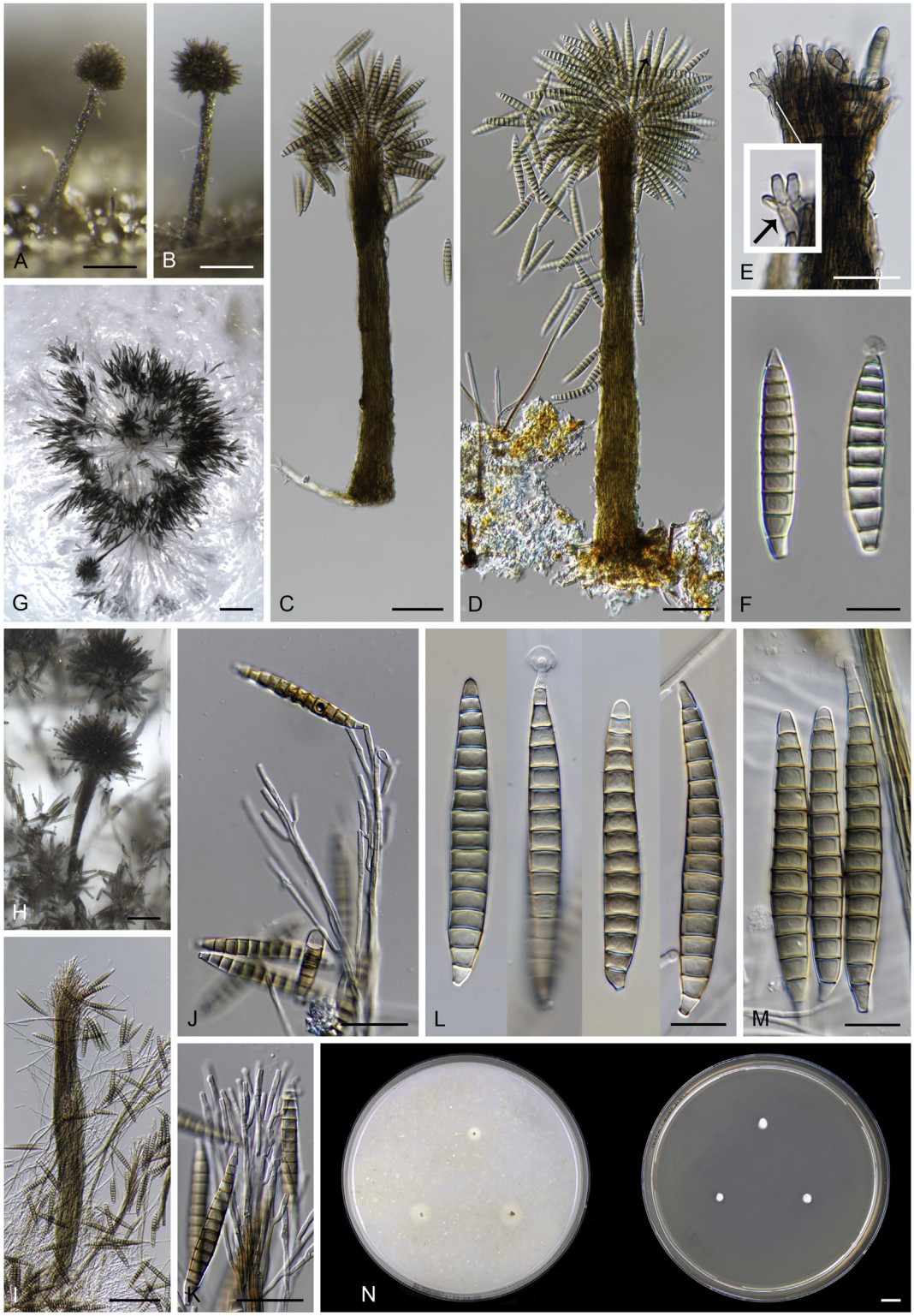

Fig. 17. *Gamsomyces stilboideus* (CBS 146494). **A–D**. Synnemata. **E**. Upper part of the synnema with conidiogenous cells (arrow indicates percurrently elongating conidiogenous cells). **F, L, M.** Conidia. **G, H.** Synnemata and densely branched conidiophores with conidia. **J, K**. Conidiophores with conidia. **A–F**. On natural substrate. **G–M**. On CBSOA. **N**. Colonies on CBSOA and MEA after 2 wk. Bars: A, B, H = 100 µm, C, D, I = 50 µm, E, J, K = 25 µm, F, L, M = 10 µm, G = 200 µm, N = 1 cm.

former species since Rao & de Hoog (1986) may not be accurate and needs to be confirmed with new specimens or revision of herbarium material.

Gamsomyces longisporus is similar to *G. stilboideus* (Castañeda-Ruiz & Arnold 1985) but differs from the latter species by longer conidia, 50–80 µm *fide* Ellis (1976), 95 µm *fide* Hughes (1978) *vs* 30–55 µm *fide* Castañeda-Ruiz & Arnold (1985), with generally more septa 8–20 *vs* 6–11. The size of conidia in our material matches that of the holotype (Ellis 1976).

Bactrodesmium ramosius (Matsushima 1993), described from decaying wood of a broad-leaf tree in Amazonia, is highly similar to *G. longisporus* in morphology of sporodochial conidiomata, transversely septate conidia with a mucilaginous cap and densely branched conidiophores formed *in vitro*, but it differs in shorter (40–64 µm) conidia with less septa, 8–12. *Bactrodesmium fruticosum* (Matsushima 1993) and *B. guamense* (Matsushima 1981) are well comparable to *G. longisporus*; *in vitro*, they produce sporodochia with conidiophores branched

in a penicillate fashion and brown, transversely septate conidia, although lacking the mucilaginous cap. However, the conidia of *B. fruticosum* are illustrated with the basal frill of the wall suggesting rhexolytic secession (Matsushima 1993).

Gamsomyces stilboideus (R.F. Castañeda & G.R.W. Arnold) Hern.-Restr. & Réblová, **comb. nov.** MycoBank MB834450. Fig. 17.

Basionym: *Bactrodesmium stilboideum* R.F. Castañeda & G.R.W. Arnold, Revta. Jardín bot. Nac. Univ. Habana 6(1): 48. 1985.

Synonym: *Stigmina longispora* var. *stilboidea* (R.F. Castañeda & G.R.W. Arnold) J. Mena & Mercado, Rep. de Investigación del Instituto de Ecología y Sistemática, Academia de Ciencias de Cuba, Ser. Bot. 17: 10. 1987.

Description on the natural substrate: *Asexual morph*: *Conidiomata* synnematous, scattered, superficial, dark brown to dark olivaceous brown, 380–455 µm long and 30–45 µm wide. *Conidiophores* macronematous, fasciculate, unbranched or branched, brown, septate. *Conidiogenous cells* terminal, integrated, monoblastic, 6.5–18.5 × 2.5–4 µm, subcylindrical, brown, elongating percurrently. *Conidia* 46–69 × 7–9 µm (mean ± SD = 57.7 ± 6.2 × 8 ± 0.6 µm), fusiform, usually straight or slightly flexuous, truncate at the base, rounded to subulate or capitate at the apex with a mucilaginous cap, 10–13-septate, smooth, brown, paler towards both ends, apical cell hyaline to subhyaline, secession schizolytic. *Sexual morph*: unknown.

Description on OA: *Conidiomata* synnematous, scattered, superficial, dark brown, up to 630 µm long and 22–60 µm wide. *Conidiophores* macronematous, fasciculate, unbranched or branched, subhyaline to brown, septate. *Conidiogenous cells* terminal, integrated, monoblastic, 9–20 × 2–3 µm, subcylindrical, brown. *Conidia* 42–90 × 6.5–10 µm (mean ± SD = 75.4 ± 12.9 × 8.8 ± 0.9 µm), fusiform, usually straight or slightly flexuous, truncate at the base, rounded to subulate or capitate at the apex with a mucilaginous cap, (5–)14–16-septate, smooth, brown, paler towards both ends, apical cell hyaline to subhyaline, secession schizolytic.

Culture characteristics: Colonies on MEA 2–4 mm after 2 wk, circular, convex, margin entire, lanose, floccose, pale purplish grey; reverse buff to smoke grey. Colonies on CBSOA 5–6 mm after 2 wk, circular, flat becoming slightly convex centrally, margin entire, lanose centrally, smooth towards the margin, colony centre lavender grey to pale olivaceous grey, white towards the margin; reverse not different from the colony surface. Sporulation on CBSOA after 4 wk or after prolonged incubation.

Habitat and distribution: *Gamsomyces stilboideus* is a saprobe on decaying wood of an unidentified host and dead leaves of *Calyptronoma plumeriana.* The species is known in Middle America in Cuba and Puerto Rico (Castañeda-Ruiz & Arnold 1985, this study)

Specimen examined: **USA**, Puerto Rico, on dead submerged twig, 19 Jul 2018, M. Hernández-Restrepo MHR18017 (culture CBS 146494).

Notes: *Gamsomyces stilboideus* was described from fallen leaves of *Calyptronoma plumeriana* in Cuba (Castañeda-Ruiz & Arnold 1985). Our isolate of *G. stilboideus* is another record of this species from the Caribbean, although the conidia in the holotype tend to be shorter and slightly narrower (30–55 × 7–8 µm *fide* Castañeda-Ruiz & Arnold 1985). *Gamsomyces stilboideus* and *G. longisporus* are well distinguishable by size of conidia based on their protologues (Ellis 1976, Castañeda-Ruiz & Arnold 1985), but the conidial size of our specimens of these species partially overlapped on the natural substrate causing their identification difficult. However, both species are well distinguishable by DNA data and characters in culture, *G. stilboideus* differs in the formation of synnemata and shorter and wider (42–90 × 6.5–10 µm) (5–)14–16-septate conidia, while *G. longisporus* forms exclusively sporodochia and longer and narrower 41–163.5 × 5.5–8 µm (6–)14–25-septate conidia.

Helicoascotaiwania Dayarathne, Maharachch. & K.D. Hyde, Front. Microbiol. 10(840): 22. 2019.

Type species: *Helicoascotaiwania farinosa* (Linder) Réblová, Hern.-Restr. & J. Fourn.

Notes: *Helicoascotaiwania* is a member of the *Pleurotheciales* and accommodates saprobic freshwater species morphologically reminiscent of *Ascotaiwania* (*Savoryellales*). It is characterised by immersed, flask-shaped, non-stromatic perithecial ascomata lying mostly horizontally to the substrate, cylindrical, stipitate asci with a prominent apical plug and a shallow non-amyloid ring in the ascal apex, early deliquescing paraphyses, transversely septate ascospores with middle cells brown and end cells hyaline to subhyaline and a helicosporous asexual morph, which has

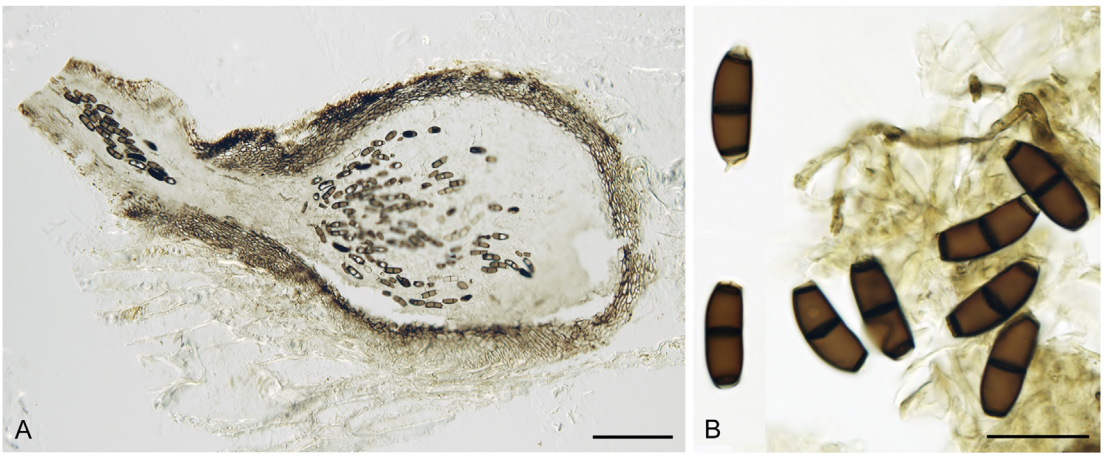

Fig. 18. *Helicoascotaiwania farinosa* (ILLS 53605). **A**. Vertical section of the ascoma. **B**. Ascospores. **A, B**. On natural substrate. Bars: A = 100 µm, B = 20 µm.

Fig. 19. *Helicoascotaiwania lacustris*. **A**. Ascomata. **B–D**. Vertical sections of the ascomata. **E**. Ascomal wall. **F**. Asci with ascospores. **G**. Ascal apex with a prominent ascal plug (indicated by arrows). **H–J**. Ascal apex with a shallow, refractive apical ring (indicated by arrows). **K, L**. Ascospores. **M**. Paraphyses. **A–M**. On natural substrate. **N**. Colonies on MLA, OA and PCA after 4 wk. Images: A PRA-00016152, B–E PRA-00016151, F, L PRA-00016154, G–K, M PRA-00016153, N CBS 145963. Bars: A = 500 µm, B–D = 250 µm, E–M = 20 µm, N = 1 cm.

been linked to only one species. A new combination and a new species are proposed below.

Key to species of *Helicoascotaiwania*

1a. Ascomatal wall darkest on the outside, asci (6.5–) 9–10 µm wide……..*H. farinosa*

1b. Ascomatal wall darkest on the innermost side, asci 11–14.5(–16) µm wide……...*H. lacustris*

Helicoascotaiwania farinosa (Linder) Réblová, Hern.-Restr. & J. Fourn., **comb. nov.** MycoBank MB832929. Fig. 18.

Basionym: *Helicoön farinosum* Linder, Ann. Mo. bot. Gdn 16: 324. 1929.

Synonyms: *Ascotaiwania hughesii* Fallah, J.L. Crane & Shearer, Can. J. Bot. 77: 89. 1999.

Helicoascotaiwania hughesii (Fallah, J.L. Crane & Shearer) Dayarathne & K.D. Hyde, Front. Microbiol. 10(840): 22. 2019.

Description: For descriptions and illustrations refer to Fallah *et al.* (1999) and Linder (1929).

Specimen examined: **U.S.A.**, Wisconsin, Vilas County, Sparkling Lake, on submerged wood, 8 Aug. 1994, P.M. Fallah P2-6 (**holotype** of *Ascotaiwania hughesii* ILLS 53605).

Notes: *Ascotaiwania hughesii* was experimentally linked with the *Helicoön farinosum* asexual morph by Fallah *et al.* (1999). The authors examined the holotype of *He. farinosum* (Linder 1929) deposited in the Farlow Herbarium (FH) and concluded that the fungus observed in the holotype of *A. hughesii* in the juxtaposition to the ascomata and also formed *in vitro* is conspecific with *He. farinosum*. In the examined holotype of *A. hughesii*, consisting of a piece of a decorticated wood, the ascomata were scattered, mostly immersed with only the tip of their necks emerging, surrounded by effuse, creamy colonies of the asexual morph. We have not seen the holotype of *He. farinosum*, but we accept Fallah's *et al.* (1999) conclusion.

A close relationship of a non-type strain of *He. farinosum* (DAOM 241947) with the ex-type strain of *A. hughesii* (isolate P2-6 = ILLS 53605, Campbell & Shearer 2004) was confirmed with DNA sequence data by Réblová *et al.* (2012). The species was positioned in the well-resolved *Pleurothecium* clade, unrelated to the *Savoryellales*, where other *Ascotaiwania* species resided (Boonyuen *et al.* 2011). Later, the order *Pleurotheciales* was introduced for this robust clade containing *He. farinosum* and its relatives (Réblová *et al.* 2016a). At that time, the generic placement of *Helicoön* was unclear pending confirmation of the phylogeny and classification of the type species *He. sessile*. Pfister (1997) isolated *He. sessile* from an *Orbilia* species, tentatively named *O. luteorubella* (*Orbiliomycetes*). However, its ITS1-5.8S sequence (U72605, Pfister 1997) shows 99 % similarity with the ITS sequences of numerous strains of *Sarocladium kiliense* and *S. strictum* of the *Hypocreales* (*Sordariomycetes*), an unlikely relationship suggestive of a contaminated or mislabelled culture. Other, recently available SSU-ITS-LSU sequences of *He. sessile* (KY659207 unpublished), a strain isolated from pond water in Austria, showed 98.84 % similarity with *Orbilia luteorubella* (H.B. 9705), thus attesting to the relationship between sexual and asexual morphs of *Orbilia* suggested by Pfister (1997).

Dayarathne *et al.* (2019) proposed the generic name *Helicoascotaiwania* typified by *A. hughesii*. However, the correct epithet for the type species of *Helicoascotaiwania* is "*farinosa*" since *He. farinosum* 1929 has a priority over *A. hughesii* 1999. Therefore, a new combination, along with full synonymy, is proposed in this study.

The ascomata of *H. farinosa* in the holotype were empty or contained only clusters of ascospores with their end cells partially collapsed. The condition of the type material did not allow us to examine the ascal apex and compare it with that of *H. lacustris*.

Helicoascotaiwania lacustris Réblová & J. Fourn., **sp. nov.** MycoBank MB832930. Fig. 19.

Typification: **France**, Haute-Garonne, Carbonne, SW of route du Lançon, artificial lake in a gravel pit, ca. 200 m a.s.l., on submerged wood of a branch of *Populus* sp., 4 Apr. 2017, J. Fournier J.F. 17013 (**holotype** PRA-00016153, culture ex-type CBS 145963 = MUCL 56486).

Etymology: *Lacustre* (Latin) of or relating to a lake, referring to the habitat of this species.

Description on the natural substrate: *Sexual morph*: *Ascomata* perithecial, non-stromatic, solitary or clustered in small groups, deeply immersed to semi-immersed becoming erumpent, black, pyriform to flask-shaped, glabrous, lying horizontally or obliquely beneath the wood surface, with a curved, lateral neck. Venter 470–750 µm high, 220–340 µm diam, ellipsoidal, laterally flattened, occasionally venter 250–360 µm diam and subglobose. *Neck* (80–)150–420 µm high, 130–170 µm diam, cylindrical, mostly lateral, occasionally central, apically slightly flared, immersed, rarely prominent; the surrounding substrate stained light brownish-grey to the depth of 1–2 mm. *Ostiole* periphysate. *Ascomatal wall* leathery, 34–45(–50) µm thick, two-layered; outer layer 20–30 µm thick, consisting of several rows of light brown cells 4.5–16 × 5–7 µm of textura angularis, the two outermost rows consisting of brown thick-walled cells with wall 1–2 µm thick; inner layer 10–15 µm thick, distinctly darker than the outer layer, consisting of dark brown flattened cells 5–22.5 × 3.5–4.5 µm of textura prismatica, inwardly lined by 1–3 rows of colourless thin-walled flattened cells. Wall at the base of the neck up to 90–100 µm thick, with outer layer thickened and outwardly more pigmented. *Paraphyses* filiform, hyaline, septate, not constricted at the septa, 2.5–6.5 µm wide, tapering to 1.5–2 µm, containing minute refractive droplets, deliquescing early. *Asci* 234–265 × 11–14.5(–16) µm (mean ± SD = 250 ± 11.1 × 12.8 ± 1.4 µm), 150–190 µm long (mean ± SD = 170 ± 11.1) in the sporiferous part, cylindrical, long-stipitate. Ascal apex obtuse with a prominent, chitinoid, non-amyloid pulvillus (5–)7.5–8.5 µm wide and 6.5–7.5 µm high deeply stained by diluted blue ink or toluidin blue, apically convex with a sharp upper rim, basally broadly cylindrical, with a wide tubular canal, obscuring a shallow refractive apical ring 4.5–5 × 1–1.5 µm revealed by phase contrast illumination and to a lesser extent in 3 % KOH. *Ascospores* (22.5–)24–31(–35.5) × 6.5–9(–9.5) µm (mean ± SD = 27.4 ± 1.6 × 7.9 ± 0.5 µm), fusiform, inequilateral, straight to slightly curved in the side view, unequally 3-septate, not constricted or slightly constricted at the septa, smooth-walled, versicolorous, the middle cells olivaceous brown to deep brown, filled by a large guttule and smaller droplets, end cells hyaline, shorter and obtusely to narrowly rounded; ascospores uniseriate in the ascus when fresh, becoming obliquely oriented and overlapping when dry, no appendages or mucilaginous sheath observed. *Asexual morph*: unknown.

Culture characteristics: Colonies on MLA 12–15 mm after 4 wk, circular, convex, margin entire, velvety, floccose, funiculose becoming smooth and mucoid at the margin, zonate, whitish-grey becoming sepia to ochre-beige towards the margin, with a paler outer zone, older cultures (>8 wk) becoming brown; reverse beige. Colonies on OA 14–16 mm after 4 wk, circular, flat, margin entire, mucoid-waxy, smooth, yellowish-beige centrally becoming creamy towards the margin; reverse beige. Colonies on PCA 12–14 mm after 4 wk, circular, flat, margin undulate to fimbriate, mucoid, smooth centrally, pale sepia-beige becoming paler towards the periphery; reverse creamy. Sporulation absent on all media.

Other specimens examined: **France**, Haute-Garonne, Avignonet-Lauragais, Marbail-Bas, Lac de Rosel, artificial lake in a gravel pit, ca. 188 m a.s.l., on submerged wood of a branch *Populus* sp., 16 Jan. 2007, J. Fournier J.F. 07010 (PRA-00016151); *ibid.*, Carbonne, SW of route du Lançon, artificial lake in a

gravel pit, ca. 200 m a.s.l., on submerged wood of a branch of *Populus* sp., 14 Aug. 2018, J. Fournier J.F. 18068 (PRA-00016154, culture CBS 145964); *ibid*., on submerged wood of a branch of *Salix atrocinerea*, 14 Aug. 2018, J. Fournier J.F. 18072 (PRA-00016155, culture CBS 146144); *ibid.,* Martres-Tolosane, Balet, artificial lake in a gravel pit, ca. 256 m a.s.l., on submerged decorticated branch of *Populus* sp., 17 May 2008, J. Fournier J.F. 08131 (PRA-00016152).

Habitat and distribution: All specimens of *H. lacustris* originate from small artificial lakes in gravel pits in lowlands, strongly suggesting a preference for lentic habitats. In these lakes, water temperature can be high in summer. Submerged, decorticated twigs of the *Salicaceae* (mostly *Populus*) appear to be the regular host. The species is known in Europe in France so far.

Notes: *Helicoascotaiwania lacustris* differs from *H. farinosa* by anatomy of the ascomatal wall, shorter and broader asci, somewhat broader ascospores and the presence of a shallow refractive apical ring which is obscured by a prominent chitinoid pulvillus in the ascal apex. The asexual morph of *H. lacustris* is unknown. No conidia or conidiophores were formed on any of the used media, even after prolonged cultivation.

Ascomata of *H. lacustris* vary from subglobose to ellipsoidal, lying vertically or horizontally in the substrate. The neck is immersed, rarely emerged, most often opening flush with the host surface appearing as an ellipsoidal black dot up to 200 µm in the broadest place. The anatomy of the ascomatal wall of *H. lacustris* is unusual in this genus. Compared to *H. farinosa* whose ascomatal wall is composed of compressed brown cells darker on the outside (Fig. 18) (Fallah *et al.* 1999, fig. 11), the wall of *H. lacustris* is two-layered; the innermost rows of cells of the inner layer are composed of strongly flattened, thick-walled, brown cells which are significantly darker than the brown cells of the outer layer.

The ascal apex of *H. lacustris* contains two structures. The apical plug with a convex discoid apex and a broadly cylindrical base united by a canal that is apically occluded, and a shallow, refractive apical ring, usually obscured by the plug but clearly visible in empty or half-empty asci or with a phase contrast illumination (Fig. 19G–J). A similar configuration of the apical plug is commonly encountered in species referred to *Ascotaiwania sensu lato*. The size of the apical plug of *H. farinosa* is given nearly twice as big as that of *H. lacustris*, 9–13.5 µm *fide* Fallah *et al.* (1999). The refractive ring has never been reported for *H. farinosa*.

Kaseifertia Réblová, Hern.-Restr. & J. Fourn., **gen. nov.** MycoBank MB832924.

Etymology: The generic name is a tribute to our colleague and friend Keith A. Seifert for his contribution to mycology.

Type species: *Kaseifertia cubense* (R.F. Castañeda & G.R.W. Arnold) Réblová, Hern.-Restr. & J. Fourn.

Description: *Asexual morph*: *Colonies* effuse or with sporodochial conidiomata. *Conidiophores* semi-macronematous or micronematous, fasciculate, simple or branched, subhyaline. *Conidiogenous cell* integrated, terminal, monoblastic or polyblastic. *Conidia* dry, solitary, curved, clavate, pigmented, transversely septate, euseptate. Conidia secede schizolytically. *Sexual morph*: unknown.

Kaseifertia cubense (R.F. Castañeda & G.R.W. Arnold) Réblová, Hern.-Restr. & J. Fourn., **comb. nov.** MycoBank MB832925.

Basionym: *Trichocladium cubense* R.F. Castañeda & G.R.W. Arnold [as "*cubensis*"], Revta Jardín bot. Nac., Univ. Habana 6: 53. 1985.
Synonym: *Bactrodesmium cubense* (R.F. Castañeda & G.R.W. Arnold) Zucconi & Lunghini, Mycotaxon 63: 324. 1997.

Description: For description and illustration refer to Castañeda-Ruiz & Arnold (1985) and Zucconi & Lunghini (1997).

Habitat and distribution: *Kaseifertia cubense* occurs on fallen leaves of *Coccoloba uviferae* and leaf litter and decaying wood of *Quercus ilex*. The species is known in Middle America in Cuba and in Europe in Italy (Castañeda-Ruiz & Arnold 1985, Zucconi & Lunghini 1997).

Notes: The Blastn searches (GenBank accessed 23/10/2019) for possible relatives of a non-type strain of *B. cubense* CBS 680.96 (Zucconi & Lunghini 1997) using ITS, LSU, SSU and *tef1-α* sequences always showed this species nested in the *Pleosporales* but distantly related to all its members. Because of the lack of close relatives and new data, we follow the results of a phylogenetic analysis inferred from a combined dataset of ribosomal and protein-coding loci; *B. cubense* was resolved as a member of the suborder *Massarineae* and positioned on a separate branch as sister to the *Morosphaeriaceae* (Tanaka *et al.* 2015, fig. 1). Therefore, a new bactrodesmium-like genus *Kaseifertia* is introduced for *B. cubense* and a new combination is proposed.

In the protologue of *K. cubense*, Castañeda-Ruiz & Arnold (1985) described the species with effuse colonies on fallen leaves of *Coccoloba uviferae* in Cuba, while Zucconi & Lunghini (1997), who studied *K. cubense* on leaf litter of *Quercus ilex* and decaying wood in Italy, stated that the fungus formed sporodochia. Zucconi & Lunghini (1997) examined the type of *K. cubense* and concluded that the collections from Italy match the protologue in all other respects, and that specimens from Cuba and Italy are conspecific.

Neoascotaiwania Hern.-Restr., R.F. Castañeda & Guarro, Stud. Mycol. 86: 88. 2017.

Type species: *Neoascotaiwania terrestris* Hern.-Restr., R.F. Castañeda & Guarro, Stud. Mycol. 86: 90. 2017.

Notes: Based on phylogenies inferred from the LSU gene, Hernández-Restrepo *et al.* (2017) questioned the monophyly of *Ascotaiwania* and introduced a new genus *Neoascotaiwania* for *N. terrestris*, the type species, and *N. limnetica* (Chang *et al.* 1998, Réblová *et al.* 2016a). A third species, *N. fusiformis* (Yang *et al.* 2016), is assigned to the genus in this study based on the evidence from molecular DNA data. *Neoascotaiwania* was segregated from *Ascotaiwania* to accommodate morphologically similar fungi characterised by ascomata variably oriented on the host (upright, obliquely oriented or lying horizontally), 3-septate pigmented ascospores with hyaline end cells, asci with a smaller and shallow apical ring, only partially disintegrating paraphyses and asexual morphs forming effuse colonies of solitary, pigmented phragmoconidia.

Key to species of *Neoascotaiwania*

1a. Conidia 2-septate, 29.5–38.5 × 18.5–25 µm…*N. fusiformis*
1b. Conidia with more than two septa……..2

2a. Conidia (3–)5–6-septate, (30–)33–41 × 15–17.5 µm…
……...*N. limnetica*

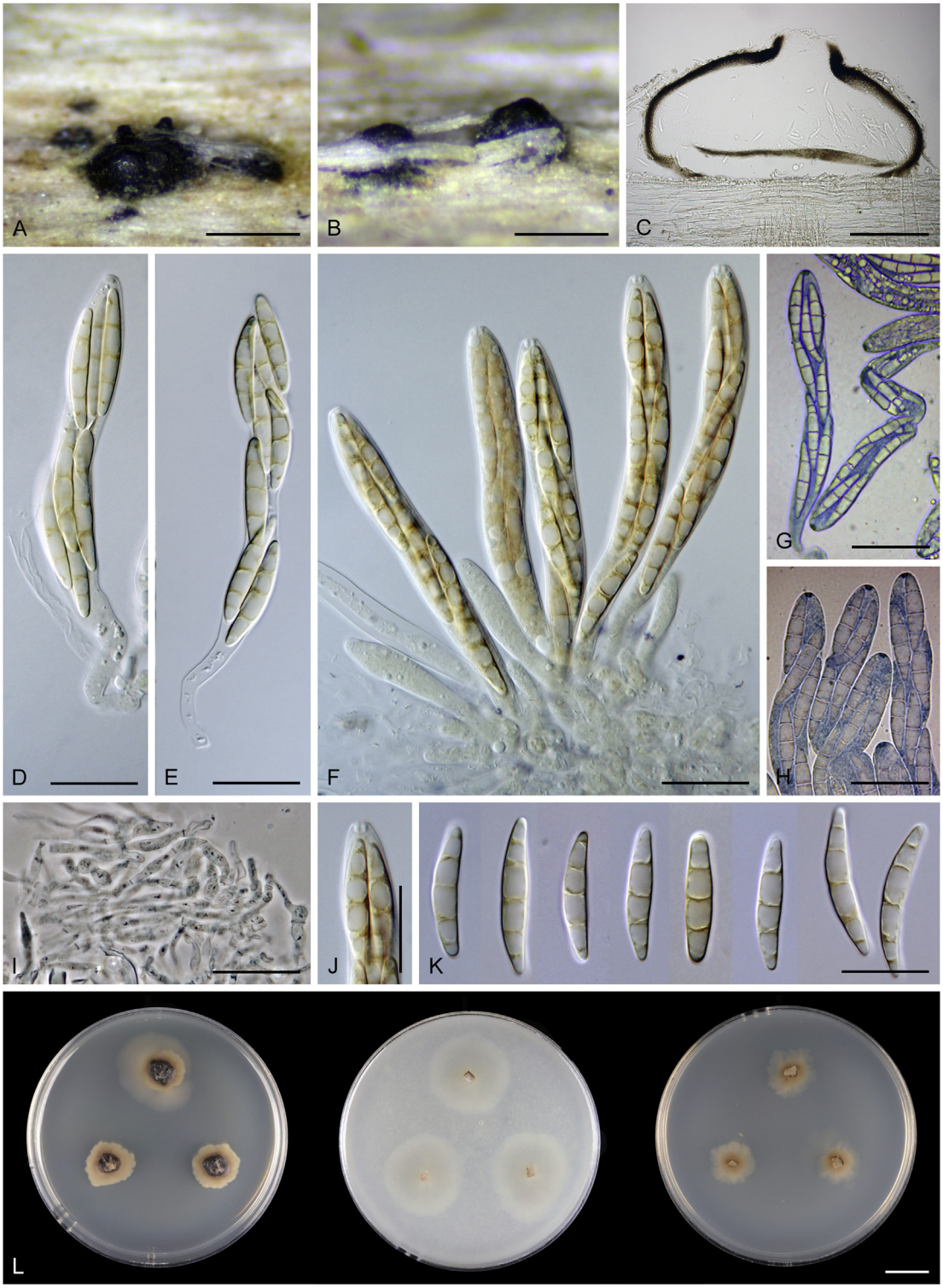

Fig. 20. *Pleurotheciella erumpens*. **A, B**. Ascomata. **C**. Vertical section of the ascoma. **D–F**. Asci with ascospores (in Melzer reagent). **G, H**. Asci beginning to swell (in water with Waterman blue ink). **I**. Paraphyses. **J**. Ascal apex with a refractive apical ring. **K**. Ascospores. **A–K**. On natural substrate. **L**. Colonies on MLA, OA and PCA after 6 wk. Images: A–C PRA-00016169, D, E, K PRA-00016171, F, I, L CBS 142447. Bars: A, B = 250 µm, C = 100 µm, D–K = 20 µm, L = 1 cm.

2b. Conidia (2–)3–4(–5)-septate, 25.5–44.5 × 13–22 µm… ……...*N. terrestris*

Neoascotaiwania fusiformis (Jing Yang, Bhat & K.D. Hyde) Réblová, Hern.-Restr. & J. Fourn., **comb. nov.** MycoBank MB832931.

Basionym: *Ascotaiwania fusiformis* Jing Yang, Bhat & K.D. Hyde, Cryptog. Mycol. 37: 469. 2016.

Description: For description and illustrations refer to Yang *et al.* (2016).

Notes: Phylogenetic analyses of the combined ribosomal and protein-coding sequences of representatives of the *Savoryellales* support *Ascotaiwania fusiformis* as a member of the well-resolved *Neoascotaiwania* clade (Figs 1, 2). Following these results, a new combination in the latter genus is proposed. *Neoascotaiwania fusiformis* is highly similar to *N. limnetica* and

N. terrestris in forming dark, effuse colonies consisting of single, dry, dark brown, transversely septate conidia. Although the conidial size of all three *Neoascotaiwania* species somewhat overlaps, they can be distinguished by the number of septa.

Pleurotheciella Réblová, Seifert & J. Fourn., Mycologia 104: 1304. 2012.

Type species: *Pleurotheciella rivularia* Réblová, Seifert & J. Fourn., Mycologia 104: 1304. 2012.

Notes: *Pleurotheciella* (Réblová *et al.* 2012) accommodates freshwater, non-stromatic perithecial ascomycetes with minute, brown or black ascomata with a papilla or rostrate neck, disintegrating paraphyses, cylindrical-clavate asci with a distinct, non-amyloid apical annulus, hyaline, transversely septate ascospores, and brown or hyaline, macronematous conidiophores and hyaline, aseptate or septate conidia formed holoblastically on short denticles on sympodially elongating conidiogenous cells. Of the 12 known species of *Pleurotheciella*, sexual morphs have been reported for two other species only, *P. centenaria* (Réblová *et al.* 2012) and *P. fusiformis* (Luo *et al.* 2018). Members of the genus were collected on submerged decaying wood in lentic and lotic habitats in temperate, subtropical and tropical zones in Asia in China and Thailand, Europe in France, Melanesia in Papua New Guinea and North America in Canada (Matsushima 1971, Réblová *et al.* 2012, 2016a, Luo *et al.* 2018, Hyde *et al.* 2018).

Key to species of *Pleurotheciella*

1a. Sexual morph unknown, conidiophores hyaline or brown, up to 390 µm long……2
1b. Sexual morph known, conidiophores hyaline, up to 50 µm long……10

2a. Conidiophores dark brown at the base becoming paler towards the tip……3
2b. Conidiophores hyaline……9

3a. Conidiophores up to 50 µm long……..4
3b. Conidiophores 50 µm or longer……6

4a. Conidia 1-septate……5
4b. Conidia 0–3-septate, 15.5–17.5 × 3–4 µm, broadly lunate to suballantoid……*P. aquatica*

5a. Conidia 13–23 × 3–4 µm, broadly lunate……*P. lunata*
5b. Conidia 10–14 × 2.5–3.5 µm, subcylindrical to obovoid……*P. saprophytica*

6a. Conidia aseptate, 25–28 × 5.5–6.5 µm, subcylindrical, slightly curved……..*P. submerse*
6b. Conidia 1-septate……...7

7a. Conidiophores up to 250 µm long……8
7b. Conidiophores 250 µm or longer, conidia 19–25 × 4.5–6 µm, fusiform, subcylindrical to obovoid-subclavate……*P. krabiensis*

8a. Conidia 12.5–16.5 × 3.5–4.5 µm, fusoid or slightly clavate, straight……...*P. uniseptata*
8b. Conidia 16–21 × 5.5–7 µm, narrowly obovoid or subclavate……*P. tropica*

9a. Conidia 3-septate, (14–)18–22.5 × 4–5.5 µm……
……..*P. centenaria*
9b. Conidia aseptate, 17–19 × 4–5 µm……*P. guttulata*

10a. Ascospores up to 5 µm wide……11
10b. Ascospores 5 µm or wider, 14.5–17.5(–18) × (5–)5.5–6(–6.5) µm, 3-septate, asci 103–116(–120) × 9–9.5 µm, conidia 12.5–16.5(–17.5) × 4.5–5 µm, 0–2-septate, ellipsoidal to obovoid……...*P. rivularia*

11a. Ascospores 3–5-septate, (19–)21–26.5(–30.5) × 4–5 µm, asci (84.5–)90–111 × 9–12(–13.5) µm, asexual morph unknown……..*P. erumpens*
11b. Ascospores 1-septate, 31.5–36.5 × 3.5–4.5 µm, asci 76–91 × 8–9 µm, conidia 16–18 × 3–4 µm, 0–1-septate, lunate to suballantoid……*P. fusiformis*

Pleurotheciella erumpens Réblová & J. Fourn., **sp. nov.** MycoBank MB832932. Fig. 20.

Typification: **France**, Ariège, Rimont, Las Muros, Peyrau brook, 410 m a.s.l., on submerged wood of a branch of a coniferous tree, 15 Sep. 2016, J. Fournier J.F. 16055 (**holotype** PRA-00016170, culture ex-type CBS 142447).

Etymology: *Erumpens* (Latin) meaning breaking or bursting out, referring to immersed ascomata that become gradually erumpent.

Description on the natural substrate: *Sexual morph*: *Ascomata* perithecial, non-stromatic, solitary or rarely aggregated, immersed, gradually erumpent, black, subglobose to ellipsoidal-oblong, frequently laterally or vertically flattened, with a flattened, usually less pigmented base, glabrous, vertical or lying horizontally in the substrate. Venter 130–200 µm high when subglobose, up to 420 µm high when ellipsoidal-oblong, 170–350 µm diam, with a rostrate to conical, central to eccentric papilla 40–60 µm high; the surrounding substrate stained light brownish-grey to a depth of 0.3–0.4 mm. *Ostiole* periphysate. *Ascomatal wall* leathery, fragile, 20–25 µm thick at sides, 30–35 µm thick at the apex, ca. 15 µm thick at the base, two-layered; outer layer composed of 2–3 layers of thick-walled, dark brown polyhedral cells with 1–2 µm thick wall of textura angularis to textura prismatica, inner layer of light brown, thin-walled elongated cells with 0.5–1 µm thick wall of textura prismatica, inwardly becoming subhyaline. *Paraphyses* abundant, septate, hyaline, thin-walled, 3.5–4.5(–6.5) µm wide, tapering apically to ca. 2 µm, longer than the asci. *Asci* (84.5–)90–111 × 9–12(–13.5) µm (mean ± SD = 101.4 ± 9.2 × 10.9 ± 0.7 µm), in the sporiferous part (71–)75–92(–94) µm long, unitunicate, cylindrical-clavate to slightly fusiform, 8-spored, apically obtuse, apical ring short-cylindrical to slightly wedge-shaped, non-amyloid, refractive, 2.5–3 µm wide, ca. 2 µm high, stained by diluted Waterman blue ink, Congo red or toluidin blue. *Ascospores* (19–)21–26.5(–30.5) × 4–5 µm (mean ± SD = 25.5 ± 2.6 × 4.6 ± 0.3 µm), fusiform slightly inequilateral with narrowly rounded ends, straight to slightly curved, hyaline, 3–5-septate, rapidly swollen and constricted at the septa when observed in water or lactic acid with Waterman blue ink, with a large guttule in each cell, smooth-walled, irregularly 2- to 3-seriate in the ascus, lacking a mucilaginous sheath or appendages. *Asexual morph*: unknown.

Culture characteristics: Colonies on MLA 11–12 mm after 6 wk, circular, flat, convex centrally, margin lobate, mucoid-waxy, glistening, smooth, somewhat funiculose and sparsely floccose

on the inoculation block, dark brown becoming beige towards the margin, older cultures (>8 wk) becoming dark brown and submerged growth more prominent; reverse beige. Colonies on OA 16–17 mm after 6 wk, circular, flat, margin entire, mucoid, smooth, beige centrally, creamy becoming whitish at the margin; reverse creamy. Colonies on PCA 10–11 mm after 6 wk, circular, flat, margin lobate, mucoid, smooth, sepia centrally becoming beige towards the margin; reverse beige. Sporulation absent on all media.

Habitat and distribution: *Pleurotheciella erumpens* occurs on submerged decaying wood of various deciduous or coniferous trees such as *Abies alba*, *Alnus glutinosa*, *Alnus incana*, *Fraxinus excelsior*, *Hedera helix* and *Sambucus nigra*. It occurs exclusively in lotic habitats and seems to prefer acid or neutral water. So far, it is known from France and Spain, and it was collected at the altitude ranging from 400 to 1 400 m.

Other specimens examined: **France**, Ariège, Castelnau-Durban, L'Artillac brook, 410 m a.s.l., on submerged wood of a branch of *Abies alba*, 24 Jul. 2014, J. Fournier J.F. 14073 (PRA-00016166); *ibid*., Clermont, Le Pujol brook along D 119 road, 400 m a.s.l., on submerged wood of a branch of *Fraxinus excelsior*, 31 Jul. 2009, J. Fournier J.F. 09220 (PRA-00016164); *ibid*., Illier, Laramade, Vicdessos stream, 630 m a.s.l., on submerged wood of a branch of *Hedera helix*, 25 Nov. 2014, J. Fournier J.F. 14164 (PRA-00016168); *ibid*., Montségur, Le Lasset brook along D 9 road, ca. 800 m a.s.l., on submerged wood of a branch of *Alnus glutinosa*, 16 Nov. 2014, J. Fournier J.F. 14158 (PRA-00016167); *ibid*., Orlu, Jasse de Justuniac, Oriège stream, 1 200 m a.s.l., on submerged wood of a branch of *Fraxinus excelsior*, 29 Sep. 2015, J. Fournier J.F. 15133 (PRA-00016169); *ibid*., Rimont, Combelongue, Le Baup brook along D 18b road, 480 m a.s.l., on submerged wood of a branch of *Fraxinus excelsior*, 2 Dec. 2006, J. Fournier J.F. 06319 (PRA-00016160); *ibid*., Rimont, Le Baup brook along D 18b road, 510 m a.s.l., on submerged wood of a branch of *Alnus glutinosa*, 17 Nov. 2006 (incubated in moist chamber until 25 Nov. 2006), J. Fournier J.F. 06308 (PRA-00016159); *ibid*., Sainte-Croix-Volvestre, State Forest, Sabine brook, on submerged wood of a branch of *Sambucus nigra*, 23 Jul. 2009, J. Fournier J.F. 09210 (PRA-00016163); *ibid*., Ustou, Cirque de Cagateille, small stream, 1 150 m a.s.l., on submerged wood of a branch of *Abies alba*, 31 Aug. 2009, J. Fournier J.F. 09240 (PRA-00016165); *ibid*., Deux Sèvres, L'Hermitain, La Dame de Chambrille, on submerged wood of a branch of *Sambucus nigra*, 17 Apr. 2008, J. Fournier J.F. 08068 (PRA-00016161); *ibid*., Hautes-Pyrénées, Asque, La Gourgue, Arros brook, on submerged wood of a branch of *Fraxinus excelsior*, 29 May 2009, J. Fournier J.F. 09130 (PRA-00016162); *ibid*., Puy-de-Dôme, St Alyre d'Arlanc, Bois de Chelles, rivulet, 850 m a.s.l., on submerged wood of a branch of *Abies alba*, 22 Apr. 2019, J. Fournier J.F. 19012 (PRA-00016173); *ibid*., Savoie, Planay, Doron de Pralognan stream, Pont de Pierra, 1 207 m a.s.l., on submerged wood of a branch of *Alnus incana*, 17 Jun. 2018, J. Fournier J.F. 18028 (PRA-00016172). **Spain**, Asturias, Somiedo, La Farrapona, Carbonea, 1 400 m a.s.l., on submerged wood of a branch of *Alnus glutinosa*, 9 Jun. 2017, J. Fournier J.F. 17034 (PRA-00016171).

Notes: *Pleurotheciella rivularia* (Réblová *et al.* 2012) resembles *P. erumpens* in having 3-septate ascospores and asci of a comparable length, but differs by shorter and wider [14.5–17.5(–18) × (5–)5.5–6(–6.5) µm] ascospores and narrower (9–9.5 µm) asci. *Pleurotheciella fusiformis* (Luo *et al.* 2018) is distinguished from *P. erumpens* in having smaller (76–91 × 8–9 µm) asci and longer (31.5–36.5 µm), 1-septate, elongate-fusiform ascospores.

The ascomatal morphology of *P. erumpens* is highly variable. The ascomata are immersed to variously erumpent, a common feature of many aquatic ascomycetes. Their shape is ranging from subglobose to ellipsoidal-oblong with a central or eccentric to lateral papilla or rostrate neck. The soft hyaline neck observed in PRA-00016159 is likely related to the incubation in moist chamber at room temperature since we did not see this feature on the natural substrate.

Asci and ascospores of *P. erumpens* are consistent in length but vary in width, apparently concerning the mounting medium. We observed that asci and ascospores are rapidly swelling (asci up to 13–15 µm wide; ascospores up to 5–5.5 µm wide) in media containing Congo red or Waterman blue ink and they are slightly wider than those mounted in water, lactic acid, lactophenol with cotton blue or in Melzer reagent. The swollen ascospores become also constricted at the septa. In Fig. 20G–H is captured a moment when ascospores and asci begin to swell in a medium with Waterman blue ink. On the other hand, the asci mounted in Melzer reagent in Fig. 20D–F exhibit the original "non-swollen" condition.

Pleurotheciella erumpens occurs on wood of both deciduous and coniferous trees, which is most unusual in aquatic ascomycetes. The two other common species sharing this lack of host specificity known to us are *Jahnula aquatica* and "*Trematosphaeria*" *hydrela* of the *Dothideomycetes*.

Other excluded species of *Bactrodesmium* or species of uncertain status

Although the majority of *Bactrodesmium* is morphologically well characterised, we lack DNA sequence data to demonstrate their phylogenetic relationships. Moreover, only a handful of species exists in axenic culture. The systematics of *Bactrodesmium* is also complicated by the fact that many species exist in a single exemplar and they were not seen or recollected since the mycological authorities described them. Based on published data and our results, bactrodesmium-like phenotypes occur in several unrelated groups. Since morphology exhibits only one side of the coin and may not be indicative of phylogenetic relationships, we have not completed a revision of types. The thorough revision of the types should follow the recollection of individual species, which should be obtained in pure culture and studied using DNA sequence data. Following the present narrower delimitation of *Bactrodesmium*, several species and varieties were excluded from the genus and are listed below. Accepted names are written in bold. They include species with effuse colonies or synnemata or sporodochial species that were transferred to other genera in unrelated groups or whose systematic placement remains unknown. Their hosts, substrates and current taxonomic treatment are summarised in Table 3, including those taxonomically reassessed in this study.

Bactrodesmiella masonii (S. Hughes) M.B. Ellis, Mycol. Pap. 72: 14. 1959.
Basionym: *Bactrodesmium masonii* S. Hughes, Can. J. Bot. 31: 654. 1953.

Notes: *Bactrodesmium masonii* is unique among other species of the genus by forming conidia singly or in short basipetal chains on percurrently elongating conidiogenous cells. Based on these diagnostic characters, Ellis (1959) introduced a new genus *Bactrodesmiella* typified by *B. masonii*.

Bactrodesmium coryphae Syd. & P. Syd., Annls mycol. 18: 103. 1920.

Notes: The species is known from a single collection made on fallen leaves of *Corypha* sp. in Philippines (Sydow & Sydow

Table 3. Disposition of *Bactrodesmium* species which are not accepted in the genus (E = effuse colonies, S = sporodochium, SYN = synnema).

Name in Index Fungorum	Colony	Substrate and host of the type	Current name	Current ordinal position	Reference
Bactrodesmium gabretae	S	needles of *Picea abies*	***Aphanodesmium gabretae***	*Helotiales*	Koukol & Kolářová (2010), This study
B. caulincola var. *caulincola*	E	herbaceous stem of the *Apiaceae*	*Clasterosporium caulincola*	*Magnaporthales*	Saccardo (1886)
B. caulincola var. *pellucidum*	E	herbaceous stem	*Camposporium pellucidum*	*Pleosporales*	Hughes (1951)
B. coryphae	E	fallen leaves of *Corypha* sp.	*B. coryphae*	Unknown	Sydow & Sydow (1920)
B. cubense	E/S	fallen leaves of *Cocoloba uvifera*	***Kaseifertia cubense***	*Pleosporales*	Tanaka *et al.* (2015), This study
B. clavulatum	E	bark of *Eucalyptus* sp.	*Polyschema clavulatum*	*Pleosporales*	Ellis (1976)
B. fasciculare	E	wood of *Betula alba*	*Pleotrichocladium opacum*	*Pleosporales*	Hernández-Restrepo *et al.* (2017)
B. fusiforme	S	beech test blocks	*B. fusiforme*	Unknown	Udaiyan (1991), Nom. inval., Arts 40.1, 40.3
B. heimii	SYN	on old ant nest	*B. heimii*	Unknown	Ciferri (1962)
B. indicum	S	beech test blocks	*B. indicum*	Unknown	Udaiyan (1991), Nom. inval., Arts 40.1, 40.3
B. longisporum	SYN/S	wood of *Alnus* sp.	***Gamsomyces longisporus***	*Sclerococcales*	This study
B. masonii	S	cupule of *Fagus sylvatica*	*Bactrodesmiella masonii*	Unknown	Ellis (1959)
B. mastigophorum	E	living leaves of *Parashoria plicata*	*B. mastigophorum*	Unknown	Sydow & Sydow (1920)
B. microleucurum	E	dead culms of *Chusquea cummingii*	*B. microleucurum*	Unknown	Ellis (1965)
B. obliquum var. *suttonii*	S	bark of *Pseudotsuga menziesii*	*Stuartella suttonii*	Dothideomycetes inc. sed.	Funk & Shoemaker (1983)
B. opacum	E	wood of *Cedrus* sp.	*Ellisembia opaca*	Sordariomycetes inc. sed.	Subramanian (1992)
B. papyricola	E	paper	*B. papyricola*	Unknown	Ellis (1959)
B. rahmii	S	dead branch of *Picea sitchensis*	*B. rahmii*	Unknown	Ellis (1976)
B. robustum	S	bark of *Acer* sp.	*Stigmina robusta*	*Capnodiales*	Sutton (1973)
B. stilboideum	SYN	fallen leaves of *Calyptronoma plumeriana*	***Gamsomyces stilboideus***	*Sclerococcales*	This study

Remark: Species names given in bold are taxonomic novelties.

1920). It is characterised by oblong, brown, 2–3-septate conidia arising from tips of branched hyphae that form effuse, olivaceous black colonies densely covering the substrate surface.

Bactrodesmium fusiforme Udaiyan [as "*fusiformis*"], J. Econ. Taxon. Bot. 15: 634. (1992) 1991. (Nom. inval., Arts 40.1, 40.3)

Notes: The species was described from beech test blocks in cooling towers from India, however it was not validly published as no type has been indicated (Udaiyan 1991).

Bactrodesmium heimii Cif. [as "*heimi*"], Atti Ist. bot. Univ. Lab. crittog. Pavia, sér. 5, 19: 93. 1962.

Notes: *Bactrodesmium heimii* was collected in galleries of an old ant nest of *Reticulitermes lucifugus* in the rotten trunk of *Quercus suber* in Sardinia (Ciferri 1962). Based on the conidiophore and conidium morphology given in the protologue and illustration provided earlier by Heim *et al.* (1951) based on French material, this species is remarkably similar to *Phragmocephala*, a polyphyletic dematiaceous synnematal hyphomycete currently placed in the *Pleosporales* (Su *et al.* 2015, Hernández-Restrepo *et al.* 2017) and *Pleurotheciales* (Réblová *et al.* 2016a).

Bactrodesmium indicum Udaiyan [as "*indica*"], J. Econ. Taxon. Bot. 15: 632. (1992) 1991. (Nom. inval., Arts 40.1, 40.3)

Notes: The species was described from beech test blocks in cooling towers from India, however it was not validly published as no type was indicated (Udaiyan 1991).

Bactrodesmium mastigophorum Syd. & P. Syd., Annls mycol. 18: 103. 1920.

Notes: This species is known only from the original locality in the Philippines. It forms effuse colonies on living leaves of *Parashoria plicata* and brown, septate conidia terminating in a long, apical flagellum born on short hyphae (Sydow & Sydow 1920).

Bactrodesmium microleucurum (Speg.) M.B. Ellis, Mycol. Pap. 103: 37. 1965.
Basionym: *Coniosporium microleucurum* Speg., Boln Acad. nac. Cienc. Córdoba 25: 112. 1921.

Notes: The species is known only from the holotype collected on dry, dead culms of a grass *Chusquea cummingii* in Chile. It forms

effuse colonies and brown transversely septate conidia with dark bands at the septa and the apical cell often larger than the other cells (Ellis 1965).

Bactrodesmium papyricola C. Moreau & M. Moreau ex M.B. Ellis, Mycol. Pap. 72: 3. 1959.

Notes: This species is known only from the type made on a paper in French Guinea. It is characterised by effuse colonies and ovoid, brown, transversely septate conidia that become progressively paler towards the base and have a thick band at the septum near the apex (Moreau & Moreau 1957, Ellis 1959).

Bactrodesmium rahmii Ellis, More dematiaceous Hyphomycetes: 68. 1976.

Notes: This species is known so far from coniferous hosts, *Picea* sp. in Switzerland (holotype) (Ellis 1976) and *P. sitchenis* in Canada (Hughes & White 1983i). It is characterised by sporodochia and distoseptate conidia, occasionally with oblique or longitudinal septa in the apical cells. Conidia are seceding rhexolytically. Considering the distant relationship between *Bactrodesmium* (*Savoryellales*) with euseptate conidia and its segregate *Aphanodesmium gabretae* (*Helotiales*) having distoseptate conidia, *B. rahmii* is not accepted in the genus until its systematic position is verified with DNA data.

Camposporium pellucidum (Grove) S. Hughes, Mycol. Pap. 36: 9. 1951.
Basionym: *Bactrodesmium caulincola* var. *pellucidum* Grove, J. Bot., 24: 200. 1886.
Synonym: *Clasterosporium caulincola* var. *pellucidum* (Grove) Sacc. & Traverso, Syll. fung. 19: 304. 1910.

Notes: Hughes (1951) reviewed the genus *Camposporium* (*Pleosporales*), introduced by Harkness (1884), and proposed a new combination *C. pellucidum* based on *Bactrodesmium caulincola* var. *pellucidum*. The species is characterised by effuse colonies and transversely septate, cylindrical-fusiform, pigmented conidia terminating in a subulate, hyaline extension and arising holoblastically from short denticles on sympodially elongating conidiogenous cells. It occurs on herbaceous stems, decaying leaves, wood, cupules of *Fagus sylvatica* and also fruits of *Aesculus hippocastanum*, occasionally conidia were observed in stream foam (Hughes 1951, Grove 1886, Patil 1998).

Clasterosporium caulincola (Corda) Sacc., Syll. fung. 4: 393. 1886.
Basionym: *Sporidesmium caulincola* Corda, in Sturm, Deutschl. Fl., 3 Abt. (Pilze Deutschl.) 2: 43. 1829.
Synonym: *Bactrodesmium caulincola* (Corda) Grove, J. Bot. 24: 200. 1886.

Notes: The species forms effuse colonies on dead herbaceous stems and brown, fusiform, transversely septate conidia lacking apical flagellum or extension. The species is currently classified in the genus *Clasterosporium*, a member of the *Magnaporthales* (Zhang *et al.* 2016).

Ellisembia opaca (Cooke & Harkn.) Subram., Proc. Indian natn Sci. Acad., Part B. Biol. Sci. 58: 184. 1992.
Basionym: *Bactrodesmium opacum* Cooke & Harkn., Grevillea 12: 95. 1884.
Synonyms: *Clasterosporium harknessii* Sacc., Syll. fung. 4: 385. 1886.
Sporidesmium harknessii (Sacc.) M.B. Ellis, Mycol. Pap. 70: 24. 1958.

Notes: Synonymy according to Subramanian (1992). In his survey of *Sporidesmium* and related taxa, Subramanian (1992) introduced *Ellisembia* and cited *E. opaca* among 12 accepted species. *Ellisembia* is a polyphyletic genus, some of its species are members of the *Chaetosphaeriales*, while others are nested in the *Sordariomycetidae* as an *incertae sedis* lineage; the systematic placement of the type species *E. coronata* remains unknown.

Pleotrichocladium opacum (Corda) Hern.-Restr., R.F. Castañeda & Gené, Stud. Mycol. 86: 75. 2017.
Basionym: *Sporidesmium opacum* Corda, Icon. fung. 1: 7. 1837.
Synonyms: *Xenodochus opacus* (Corda) Bonord., Handb. Allgem. mykol.: 49. 1851.
Clasterosporium opacum (Corda) Sacc., Syll. fung. 4: 387. 1886.
Trichocladium opacum (Corda) S. Hughes, Trans. Br. mycol. Soc. 35: 154. 1952.
Sporidesmium fasciculare Corda, Icon. fung. 1: 7. 1837.
Dicoccum fasciculare (Corda) Bonord., Handb. Allgem. mykol.: 48. 1851.
Clasterosporium fasciculare (Corda) Sacc., Syll. fung. 4: 387. 1886.
Bactrodesmium fasciculare (Corda) E.W. Mason & S. Hughes, in Walsh & Rimington, Nat. Hist. Scarborough Distr. 1: 159. 1953. (Nom. inval., Art. 41.5)

Notes: Synonymy according to Hughes (1952) and Ellis (1959). For more information and phylogeny refer to Hernández-Restrepo *et al.* (2017). For taxonomic placement of *B. fasciculare sensu* Mason & Hughes (1953) see notes under *B. obovatum*.

Polyschema clavulatum (Cooke & Harkn.) M.B. Ellis [as "*clavulata*"], More Dematiaceous Hyphomycetes: 370. 1976.
Basionym: *Bactrodesmium clavulatum* Cooke & Harkn., Grevillea 12: 92. 1884.
Synonyms: *Clasterosporium clavulatum* (Cooke & Harkn.) Sacc., Syll. fung. 4: 390. 1886.
Stigmina clavulata (Cooke & Harkn.) Pound & Clem., Minn. bot. Stud. 1(Bulletin 9): 661. 1896.

Notes: The species is known so far in the USA on decorticated wood of *Eucalyptus*. It is characterised by effuse colonies and pigmented, transversely septate conidia borne on monotretic conidiogenous cells. Based on these morphological traits, Ellis (1976) excluded *B. clavulatum* from the genus and proposed a combination in *Polyschema.*

Stigmina robusta (Cooke & Ellis) B. Sutton, Mycol. Pap. 132: 117. 1973.
Basionym: *Arthrobotryum robustum* Cooke & Ellis, Grevillea 7: 7. 1878.
Synonyms: *Wettsteiniella robusta* (Cooke & Ellis) Kuntze, Revis. gen. pl. 2: 875. 1891.
Bactrodesmium robustum (Cooke & Ellis) S. Hughes, Can. J. Bot. 36: 739. 1958.

Notes: The present species occurs on decaying bark of *Acer* sp. and *Populus* spp. and it is known from North America in Canada and the USA (Hughes 1958, Sutton 1973). It is characterised by superficial or semi-immersed sporodochia, monoblastic conidiogenous cells that are almost cupulate with a ragged, flared

annellation and pigmented, transversely septate conidia with inconspicuous marginal frill. Based on these features, Sutton (1973) excluded this species from *Bactrodesmium* and proposed a new combination in *Stigmina*.

Stuartella suttonii A. Funk & Shoemaker, Can. J. Bot. 61: 2277. 1983.
Synonym: *Bactrodesmium obliquum* var. *suttonii* S. Hughes & G.P. White, Fungi Canadenses 254: 1. 1983.

Notes: Hughes & White (1983b) described *B. obliquum* var. *suttonii* from the West coast of Canada from various coniferous trees except *Picea* spp., which is restricted as a host of the type variety of *B. obliquum* (Sutton 1967, Hughes & White 1983e). Both varieties produce sporodochia; the var. *suttonii* differs from var. *obliquum* by the absence of longitudinal or oblique septa in the end cells of conidia. The connection between *Stuartella suttonii* and *B. obliquum* var. *suttonii* was experimentally confirmed by Funk & Shoemaker (1983); the species is a member of the *Dothideomycetes* genera *incertae sedis*. *Bactrodesmium obliquum* var. *obliquum* is accepted in the genus until its phylogenetic relationships are determined. Its sexual-asexual connection remains unknown.

DISCUSSION

The five-gene phylogenetic analyses (Figs 1, 2) revealed *Bactrodesmium*, including *B. abruptum*, *B. diversum*, *B. leptopus*, *B. obovatum*, *B. pallidum* and *B. spilomeum*, as a well-resolved monophyletic clade in the *Savoryellales*. *Bactrodesmium* has been a broadly delimited genus encompassing saprobes on decaying wood and bark, palm rachis and fallen leaves or paper but also epiphytes on living leaves in temperate, subtropical and tropical regions of Southern and Northern hemispheres (e.g. Sydow & Sydow 1920, Ellis 1959, 1963, 1965, Ciferri 1962, Holubová-Jechová 1972, Sutton 1977, Hughes 1978, Palm & Stewart 1982, Hughes 1983, Hughes & White 1983a–i, Rao 1983, Castañeda-Ruiz 1985, Kirk 1985, 1986, Matsushima & Matsushima 1995, Mercado *et al*. 1995, Cooper 2005). Based on the phylogenetic evidence and comparative morphology of six species characterised in this study, the generic concept of *Bactrodesmium* was emended. The genus is delimited to dematiaceous hyphomycetes forming sporodochial conidiomata in the substrate, fasciculate, simple or sparsely or penicillately branched mononematous conidiophores, holoblastic conidiogenous cells and solitary, dry, acrogenous, pigmented conidia sometimes with thick bands over transverse septa. Conidiophores are usually hyaline to subhyaline to pale brown and thin-walled, but in some species, they are brown to dark brown or reddish-brown and thick-walled, i.e. *B. globosum* (Holubová-Jechová 1972). Although longitudinal or oblique septa are unusual in *Bactrodesmium*, species with dictyoconidia such as *B. obliquum*, *B. peruvianum* and *B. pithoideum* (Sutton 1967, 1975, 1977), are accepted in the genus until their systematic placement is determined with DNA sequence data. All 35 accepted species are saprobes thriving on decaying wood or bark of deciduous or coniferous trees, rarely on dead palm rachis except for *B. novageronense*, which forms conidiomata on fallen leaves.

Of the five gene markers used to assess relationships of *Bactrodesmium*, only three possess species resolving power. The ITS region, a standard DNA barcode for fungi, which, however, may not always contain enough variation for discriminating among all species (Schoch *et al*. 2012), was insufficient to identify all studied *Bactrodesmium*. We encountered difficulties in distinguishing between *B. abruptum* and *B. obovatum*; their ITS loci exhibited high sequence identity but also polymorphism among strains of each species. The intragenomic ITS variation has been reported for various fungal groups (e.g. O'Donnell & Cigelnik 1997, Hibbett *et al*. 2011, Hughes *et al*. 2018, Stadler *et al*. 2020), which can make identification, interpretation of phylogenies and taxonomic conclusions based solely on this marker problematic. Only protein-coding loci, *rpb2* and *tef1-α*, could distinguish among all six *Bactrodesmium*. The *tef1-α* locus is relatively easy to amplify, which makes it slightly superior to *rpb2*, which in turn may be difficult to amplify. Thus, the *tef1-α* gene, which has been suggested the universal secondary fungal barcode (Robert *et al*. 2011, Stielow *et al*. 2015), is suitable as a secondary identification marker for *Bactrodesmium*.

The conidiogenous cells of *Bactrodesmium* are described as either polyblastic (*B. betulicola*, *B. diversum*, *B. globosum* and *B. hebridense*) or monoblastic (*B. abruptum*, *B. ellipsoideum*, *B. indicum*, *B. leptopus*, *B. obovatum*, *B. pallidum*, *B. spilomeum*, *B. ramosius*, *B. simile*, *B. traversoanum* and *B. xerophilum*), but often this diagnostic character is omitted from the descriptions. However, only *B. betulicola* (Holubová-Jechová 1972) and *B. pithoideum* (Sutton 1975) form conidia on bluntly rounded denticles on polyblastic, sympodially elongating conidiogenous cells, an unusual character confirmed by Hughes & White (1983f, g) in Canadian material of these species. Moreover, *B. pithoideum* forms either sporodochia or the colonies are effuse, scattered, sometimes pulvinate (Sutton 1975, Hughes & White 1983g). We prefer not to segregate the two latter species from *Bactrodesmium* until their placement is verified with DNA sequence data.

Determination of the mechanism of a conidial secession of *Bactrodesmium* is complicated by the fact that on the natural substrate conidia are released and often bear a minute frill of the wall at the base suggesting the rhexolytic secession, while in culture conidia do not secede readily. This variability is a source of inconsistent view of the detachment of conidia and the reason it was considered both schizolytic and rhexolytic. Moreover, descriptions of many *Bactrodesmium* are based on observations on the natural material only and the mode of conidial secession is unknown. Species of *Bactrodesmium* with a rhexolytic detachment include *B. biformatum*, *B. cedricola*, *B. curvatum*, *B. diversum*, *B. hebridense*, *B. linderi*, *B. mucosum*, *B. palmicola*, and *B. simile* (Ellis 1963, Palm & Stewart 1982, Hughes 1983, Hughes & White 1983h, Kirk 1985, 1986, Matsushima & Matsushima 1995, Mercado *et al*. 1995, Hernández-Restrepo *et al*. 2013, Arias *et al*. 2016). *Bactrodesmium* species reported to have schizolytic secession are *B. betulicola*, *B. moenitum*, *B. nothofagi*, *B. obovatum*, *B. pithoideum*, *B. pluriseptatum*, and *B. pusillum* (Palm & Stewart 1982; Hughes & White 1983a, f, g, Hughes 1984, Révay 1993, Cooper 2005, Markovskaja 2006). Moreover, Hughes & White (1983a) considered the basal frill in conidia of *B. obovatum* as a result of the mechanical rupture of the conidiogenous cell rather than an indication of rhexolytic detachment. On the contrary, Hughes (1983) and Hughes & White (1983h) regarded the presence of a minute frill in conidia of *B. biformatum* and *B. cedricola* significant, and the secession was described as rhexolytic. These examples illustrate the difficulty to define the mode of conidial detachment in *Bactrodesmium*.

Conidia with a frill of the wall at the base were frequently observed in our specimens, while in culture the conidia usually remained attached indicating that the natural mechanism of segregation is often not completing. When detached, conidia with and without a noticeable frill were present. Multiple secession patterns of several *Bactrodesmium* are captured *in vitro* in Fig. 5 and described above. During rhexolytic secession, the conidiogenous cells or specialised supporting cells below conidium may degenerate enzymatically, or may fracture at the built-in zone of weakness or are thinner-walled than the cells above and below them and collapse (Carmichael 1971, Cole & Samson 1979). Based on our observations we conclude that the secession of conidia of *Bactrodesmium sensu stricto* is rhexolytic. However, the conidial secession varies in bactrodesmium-like species that belong to distantly related groups, i.e. *A. gabretae* (rhexolytic), *B. obliquum* var. *suttonii* (as *Stuartella suttonii*) (rhexolytic), or *G. longisporus* and *G. stilboideus* (schizolytic) and *K. cubense* (schizolytic). It seems that the mode of conidial detachment is taxonomically significant. Cultivation studies and re-evaluation of the mode of conidial secession in *Bactrodesmium* is needed to evaluate a taxonomic significance of conidial separation.

In the morphology of brown, transversely septate, solitary conidia, *Bactrodesmium* is similar to *Bactrodesmiastrum*, *Bactrodesmiella*, *Janetia*, *Listeromyces* and *Vanakripa*. *Bactrodesmiastrum* (*Fuscosporellales*) is a small genus containing five species characterised by effuse colonies, pigmented, macronematous, sometimes moniliform conidiophores and holoblastic, terminal, integrated or discrete usually pigmented conidiogenous cells (Holubová-Jechová 1984, Hernández-Restrepo *et al*. 2015, Li *et al*. 2017). Members of *Bactrodesmiella* (Ellis 1971) occur on litter or decaying bark and differ from *Bactrodesmium* by percurrently elongating conidiogenous cells and conidia arranged in short chains; its systematic placement is unknown. *Janetia* (Ellis 1976) includes species forming effuse colonies or indeterminate synnemata; conidiophores are often reduced to conidiogenous cells which are sympodially elongating with denticles bearing pigmented phragmoconidia. *Listeromyces* (Penzig & Saccardo 1902) is a monotypic genus whose conidiomata can be interpreted as either synnematal or sporodochial. It occurs on decaying wood and is characterised by conidiophores arising from a stromatic base and bearing short monoblastic conidiogenous cells with distoseptate conidia and phialidic synanamorph *in vitro* (Goos 1971, Ellis 1976). *Vanakripa* forms sporodochia on decaying wood and is distinctive by pigmented, septate or non-septate conidia which remain attached to the hyaline so called separating cell after rhexolytic secession (Bhat & Kendrick 1993).

In the absence of molecular DNA data, the classification of *Bactrodesmium* has always been challenging. The occurrence of bactrodesmium-like phenotypic traits in distinct clades implies that they are a result of convergent evolution, and the genus is polyphyletic. In this study, four species were segregated from *Bactrodesmium* into three unrelated genera, *Aphanodesmium* (*Helotiales*), *Gamsomyces* (*Sclerococcales*) and *Kaseifertia* (*Pleosporales*). Following the emended description of *Bactrodesmium*, phylogenetic evidence and morphological comparison of known species, several other species are not recognised in the genus (Table 3). Interestingly, the majority of excluded species with effuse colonies inhabit fallen or living leaves or herbaceous stems, while species accepted in *Bactrodesmium* are generally lignicolous. The substrate preference of species with synnemata is not unambiguous.

Bactrodesmium species, excluded from the genus and characterised by synnemata, include *B. heimii*, *G. longisporus* and *G. stilboideus*; *G. longisporus* forms also sporodochial conidiomata (Ellis 1976, Chang 1997, Heredia *et al*. 2018, this study). Due to the revealed relationship of *G. longisporus* and *G. stilboideus* as a new evolutionary lineage in the Sclerococcales, *B. heimii*, which is morphologically reminiscent of *Phragmocephala*, is not accepted in *Bactrodesmium*. On the other hand, we do not exclude the possibility that other synnematal species may be included in *Bactrodesmium* based on molecular evidence. The conidiomatal structures such as synnema and sporodochium, their anatomy, intermediate or transitional forms and importance in classification have been addressed several times. Concerning the presence of pseudoparenchymatous tissue at the base of the synnema, there can be no apparent difference between sporodochium and synnema. Sutton (1980) proposed an experimental classification system for coelomycetous fungi, which he based on the conidium-ontogeny system proposed earlier by Hughes (1953) and subsequently refined by Tubaki (1958), Barron (1968), and Cole & Samson (1979). He stated that different categories of conidiomata are continuous and indistinguishable from each other (Sutton 1980). In some species, conidiomata can be interpreted either as synnematal and/or sporodochial, e.g. in asexual morphs of *Nectria*. For example *N. cinnabarina* (asexual morph *Tubercularia vulgaris*) forms long, stipitate sporodochia interpreted as synnemata (Okada & Tubaki 1987), compared to *N. pseudocinnabarina* which forms only synnemata (Hirooka *et al*. 2012), while other *Nectria* form non-stipitate sporodochia. Sutton & Cole (1983) and Rao & de Hoog (1986) discussed the arrangement of conidiophores on the examples of *Thozetella* and *B. longisporum* and questioned the taxonomic value of sporodochium *vs* synnema concluding that under different environmental conditions this character may show remarkable variation.

Although we studied strains of several *Bactrodesmium sensu stricto*, the epitype was proposed only for *B. diversum*. Strains of other species do not come from the same country or region as the holotypes. The *B. diversum* holotype (Spain) and all newly collected strains (France) originate from the southwestern Pyrenees in the southern and northern parts of this mountainous region; localities are ca. 180 km apart. Thus, the French collections were suitable for selecting the epitype. Regarding *A. cubense* (Elba Island *vs* Cuba – holotype) and *G. longisporus* (India, Japan *vs* United Kingdom – holotype), the available strains are from different continents and cannot be considered eligible candidates. Although the strain of *G. stilboideus* (Puerto Rico) originates in Middle America in the Caribbean as well as the holotype (Cuba), it is not the most typical representative of this species. The conidia of our strain are slightly longer, wider and with more septa (see above) and expand the known variability of this species.

The genus *Dematiosporium* was revised to include lignicolous freshwater fungi forming effuse colonies and dictyosporous, dark brown conidia with pores at each cell. The genus is remarkably similar to *Monodictys* (Hughes 1958), typified by *M. putredinis*. *Monodictys* and *Dematiosporium* share several morphological traits such as effuse colonies without setae, micronematous conidiophores and single, dry, brown to black, dictyosporous conidia formed on the terminal, integrated, monoblastic

conidiogenous cells (Hughes 1958, Ellis 1971). Although the majority of *Monodictys* are saprobes on decaying wood or plant debris in terrestrial, freshwater, seawater or brackish habitats and are cosmopolitan in distribution, some species, e.g. *M. putredinis* and *Monodictys* sp., were confirmed to induce soft rot (Eslyn *et al*. 1975, Eslyn & Highley 1976, Udaiyan & Manian 1991).

Monodictys putredinis, the asexual morph of *Ohleria brasilensis* (Samuels 1980), and seven other species (*M. aershanensis*, *M. arctica*, *M. austrina*, *M. capensis*, *M. castaneae*, *M. nigrospermum*, *M. cf. pelagica*), whose sequence data are available in GenBank are positioned in various families or *incertae sedis* clades in the *Pleosporales* and *Sordariales* (Day *et al*. 2006, Prasanna Kumar 2013, Tanaka *et al*. 2015, Hernández-Restrepo *et al*. 2017, Vu *et al*. 2019). Relationships of other *Monodictys* species can be estimated through their life histories. *Monodictys pelagica* is the asexual morph of *Nereiospora cristata* (*Microascales*, *Sordariomycetes*) (Mouzouras & Jones 1985) and several other monodictys-like fungi were reported as asexual morphs of *Aquastroma magniostiolata* (*Pleosporales*) (Tanaka *et al*. 2015), *Ascotaiwania latericolla* and *A. lignicola* (*Savoryellales*) (Chang 2001, this study), *Hyaloscypha monodictys* (*Helotiales*, *Leotiomycetes*) (as *H. albohyalina* var. *monodictys*, Hosoya & Huhtinen 2002, see also Han *et al*. 2014, Fehrer *et al*. 2019) and *Tubeufia amazonensis* and *T.* cf. *paludosa* (*Tubeufiales*, *Dothideomycetes*) (Samuels *et al*. 1978). A phialidic synanamorph was reported for *M. levis* (*incertae sedis*) *in vitro* (Wiltshire 1938). The newly published occurrence of three monodictys-like species in the *Savoryellales* and the systematic placement of *Monodictys s. str.* and other monodictys-like fungi in several fungal classes demonstrate that the present generic concept is polyphyletic and strongly calls for targeted morphological and molecular phylogenetic studies needed to resolve the taxonomy of the genus.

Our combined five-gene phylogenetic analyses consistently show *Bactrodesmium*, *Canalisporium*, *Dematiosporium*, *Neoascotaiwania* and *Savoryella* as monophyletic strongly supported genera of the *Savoryellales* and together with morphological characters provide evidence to recognise them as separate taxa. Only *Ascotaiwania* cannot be resolved with the current sampling. In the survey of the *Savoryellales*, Dayarathne *et al*. (2019) proposed a broadly delimited *Ascotaiwania*, but the authors did not consider the diversity and taxonomic significance of asexual characters nor they analysed the ITS sequence data. Dayarathne *et al*. (2019) reduced *Neoascotaiwania* to the synonymy with *Ascotaiwania* and accepted *Bactrodesmium* (based on *B. pallidum*) in the latter genus by analysing the combined LSU-SSU-*rpb2*-*tef1*-*α* data. However, the nested position of a single species of *Bactrodesmium* in the *Ascotaiwania* clade merely demonstrated that the delimitation of *Ascotaiwania* may not correspond with a monophyletic genus and that application of the name requires much improved sampling.

Although the relationship of *Ascotaiwania* species included in the phylogenetic analysis seems clear when their ascospores, asci and ascomata are compared, it is difficult to reconcile their different asexual morphs with this relationship. *Ascotaiwania latericolla* and *A. lignicola* are the only species of the genus with dictyosporous conidia. The other *Ascotaiwania* were additionally linked to morphologically different monotosporella-, triadelphia- or trichocladium-like asexual morphs with phragmoconidia, i.e. *A. hsilio* (Chang 2001), *A. mitriformis* (Ranghoo & Hyde 1998), *A. sawadae* (Sivichai *et al*. 1998), and *A. uniseptata* (Réblová *et al*. 2016a). Given a close relationship of *A. latericolla* and *A. lignicola*, representing the core of the genus, the dictyosporous, pigmented, dry, solitary conidia may serve as a diagnostic character to recognise *Ascotaiwania sensu stricto*, and the asexual characters may play an important role in delimitation of the genus and its possible segregates. Because of the high degree of similarity in sexual morphological traits of *Ascotaiwania* and because of the lack of sequence data for majority of its species or insufficient DNA data that consists only of fragments of the LSU gene (*A. uniseptata*, *A. mitriformis*), we refrain from making any nomenclatural changes or proposing new genera based on limited sampling. Based on the current sampling of the *Savoryellales*, it became evident that sporodochial conidiomata (*Bactrodesmium*, *Canalisporium*) and effuse colonies (*Ascotaiwania*, *Dematiosporium*, *Neoascotaiwania* and *Savoryella*) are generic diagnostic characters.

Pleurotheciella erumpens and *H. lacustris* represent new additions to the *Pleurotheciales*. *Pleurotheciella* is remarkably similar to *Pleurothecium* (Höhnel 1919) in the morphology of the macronematous conidiophores, hyaline conidia borne on holoblastic denticulate conidiogenous cells seceding schizolytically, non-stromatic dark brown ascomata, cylindrical-clavate asci with a distinct apical annulus and hyaline, ellipsoidal to fusiform, transversely septate ascospores. Although the first observations of dactylaria-like conidiophores of *Pleurotheciella* were made only *in vitro*; conidiophores were hyaline, often reduced to conidiogenous cells (Réblová *et al*. 2012), species subsequently added to the genus were confirmed to produce macronematous, brown or hyaline conidiophores on the natural substrate (Réblová *et al*. 2016a, Luo *et al*. 2018).

Helicoascotaiwania, typified by *H. farinosa*, was segregated from *Ascotaiwania* (*Savoryellales*) by coiled conidia of the *Helicoön*-type and DNA sequence data (Campbell & Shearer 2004, Boonyuen *et al*. 2011, Réblová *et al*. 2012, 2016a, Dayarathne *et al*. 2019). It is the only member of the *Pleurotheciales* with this kind of conidial morphology. *Helicoascotaiwania* forms a well-resolved clade in the five-gene phylogeny and is distinguished from other genera of the order by versicolorous, septate ascospores, and asci with a prominent ascal plug obscuring the apical ring. Our new species *H. lacustris* is the first member of the genus reported from Europe.

ACKNOWLEDGEMENTS

This study was supported by long-term research development projects of the Institute of Botany, Czech Academy of Sciences RVO 67985939 (M.R.) and the University Hospital Hradec Králové MH CZ – DRO (UHHK, 00179906) (J.N.). We thank Keith Seifert for a discussion on the rhexolytic conidiogenesis and conidiogenesis in general. We thank the curators of ILLS and K herbaria, Andrew N. Miller and Angela Bond, for the loan of specimens. Peter Johnston is acknowledged for his assistance to M. R. in obtaining the Manaaki Whenua Fellowship in 2005 and collecting permit for New Zealand. We are grateful to Ken Hudson from CABI (Mycology Publications) for providing necessary literature. We thank the French Ministry of Environment for assistance in obtaining the collecting permit for France. We thank Václav Štěpánek for preparing several *Bactrodesmium* sequences during preparation of this study. We thank Shaun Pennycook for grammatical review of new names and reviewers for their comments and suggestions.

REFERENCES

Arias RM, Heredia G, Castañeda-Ruiz RF (2016). Two new species of *Bactrodesmium* and *Dictyoaquaphila* from Mexico. *Mycotaxon* **131**: 291–295.

Barbosa FR, Gusmão LFP (2011). Conidial fungi from semi-arid Caatinga Biome of Brazil. Rare freshwater hyphomycetes and other new records. *Mycosphere* **2**: 475–485.

Barron GL (1968). *The genera of hyphomycetes from soil*. Williams & Wilkins Co., Baltimore, USA.

Berkeley MJ, Broome CE (1865). Notices of British fungi (1038–1062). *Annals and Magazine of Natural History, Ser. 3* **15**: 400–404.

Bhat DJ, Kendrick WB (1993). Twenty-five new conidial fungi from the Western Ghats and the Andaman Islands (India). *Mycotaxon* **49**: 19–90.

Boonyuen N, Suetrong S, Sivichai S, *et al*. (2011). *Savoryellales* (*Hypocreomycetidae*, *Sordariomycetes*): a novel lineage of aquatic ascomycetes inferred from multiple-gene phylogenies of the genera *Ascotaiwania*, *Ascothailandia*, and *Savoryella*. *Mycologia* **103**: 1351–1371.

Cai L, Zhang K, McKenzie EH, *et al*. (2003). Freshwater fungi from bamboo and wood submerged in the Liput River in the Philippines. *Fungal Diversity* **13**: 1–12.

Campbell J, Shearer CA (2004). *Annulusmagnus* and *Ascitendus*, two new genera in the *Annulatascaceae*. *Mycologia* **96**: 822–833.

Carmichael JW (1971). Blastospores, aleuriospores, chlamydospores. In: *Taxonomy of fungi imperfecti* (Kendrick B, ed). Univ. Toronto Press, Toronto, Ontario: 50–65.

Castañeda-Ruiz RF (1985). *Deuteromycotina de Cuba. II. Hyphomycetes*. Instituto de investigacions Fundamentales en Agricultura Tropical - Alejandro de Humboldt, Cuba.

Castañeda-Ruiz RF, Arnold GRW (1985). Deuteromycotina de Cuba. I. Hyphomycetes. *Revista del Jardín Botánico Nacional* **6**: 47–67. Universidad de la Habana.

Castañeda-Ruiz RF, Guerrero B, Adamo GM, *et al*. (2009). A new species of *Selenosporella* and two microfungi recorded from a cloud forest in Mérida, Venezuela. *Mycotaxon* **109**: 63–74.

Castañeda-Ruiz RF, Heredia G, Gusmao LFP, *et al*. (2016). Fungal diversity of Central and South America. In: *Biology of microfungi* (De-Wei L, ed). Springer International Publishing, Switzerland: 197–218.

Castlebury LA, Rossman AY, Sung GH, *et al*. (2004). Multigene phylogeny reveals new lineage for *Stachybotrys chartarum*, the indoor air fungus. *Mycological Research* **108**: 864–872.

Chang HS (1997). Eight more dematiaceous hyphomycetes new for Taiwan. *Botanical Bulletin- Academia Sinica* **38**: 197–204.

Chang H (2001). *Trichocladium* anamorph of *Ascotaiwania hsilio* and *Monodictys*-like anamorphic states of *Ascotaiwania lignicola*. *Fungal Science* **16**: 35–38.

Chang HS, Hsieh SY, Jones EBG, *et al*. (1998). New freshwater species of *Ascotaiwania* and *Savoryella* from Taiwan. *Mycological Research* **102**: 709–718.

Cheng X-L, Li W, Zhang T-Y (2014). A new species of *Phaeoisaria* from intertidal marine sediment collected in Weihai, China. *Mycologia* **127**: 17–24.

Chew HF, Jungkind DL, Mah DY, *et al*. (2010). Post-traumatic fungal keratitis caused by *Carpoligna* sp. *Cornea* **29**: 449–452.

Ciferri R (1962). Schedae mycologicae 35–98. *Atti dell'Istituto Botanico della Università e Laboratorio Crittogamico di Pavia, Sér. 5* **19**: 85–139.

Cole GT, Samson RA (1979). *Patterns of development in conidial fungi*. Pitman Publishing Limited, London, England.

Cooke MC (1883). Saccardo's sylloge fungorum. *Grevillea* **12**: 34–35.

Cooper JA (2005). New Zealand hyphomycete fungi: additional records, new species, and notes on interesting collections. *New Zealand Journal of Botany* **43**: 323–349.

Crous PW, Verkley GJM, Groenewald JZ, *et al*. (2019). *Fungal biodiversity*. Westerdijk Fungal Biodiversity Institute, Utrecht, The Netherlands. Westerdijk Laboratory Manual Series 1.

Day MJ, Gibas CFC, Fujimura KE, *et al*. (2006). *Monodictys arctica*, a new hyphomycete from the roots of *Saxifraga oppositifolia* collected in the Canadian High Arctic. *Mycotaxon* **98**: 261–272.

Dayarathne MC, Maharachchikumbura SSN, Jones EBG, *et al*. (2019). Phylogenetic revision of *Savoryellaceae* and evidence for its ranking as a subclass. *Frontiers in Microbiology* **10**: 1–26.

de Hoog GS, Gerrits van den Ende AH (1998). Molecular diagnostics of clinical strains of filamentous *Basidiomycetes*. *Mycoses* **41**: 183–189.

Diederich P, Ertz D, Lawrey JD, *et al*. (2013). Molecular data place the hyphomycetous lichenicolous genus *Sclerococcum* close to *Dactylospora* (*Eurotiomycetes*) and *S. parmeliae* in *Cladophialophora* (*Chaetothyriales*). *Fungal Diversity* **58**: 61–72.

Ellis MB (1959). *Clasterosporium* and some allied dematiaceae-phragmosporae. II. *Mycological Papers* **72**: 1–75.

Ellis MB (1963). Dematiaceous hyphomycetes IV. *Mycological Papers* **87**: 1–42.

Ellis MB (1965). Dematiaceous hyphomycetes VI. *Mycological Papers* **103**: 1–46.

Ellis MB (1971). *Dematiaceous hyphomycetes*. Commonwealth Mycological Institute, Kew, Surrey, England.

Ellis MB (1976). *More dematiaceous hyphomycetes*. Commonwealth Mycological Institute, Kew, Surrey, England.

Eslyn WE, Highley TL (1976). Decay resistance and susceptibility of sapwood of fifteen tree species. *Phytopathology* **66**: 101–117.

Eslyn WE, Kirk TH, Effland MJ (1975). Changes in the chemical composition of wood caused by six soft rot fungi. *Phytopathology* **66**: 473–476.

Fallah PM, Crane JL, Shearer CA (1999). Freshwater ascomycetes: two new species of *Ascotaiwania* from North America. *Canadian Journal of Botany* **77**: 87–92.

Fehrer J, Réblová M, Bambasová V, *et al*. (2019). The root-symbiotic *Rhizoscyphus ericae* aggregate and *Hyaloscypha* (*Leotiomycetes*) are congeneric: Phylogenetic and experimental evidence. *Studies in Mycology* **92**: 195–225.

Fernández FA, Lutzoni FM, Huhndorf SM (1999). Teleomorph-anamorph connections: the new pyrenomycetous genus *Carpoligna* and its *Pleurothecium* anamorph. *Mycologia* **91**: 251–262.

Figueroa R, Bran MC, Morales, *et al*. (2016). Nuevos registros de hongos anamórficos para Guatemala. *Revista Científica de la Facultad de Ciencias Químicas y Farmacia* **26**: 40–50.

Funk A, Shoemaker RA (1983). *Stuartella suttonii* n. sp., the teleomorph of *Bactrodesmium obliquum* var. *suttonii*. *Canadian Journal of Botany* **61**: 2277–2279.

Gargas A, Taylor JW (1992). Polymerase chain reaction (PCR) primers for amplifying and sequencing nuclear SSU rDNA from lichenized fungi. *Mycologia* **84**: 589–592.

Geiser DM, Gueidan C, Miadlikowska J, *et al*. (2006–2007). *Eurotiomycetes*: *Eurotiomycetidae* and *Chaetothyriomycetidae*. *Mycologia* **98**: 1053–1064.

Gooding GV, Lucas GB (1959). Factors influencing sporangial formation and zoospore activity in *Phytophthora parasitica* var. *nicotianae*. *Phytopathologia* **49**: 277–281.

Goos RD (1971). *Listeromyces insignis* refound. *Mycologia* **63**: 213–218.

Grove WB (1886). New and noteworthy fungi: Part III. *Journal of Botany* **24**: 197–206.

Guarro J, Gené J, Stchigel AM, *et al*. (2012). *Atlas of soil ascomycetes*. CBS-KNAW Fungal Biodiversity Centre, Utrecht, The Netherlands. CBS Biodiversity series 10.

Guarro J, Vieira LA, Freitas D de, *et al*. (2000). *Phaeoisaria clematidis* as a cause of keratomycosis. *Journal of Clinical Microbiology* **38**: 2434–2437.

Gueidan C, Ruibal VC, de Hoog GS, *et al*. (2008). An extremotolerant rock-inhabiting ancestor for mutualistic and pathogen-rich fungal lineages. *Studies in Mycology* **61**: 111–119.

Hall TA (1999). BioEdit 5.0.9: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symposium Series* **41**: 95–98.

Han J-G, Hosoya T, Sung G-H, *et al*. (2014). Phylogenetic reassessment of *Hyaloscyphaceae sensu lato* (*Helotiales*, *Leotiomycetes*) based on multigene analyses. *Fungal Biology* **118**: 150–167.

Harkness HW (1884). New species of California fungi. *Bulletin of the California Academy of Sciences* **1**: 29–47.

Heim R, Buchli H, Duche J, *et al*. (1951). Memoire sur l'Antennopsis ectoparasite du termite de Saintonge. *Bulletin trimestriel de la Société mycologique de France* **67**: 336–364.

Heredia G, Arias-Mota RM, Mena-Portales J, *et al*. (2018). Saprophytic synnematous microfungi. New records and known species for Mexico. *Revista Mexicana de Biodiversidad* **89**: 604–618.

Hernández-Restrepo M, Gené J, Castañeda-Ruiz RF, *et al*. (2015). Emendation of the genus *Bactrodesmiastrum* (*Sordariomycetes*) and description of *Bactrodesmiastrum monilioides* sp. nov. from plant debris in Spain. *Mycological Progress* **14**: 1–7.

Hernández-Restrepo M, Gené J, Castañeda-Ruiz RF, *et al*. (2017). Phylogeny of saprobic microfungi from Southern Europe. *Studies in Mycology* **86**: 53–97.

Hernández-Restrepo M, Mena-Portales J, Gené J, *et al*. (2013). New *Bactrodesmiastrum* and *Bactrodesmium* from decaying wood in Spain. *Mycologia* **105**: 172–180.
Hibbett DS, Ohman A, Glotzer D, *et al*. (2011). Progress in molecular and morphological taxon discovery in *Fungi* and options for formal classification of environmental sequences. *Fungal Biology Review* **25**: 38–47.
Hirooka Y, Rossman AY, Samuels GJ, *et al*. (2012). A monograph of *Allantonectria*, *Nectria*, and *Pleonectria* (*Nectriaceae*, *Hypocreales*, *Ascomycota*) and their pycnidial, sporodochial, and synnematous anamorphs. *Studies in Mycology* **71**: 1–210.
Höhnel FXR von (1904). Mykologische Fragmente. *Annales Mycologici* **2**: 38–60.
Höhnel FXR von (1919). Fünfte vorläufige Mitteilung mykologische Ergebnisse (Nr. 300–500). *Berichte der Deutschen Botanischen Gesellschaft* **37**: 153–161.
Holubová-Jechová V (1972). Lignicolous Hyphomycetes from Czechoslovakia. 2. *Bactrodesmium*. *Folia Geobotanica et Phytotaxonomica* **7**: 407–418.
Holubová-Jechová V (1984). *Bactrodesmiastrum*, a new genus of lignicolous Hyphomycetes. *Folia Geobotanica et Phytotaxonomica* **19**: 103–106.
Houbraken J, Samson RA (2011). Phylogeny of *Penicillium* and the segregation of *Trichocomaceae* into three families. *Studies in Mycology* **70**: 1–51.
Hosoya T, Huhtinen S (2002). *Hyaloscyphaceae* in Japan (7): *Hyaloscypha albohyalina* var. *monodictys* var. nov. *Mycoscience* **43**: 405–409.
Huelsenbeck JP, Ronquist F (2001). MrBayes: Bayesian inference of phylogenetic trees. *Bioinformatics* **17**: 754–755.
Hughes SJ (1951). Studies on Microfungi. III. *Mastigosporium*, *Camposporium*, and *Ceratosporium*. *Mycological Papers* **36**: 1–43.
Hughes SJ (1952). *Trichocladium* Harz. *Transactions of the British Mycological Society* **35**: 152–157.
Hughes SJ (1953). Conidiophores, conidia and classification. *Canadian Journal of Botany* **31**: 577–659.
Hughes SJ (1958). Revisiones Hyphomycetum aliquot cum appendice de nominibus rejiciendis. *Canadian Journal of Botany* **36**: 727–836.
Hughes SJ (1978). New Zealand Fungi. 25. Miscellaneous species. *New Zealand Journal of Botany* **16**: 311–370.
Hughes SJ (1983). *Bactrodesmium biformatum*. *Fungi Canadenses* **258**: 1–2.
Hughes SJ (1984). *Bactrodesmium moenitum*. *Fungi Canadenses* **261**: 1–2.
Hughes KW, Tulloss RH, Petersen RH (2018). Intragenomic nuclear RNA variation in a cryptic *Amanita* taxon. *Mycologia* **110**: 93–103.
Hughes SJ, White GP (1983a). *Bactrodesmium obovatum*. *Fungi Canadenses* **256**: 1–2.
Hughes SJ, White GP (1983b). *Bactrodesmium obliquum* var. *suttonii*. *Fungi Canadenses* **254**: 1–2.
Hughes SJ, White GP (1983c). *Bactrodesmium spilomeum*. *Fungi Canadenses* **257**: 1–2.
Hughes SJ, White GP (1983d). *Bactrodesmium traversianum*. *Fungi Canadenses* **259**: 1–2.
Hughes SJ, White GP (1983e). *Bactrodesmium obliquum* var. *obliquum*. *Fungi Canadenses* **253**: 1–2.
Hughes SJ, White GP (1983f). *Bactrodesmium betulicola*. *Fungi Canadenses* **251**: 1–2.
Hughes SJ, White GP (1983g). *Bactrodesmium pithoideum*. *Fungi Canadenses* **252**: 1–2.
Hughes SJ, White GP (1983h). *Bactrodesmium cedricola*. *Fungi Canadenses* **255**: 1–2.
Hughes SJ, White GP (1983i). *Bactrodesmium rahmii*. *Fungi Canadenses* **260**: 1–2.
Hyde KD, Chaiwan N, Norphanphoun C, *et al*. (2018). Mycosphere notes 169–224. *Mycosphere* **9**: 271–430.
Hyde KD, Norphanphoun C, Abreu VP, *et al*. (2017). Fungal diversity notes 603–708: taxonomic and phylogenetic notes on genera and species. *Fungal Diversity* **87**: 1–235.
Johnston PR, Quijada L, Smith CA, *et al*. (2019). A multigene phylogeny toward a new phylogenetic classification of *Leotiomycetes*. *IMA Fungus* **10**: 1.
Jones EBG, Eaton RA (1969). *Savoryella lignicola* gen. and sp. nov. from water-cooling towers. *Transactions of the British Mycological Society* **52**: 161–165.
Katoh K, Standley DM (2013). MAFFT multiple sequence alignment software version 7: improvements in performance and usability. *Molecular Biology and Evolution* **30**: 772–780.
Kauff F, Lutzoni F (2002). Phylogeny of the *Gyalectales* and *Ostropales* (*Ascomycota*, *Fungi*): among and within order relationships based on nuclear ribosomal RNA small and large subunits. *Molecular Phylogenetics and Evolution* **25**: 138–156.
Kirk PM (1985). New or interesting microfungi XIV. Dematiaceous hyphomycetes from Mt Kenya. *Mycotaxon* **23**: 305–352.
Kirk PM (1986). New or interesting microfungi. XV. Miscellaneous hyphomycetes from the British Isles. *Transactions of the British Mycological Society* **86**: 409–428.
Koukol O, Kolářová Z (2010). *Bactrodesmium gabretae* (anamorphic *Helotiales*), a new sporodochial species described from spruce needles. *Nova Hedwigia* **91**: 243–248.
Kusari S, Lamshoft M, Spiteller M (2009). *Aspergillus fumigatus* Fresenius, an endophytic fungus from *Juniperus communis* L. Horstmann as a novel source of the anticancer pro-drug deoxypodophyllotoxin. *Journal of Applied Microbiology* **107**: 1019–1030.
Landvik S (1996). *Neolecta*, a fruit-body-producing genus of the basal ascomycetes, as shown by SSU and LSU DNA sequences. *Mycological Research* **100**: 199–202.
Li DW, Yang CS, Jalsrai A (2017). *Bactrodesmiastrum domesticum* sp. nov. and a noteworthy hyphomycete from indoor environments. *Mycotaxon* **132**: 779–787.
Linder DH (1929). A monograph of the helicosporous Fungi Imperfecti. *Annals of the Missouri Botanical Garden* **16**: 227–348.
Liu JK, Hyde KD, Jones EBG, *et al*. (2015). Fungal Diversity Notes 1–100: Taxonomic and phylogenetic contributions to fungal species. *Fungal Diversity* **72**: 1–197.
Liu YJ, Whelen S, Hall BD (1999). Phylogenetic relationships among ascomycetes: evidence from an RNA polymerase II subunit. *Molecular Biology and Evolution* **16**: 1799–1808.
Luo ZL, Hyde KD, Bhat DJ, *et al*. (2018). Morphological and molecular taxonomy of novel species *Pleurotheciaceae* (*Pleurotheciales*) from freshwater habitats in Yunnan, China. *Mycological Progress* **17**: 511–530.
Luo ZL, Hyde KD, Liu JK, *et al*. (2019). Freshwater *Sordariomycetes*. *Fungal Diversity* **99**: 451–660.
Malloch D (1981). *Moulds: their isolation, cultivation and identification*. University of Toronto Press, Ontario, Canada.
Markovskaja S (2006). A new species of *Bactrodesmium* from Lithuania. *Mycotaxon* **97**: 337–343.
Mason EW, Hughes SJ (1953). *Bactrodesmium fasciculare*. In: *The natural history of the Scarborough district. Vol. 1. Geology and Botany* (Walsh GB, Rimington FC, eds). Scarborough Field Naturalists Society, Scarborough, England: 159.
Mason-Gamer RJ, Kellogg EA (1996). Testing for phylogenetic conflict among molecular data sets in the tribe *Triticeae* (*Gramineae*). *Systematic Biology* **45**: 524–545.
Matsushima T (1971). *Microfungi of the Solomon islands and Papua-New Guinea*. Kobe, Japan.
Matsushima T (1975). *Icones microfungorum a Matsushima lectorum*. Kobe, Japan.
Matsushima T (1981). Matsushima mycological memoirs 2. *Matsushima Mycological Memoirs* **2**: 1–68.
Matsushima T (1993). Matsushima mycological memoirs 7. *Matsushima Mycological Memoirs* **7**: 1–141.
Matsushima K, Matsushima T (1995). Fragmenta mycologica - I. *Matsushima Mycological Memoirs* **8**: 45–54.
Mena-Portales J, Gené J, Guarro J (2000). Contribución al estudio de los hifomicetos en España. XV. *Boletín de la Sociedad Micológica de Madrid* **25**: 73–82.
Mena-Portales J, Mercado SA (1987). Algunos hifomecetes de las provincias Ciudad de La Habana y La Habana. *Reporte de Investigacion del Instituto de Ecologia y Sistemática* **17**: 1–7.
Mercado SA, Heredia G, Mena-Portales J (1995). New species of dematiaceous hyphomycetes from Veracruz, Mexico. *Mycotaxon* **55**: 491–499.
Miller MA, Pfeiffer W, Schwartz T (2010). Creating the CIPRES Science Gateway for inference of large phylogenetic trees. In: *Proceedings of the Gateway Computing Environments Workshop (GCE), 14 Nov. 2010, New Orleans, LA*: 1–8.
Moreau C, Moreau M (1957). Micromycètes africains. V. *Revue de Mycologie* **22**: 1–5.
Mouzouras R, Jones EBG (1985). *Monodictys pelagica*, the anamorph of *Nereiospora cristata* (*Halosphaeriaceae*). *Canadian Journal of Botany* **63**: 2444–2447.
Nag Raj TR (1993). *Coelomycetous anamorphs with Appendage-Bearing Conidia*. Waterloo, Mycologue Publications, Ontario, Canada.
Nawawi A, Kuthubutheen AJ (1989). *Canalisporium*, a new genus of lignicolous hyphomycetes from Malaysia. *Mycotaxon* **34**: 475–487.

Nierman WC, Pain A, Anderson MJ, *et al*. (2005). Genomic sequence of the pathogenic and allergenic filamentous fungus *Aspergillus fumigatus*. *Nature* **438**: 1151–1156.
Nylander J (2008). *MrModeltest2 v. 2.3 (Program for selecting DNA substitution models using PAUP*)*. Evolutionary Biology Centre, Uppsala, Sweden.
O'Donnell K, Cigelnik E (1997). Two divergent intragenomic rDNA ITS2 types within a monophyletic lineage of the fungus *Fusarium* are nonorthologous. *Molecular Phylogenetics and Evolution* **7**: 103–116.
Okada G, Tubaki K (1986–1987). Conidiomatal structures of the stilbellaceous and allied fungi. *Sydowia* **39**: 148–159.
Olariaga I, Teres J, Martin J, *et al*. (2019). *Pseudosclerococcum golindoi* gen. et sp. nov., a new taxon with apothecial ascomata and a Chalara-like anamorph within the *Sclerococcales* (*Eurotiomycetes*). *Mycological Progress* **18**: 895–905.
Oudemans CAJA (1901). Contributions á la flore mycologique des Pays-Bas. XVII. *Nederlandsch Kruidkundig Archief, Ser. 3* **2**: 170–351.
Palm ME, Stewart EL (1982). Two new combinations in *Bactrodesmium*. *Mycotaxon* **15**: 319–325.
Pang KL, Guo SY, Alas SA, *et al*. (2014). A new species of marine *Dactylospora* and its phylogenetic affinities within the *Eurotiomycetes, Ascomycota*. *Botanica Marina* **57**: 315–321.
Patil NN (1998). Aquatic hyphomycetes of Mahabaleshwar. *Geobiosis New Reports* **17**: 90.
Penzig AJO, Saccardo PA (1901–1902). Diagnoses fungorum novorum in insula Java collectorum. Ser. III. *Malpighia* **15**: 201–260.
Peyronel B (1916). Primo Elenco di Funghi di val San Martino o valle della Germanasca. *Memorie della Reale Accademia delle Scienze di Torino, Ser. 2* **66**: 1–58.
Pfister DH (1997). Castor, pollux and life histories of fungi. *Mycologia* **89**: 1–23.
Pino-Bodas R, Zhurbenko MP, Stenroos S (2017). Phylogenetic placement within *Lecanoromycetes* of lichenicolous fungi associated with *Cladonia* and some other genera. *Persoonia* **39**: 91–117.
Prasanna Kumar C (2013). DNA barcodes for marine fungal identification and discovery. *Fungal Ecology* **6**: 408–418.
Prasher IB, Verma RK (2016). The genus *Monodictys* from Himachal Pradesh. *Kavaka* **47**: 138–142.
Rabenhorst GL (1868). Fungi Europaei exsiccati, Klotzschii herbarii vivi mycologici continuatio. *Editio nov. Series secunda. Cent* **12**: 1101–1200.
Raja HA, Miller AN, Shearer CA (2008). Freshwater ascomycetes: *Aquapoterium pinicola*, a new genus and species of *Helotiales* (*Leotiomycetes*) from Florida. *Mycologia* **100**: 141–148.
Rambaut A (2009). *FigTree v. 1.3.1*.. Computer program and documentation distributed by the author at. http://tree.bio.ed.ac.uk/software/.
Ranghoo VM, Hyde KD (1998). *Ascolacicola aquatica* gen. et sp. nov. and a new species of *Ascotaiwania* from wood submerged in a reservoir in Hong Kong. *Mycologia* **90**: 1055–1062.
Ranghoo VM, Hyde KD, Liew ECY (1999). Family placement of *Ascotaiwania* and *Ascolacicola* based on DNA sequences from the large subunit rRNA gene. *Fungal Diversity* **2**: 159–168.
Rao PR (1983). Two new species of *Bactrodesmium* from India. *Indian Journal of Mycology and Plant Pathology* **13**: 207–208.
Rao V, de Hoog GS (1986). New or critical hyphomycetes from India. *Studies in Mycology* **28**: 1–84.
Réblová M, Seifert KA (2004). *Conioscyphascus*, a new ascomycetous genus for holomorphs with *Conioscypha* anamorphs. *Studies in Mycology* **50**: 95–108.
Réblová M, Seifert KA (2011). Discovery of the teleomorph of the hyphomycete, *Sterigmatobotrys macrocarpa*, and epitypification of the genus to holomorphic status. *Studies in Mycology* **68**: 193–202.
Réblová M, Seifert KA, Fournier J, *et al*. (2012). Phylogenetic classification of *Pleurothecium* and *Pleurotheciella* gen. nov. and its dactylaria-like anamorph (*Sordariomycetes*) based on nuclear ribosomal and protein-coding genes. *Mycologia* **104**: 1299–1314.
Réblová M, Seifert KA, Fournier J, *et al*. (2016a). Newly recognised lineages of perithecial ascomycetes: the new orders *Conioscyphales* and *Pleurotheciales*. *Persoonia* **37**: 57–81.
Réblová M, Untereiner WA, Štěpánek V, *et al*. (2016b). Disentangling *Phialophora* section *Catenulatae*: disposition of taxa with pigmented conidiophores and recognition of a new subclass, *Sclerococcomycetidae* (*Eurotiomycetes*). *Mycological Progress* **16**: 27–46.
Rehner S, Buckley E (2005). A *Beauveria* phylogeny inferred from nuclear ITS and EF1-alpha sequences: evidence for cryptic diversification and links to *Cordyceps* teleomorphs. *Mycologia* **97**: 84–98.
Révay A (1993). Some new or interesting hyphomycetes from Hungary. *Nova Hedwigia* **56**: 473–482.
Rivera KG, Seifert KA (2011). A taxonomic and phylogenetic revision of the *Penicillium sclerotiorum* complex. *Studies in Mycology* **70**: 139–158.
Robert V, Szoke S, Eberhardt U, *et al*. (2011). The quest for a general and reliable fungal DNA barcode. *The Open and Applied Informatics Journal* **5**: 45–61.
Saccardo PA (1881a). *Fungi Italici Autographice Delineati (additis nonnullis extra-Italicis, asterisco notatis). Fascs 17–28. Tabs 641–1120*. Patavii, Italy.
Saccardo PA (1881b). Fungi Veneti novi vel critici V. Mycologiae Venetae addendi. Series XII. *Michelia* **2**: 241–301.
Saccardo PA (1886). Sylloge Hyphomycetum. *Sylloge Fungorum* **4**: 1–807.
Samuels GJ (1980). Ascomycetes of New Zealand 1. *Ohleria brasiliensis* new record and its *Monodictys* anamorph with notes on taxonomy and systematics of *Ohleria* and *Monodictys*. *New Zealand Journal of Botany* **18**: 515–523.
Samuels GJ, Rossman AY, Müller E (1978). Life-history studies of Brazilian Ascomycetes. 6. Three species of *Tubeufia* with, respectively, dictyosporous/pycnidial and helicosporous anamorphs. *Sydowia* **31**: 180–192.
Santa Izabel TDS, Gusmão LFP (2016). Fungal succession on plant debris in three humid forests enclaves in the Caatinga biome of Brazil. *Brazilian Journal of Botany* **39**: 1065–1076.
Sayers EW, Cavanaugh M, Clark K, *et al*. (2019). GenBank. *Nucleic Acids Research* **47**: D94–D99.
Schoch CL, Seifert KA, Huhndorf S, *et al*. (2012). Nuclear ribosomal internal transcribed spacer (ITS) region as a universal DNA barcode marker for fungi. *Proceedings of the National Academy of Sciences* **109**: 6241–6246.
Schoch C, Sung GH, López-Giráldez F, *et al*. (2009). The *Ascomycota* tree of life: a phylum-wide phylogeny clarifies the origin and evolution of fundamental reproductive and ecological traits. *Systematic Biology* **58**: 224–239.
Schweinitz von LD (1832). Synopsis fungorum in America boreali media degentium. *Transactions of the American Philosophical Society* **4**: 141–316.
Shearer CA, Motta JJ (1973). Ultrastructure and conidiogenesis in *Conioscypha* (*Hyphomycetes*). *Canadian Journal of Botany* **51**: 1747–1751.
Sivanesan A, Chang HS (1992). *Ascotaiwania*, a new amphisphaeriaceous ascomycete genus on wood from Taiwan. *Mycological Research* **96**: 481–484.
Sivichai S, Hywel-Jones N, Jones EBG (1998). Lignicolous freshwater *Ascomycota* from Thailand: 1. *Ascotaiwania sawadae* and its anamorph state *Monotosporella*. *Mycoscience* **39**: 307–311.
Spatafora JW, Sung GH, Sung JM, *et al*. (2007). Phylogenetic evidence for an animal pathogen origin of ergot and the grass endophytes. *Molecular Ecology* **16**: 1701–1711.
Stadler M, Lambert C, Wibberg D, *et al*. (2020). Intragenomic polymorphisms in the ITS region of high quality genomes of the *Hypoxylaceae* (*Xylariales*, *Ascomycota*). *Mycological Progress* **19**: 235–245.
Stamatakis A (2014). RAxML Version 8: A tool for Phylogenetic Analysis and Post-Analysis of Large Phylogenies. *Bioinformatics* **30**: 1312–1313.
Stielow JB, Lévesque CA, Seifert KA, *et al*. (2015). One fungus, which genes? Development and assessment of universal primers for potential secondary fungal DNA barcodes. *Persoonia* **35**: 242–263.
Su HY, Udayanga D, Luo ZL, *et al*. (2015). Hyphomycetes from aquatic habitats in Southern China: Species of *Curvularia* (*Pleosporaceae*) and *Phragmocephala* (*Melanommataceae*). *Phytotaxa* **226**: 201–216.
Subramanian CV (1992). A reassessment of *Sporidesmium (Hyphomycetes)* and some related taxa. *Proceedings of the Indian Academy of Sciences (Plant Sciences)* **58**: 179–190.
Sutton BC (1967). A new species of *Bactrodesmium* from white spruce. *Canadian Journal of Botany* **45**: 1777–1781.
Sutton BC (1973). Hyphomycetes from Manitoba and Saskatchewan, Canada. *Mycological Papers* **132**: 1–143.
Sutton BC (1975). *Coelomycetes* V. *Coryneum*. *Mycological Papers* **138**: 1–224.
Sutton BC (1977). Some dematiaceous *Hyphomycetes* from *Eucalyptus* leaf litter. *Boletín de la Sociedad Argentina de Botánica* **18**: 154–161.
Sutton BC (1980). *The coelomycetes, fungi imperfecti with pycnidia, acervuli and stromata*. Commonwealth Mycological Institute, Kew, Surrey, England.
Sutton BC, Cole GT (1983). *Thozetella (Hyphomycetes)*: an exercise in diversity. *Transactions of the British Mycological Society* **81**: 97–107.
Sydow P, Sydow H (1920). Weitere neue Micromyceten der Philippinen-Inseln. *Annales Mycologici* **18**: 98–104.
Tanaka K, Hirayama K, Yonezawa H, *et al*. (2015). Revision of the *Massarineae* (*Pleosporales*, *Dothideomycetes*). *Studies in Mycology* **82**: 75–136.

Tubaki K (1958). Studies on the Japanese *Hyphomycetes*. V. Leaf and stem group with a discussion of the classification of Hyphomycetes and their perfect stages. *Journal of Hattori Botanical Laboratory* **20**: 142–244.

Tubaki K (1975). Notes on the Japanese Hyphomycetes VII. *Cancellidium*, a new hyphomycetes genus. *Transactions of the Mycological Society of Japan* **21**: 357–360.

Udaiyan K (1991). Some interesting hyphomycetes from the industrial water cooling towers of Madras. *Journal of Economic and Taxonomic Botany* **15**: 627–647.

Udaiyan K, Manian S (1991). Fungi colonizing wood in the cooling tower water system at the Madras fertilizer company, Madras, India. *International Biodeterioration Bulletin* **27**: 351–371.

Untereiner WA, Yue Q, Chen L, *et al*. (2019). *Phialophora* section *Catenulatae* disassembled: New genera, species, and combinations and a new family encompassing taxa with cleistothecial ascomata and phialidic asexual states. *Mycologia* **111**: 998–1027.

Vargas-Asensio G, Pinto-Tomas A, Rivera B, *et al*. (2014). Uncovering the cultivable microbial diversity of Costa Rican beetles and its ability to break down plant cell wall components. *PLoS One* **9**(11): e113303.

Vijaykrishna D, Hyde KD (2006). Inter-and intra-stream variation of lignicolous freshwater fungi in tropical Australia. *Fungal Diversity* **21**: 203–224.

Vilgalys R, Hester M (1990). Rapid genetic identification and mapping of enzymatically amplified ribosomal DNA from several *Cryptococcus* species. *Journal of Bacteriology* **172**: 4238–4246.

Vu D, Groenewald M, de Vries M, *et al*. (2019). Large-scale generation and analysis of filamentous fungal DNA barcodes boosts coverage for kingdom fungi and reveals thresholds for fungal species and higher taxon delimitation. *Studies in Mycology* **92**: 135–154.

Wang XW, Yang FY, Meijer M, *et al*. (2019). Redefining *Humicola sensu stricto* and related genera in the *Chaetomiaceae*. *Studies in Mycology* **93**: 65–153.

White TJ, Bruns T, Lee S, *et al*. (1990). Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: *PCR protocols: a guide to methods and applications* (Innis MA, Gelfand DH, Sninsky JJ, White TJ, eds). Academic Press, San Diego, California: 315–322.

Wiltshire SP (1938). The original and modern conceptions of *Stemphylium*. *Transactions of the British Mycological Society* **21**: 211–239.

Wong MK, Hyde KD (2001). Diversity of fungi on six species of *Gramineae* and one species of *Cyperaceae* in Hong Kong. *Mycological Research* **105**: 1485–1491.

Yang J, Maharachchikumbura SSN, Bhat DJ, *et al*. (2016). *Fuscosporellales*, a new order of aquatic and terrestrial *Hypocreomycetidae* (*Sordariomycetes*). *Cryptogamie, Mycologie* **37**: 449–475.

Yu X, Dong W, Bhat DJ, *et al*. (2018). *Cylindroconidiis aquaticus* gen. et sp. nov., a new lineage of aquatic hyphomycetes in *Sclerococcaceae* (*Eurotiomycetes*). *Phytotaxa* **372**: 79–87.

Zhang S-N, Abdel-Wahab MA, Jones EBG, *et al*. (2019). Additions to the genus *Savoryella* (*Savoryellaceae*), with the asexual morphs *Savoryella nypae* comb. nov. and *S. sarushimana* sp. nov. *Phytotaxa* **408**: 195–207.

Zhang N, Castlebury LA, Miller AN, *et al*. (2006–2007). An overview of the systematics of the *Sordariomycetes* based on a four-gene phylogeny. *Mycologia* **98**: 1076–1108.

Zhang N, Luo J, Rossman AY, *et al*. (2016). Generic names in *Magnaporthales*. *IMA Fungus* **7**: 155–159.

Zhang Z, Schwartz S, Wagner L, *et al*. (2000). A greedy algorithm for aligning DNA sequences. *Journal of Computational Biology* **7**: 203–214.

Zucconi L, Lunghini D (1997). Studies on Mediterranean hyphomycetes. VI. Remarks on *Bactrodesmium*, and *B. cubense* comb. nov. *Mycotaxon* **63**: 323–328.