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

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INTRODUCTION

Fungi classified in the Pleurotheciales and Savoryellales are non-lichenized perithelial ascomycetes and dematiaceous hyphomycetes with holoblastic conidiogenesis, some of which belong to the life cycle of known sexual morphs (Boonyuen et al. 2011, Rébolová et al. 2016a). They are saprobes thriving on decay ing 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., Chew et al. 2010). Members of both orders share several sexual morphological traits such as the absence of stromatic tissue or clypeus, perithelial ascocoma, similar anatomy of the ascocameral wall, thin-walled unisecinct asc 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 as asexual morphs characterised by sporodochial conidiomata or effuse colonies, monomor- nematus conidiophores and thick-walled, dry, pigmented conidia with transverse and longitudinal septa. They are part of the life cycle of Asco ta rivia, Canalisporium, Dematosporium, Neoasco ta rivia and Savoryella (e.g. Sivichai et al. 1998, Yang et al. 2016). Members of the Savoryellales 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 rachi on sympodially extending conidiogenous cells (e.g. Fallah
In this study, we focused on Bactrodesmium, an enigmatic and little understood hyphomycete genus whose representative species B. pallidum was linked with the Savoryellases by DNA sequence data (Hernández-Restrepo et al. 2017) and accepted in the broadly delimited Ascostauwania (Dayarthine 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, Castaneda-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 subglobule, 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 rheoxolytic (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 (Castaneda-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 1983), 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 Staurella 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 stiloideum (Castaneda-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. stiloideum. Mena-Portales & Mercado (1987) regarded Stigmina a correct genus and proposed Stigmina longispora var. stiloidea.

We also collected additional representatives of the Pleurotheciales and Savoryellales such as Dematosporium 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 Ascoctaiwania (Sivanesan & Chang 1992), was made on decaying wood in New Zealand. A monodictyos-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 Pleurothecieilla (Réblova et al. 2012). Pleurothecieilla 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 Conicospichylales, Fuscosporellales, Pleurotheciales and Savoryellales. These orders were recovered...
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 hamathelial elements (Réblova et al. 2016a). The BLASTn search (Zhang et al. 2000) of nuclear ribosomal sequences of B. longisporum and B. stibioides 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.

### 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 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 144001                  | 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                   |
| Dematiopsis aquaticum   | CBS 144793                  | on submerged wood                      | Ariège, France                   |
| Gamsomyces longisporus  | CBS 118.86                  | on decaying branch                     | Kamataka, India                  |
| G. longisporus          | CBS 240.89                  | on decaying stem of bamboo             | Kyoto, Japan                     |
| G. stibioides           | 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                  | on 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.
water samples were air-dried, placed in the moist chambers and laboratory. Sediments were washed off with tap water. Fresh-lying on the ground were collected in paper bags, transferred to conidium isolates were incubated on water agar or Modiol isolator (Meopta, Czech Republic). The ascospore and obtained from fresh material with the aid of a single-spore cospores and conidia.

Means ± standard deviation (SD) based on the minimum of 20–25 water. Different growth media were selected to cover various sources of the colonies was carried out at a temperature of 23 °C. Also, MLA was selected to stimulate sporulation and mycelium growth (Malloch 1981) and also for the ability to stimulate the production of pigments in mycological or diffusing in agar (M. Rebová et al., in preparation).

For comparative purposes and culture characteristics, strains were inoculated in triplicate on five different media: commeal dextrose agar (CMD) (17 g of commeal 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 CellID (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 DNaseasy® Ultra-Clean® 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 1996, 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) IRPB2-5F/IRPB2-7cR (Liu et al. 1999) for segments 5–7 of the second largest subunit of RNA polymerase II (rpB2), and 4) EF1-983F/EF1-2218R (Rheiner & Buckley 2005) for the intermediate section of the coding region of the translation elongation factor 1-alpha (eEF1-a).

PCR was carried out in a BioRad C1000 thermal cycler (BioRad 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 (eEF1-a) 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.
| Taxon                               | Source                          | ITS    | LSU    | SSU    | rpb2   | tef1-α | Reference                      |
|------------------------------------|---------------------------------|--------|--------|--------|--------|--------|--------------------------------|
| **Adelosphaeria catenata**          | CBS 138679T                     | KT278721 | KT278707 | KT278692 | KT278743 | —      | Reblóvá et al. (2016a)        |
| **Anapleurothecium botulisporum**  | CBS 132713T                     | KY853423 | KY853483 | —      | —      | —      | Hernández-Restrepo et al. (2017) |
| **Ascoaltaewania latericolla**      | ICM 22739T                     | MN699390 | MN699407 | —      | MN704312 | —      | This study                     |
| A. **lignicola**                   | NIL 0005                        | HQ446341 | HQ446364 | HQ446284 | HQ446419 | HQ446307 | Boonyuen et al. (2011)         |
| A. **lignicola**                   | NIL 0006                        | HQ446342 | HQ446385 | HQ446285 | —      | HQ446308 | Boonyuen et al. (2011)         |
| A. **mitriformis**                 | HKUCC 3706                      | —      | AF132324 | —      | —      | —      | Ranghoo et al. (1999)          |
| A. **sawadae**                     | SS 00051                        | HQ446340 | HQ446383 | HQ446283 | HQ446418 | HQ446306 | Boonyuen et al. (2011)         |
| A. **uniseptata**                  | Sloan 5406                      | —      | KT278718 | —      | —      | —      | Reblóvá et al. (2016a)        |
| **Aspergillus fumigatus**           | INFU/Jc/KF/6, F-A, AF293        | —      | —      | —      | —      | —      | Nierman et al. (2005), Kusari et al. (2009), SSU sequence unpublished |
| **Bactrodesmiun abruptum**          | CBS 144079                      | MN699391 | MN699408 | MN699365 | MN704288 | MN704313 | This study                     |
| **B. pyriforme**                   | 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 | MN704321 | 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 | 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)
| Taxon                             | Source | GenBank accession numbers | Reference                     |
|----------------------------------|--------|---------------------------|-------------------------------|
|                                  |        | ITS          | LSU          | SSU          | rpb2          | tef1-a          |                                  |
| *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 03863 |        | —            | —            | —            | —             | —                | Boonyuen et al. (2011)         |
| *C. elegans* SS 00895            |        | —            | —            | GQ390271     | HQ446425      | HQ446311        | Boonyuen et al. (2011)         |
| *C. exiguum* SS 00809            |        | —            | —            | GQ390281     | HQ446426      | HQ446311        | Boonyuen et al. (2011)         |
| *C. granadoidia* BCC 20507T      |        | GQ390267     | HQ446420    | —            | —             | HQ446309        | Boonyuen et al. (2011)         |
| *C. pulchrum* SS 03982           |        | GQ390277     | HQ446431    | —            | —             | HQ446319        | Boonyuen et al. (2011)         |
| *Conioscypha hoehnelii* FMR 11592T |        | KY853437     | KY853497    | HF373438     | —             | —                | Hernández-Restrepo et al. (2017) |
| *C. japonica* CBS 335.93T        |        | —            | —            | JQ437465     | —             | —                | Rěblová & Seifert 2004, Rěblová et al. (2012) |
| *C. varia* CBS 113653            |        | —            | —            | JQ429281     | —             | —                | Rěblová & Seifert 2004, Rěblová et al. (2012) |
| *Cylindroconidiis aquaticus* MFLUCC 11-0294T | | MH236576 | MH236579 | — | — | — | Yu et al. (2018) |
| *Dematosporium aquaticum* CBS 144793 | | MN699402 | MN699433 | MN699385 | MN704307 | MN704330 | This study |
| *D. aquaticum* MFLU 18-1641      |        | —            | MK385855    | MN194020     | MN200286      | —                | Luo et al. (2019)              |
| *Eupenicillium javanicum* AFTOL-ID 429 | | — | EF413621 | EF413620 | EF413622 | — | Geiser et al. (2007) |
| *Fuscospora palustris* MFLUCC 16-0570T | | MG388217 | KX505090 | KX567872 | — | — | Yang et al. (2016) |
| *Fusichalara minuta* CBS 709.88 |        | —            | —            | JQ484512     | JQ492690      | —                | Rěblová et al. (2016b)         |
| *Gamsomyces longisporus* CBS 118.86 | | MT020865 | MT020877 | MT026565 | MT023101 | — | This study |
| *G. simicola* CBS 135.83T        |        | —            | —            | JQ437439     | JQ429260      | —                | Rěblová & Seifert 2004, Rěblová et al. (2012) |
| *G. stiboides* CBS 146494        |        | —            | —            | JQ429261     | —             | —                | Rěblová & Seifert 2004, Rěblová et al. (2012) |
| *Helicocoscodia axinaria* DAOMC 241947 | | JQ429145 | JQ429230 | — | — | — | Rěblová et al. (2012) |
| *H. farinosa* ILLS 53605T        |        | —            | —            | JQ49189      | —             | —                | Campbell & Shearer (2004)      |
| *H. lacusnitra* CBS 14563T, MUCL 56486T | | MN699399 | MN699430 | MN699382 | MN704304 | MN704329 | This study |
| *H. lacusnitra* CBS 145964       |        | MN699400     | MN699431    | MN699383     | MN704305      | —                | This study                     |
| *H. lacusnitra* CBS 146144       |        | MN699401     | MN699432    | MN699384     | MN704306      | —                | This study                     |
| *Melanotrigonum ovale* CBS 138743T | | KT278724 | KT278709 | KT278696 | KT278745 | — | Rěblová et al. (2016a) |
| *M. ovale* CBS 138815            |        | KT278722     | KT278711    | KT278698     | KT278747      | —                | Rěblová et al. (2016a)         |
| *Monotosporella setosa* HKUCC 3713 | | — | AF132334 | — | — | — | Rangho et al. (1999) |
| *Mucispora obscuriseptata* MFLUCC 15-0618T | | MG388218 | KX505892 | KX505897 | — | — | Yang et al. (2016) |
| *Neoascotaiwania fusiformis* MFLUCC 15-0621T | | MG388215 | KX505893 | — | KX576871 | — | Yang et al. (2016) |
| Taxon                      | Source                  | GenBank accession numbers | Reference                                         |
|---------------------------|-------------------------|---------------------------|---------------------------------------------------|
|                           |                         | **ITS**                   | **LSU**               | **SSU**               | **rpb2**               | **tef1-a**               |
| **N. fusiformis**         | MFLUCC 15-0625          | MG388216                  | XX50894              | XX50898              | —                      | —                      |
| **N. limnetica**          | CBS 126576              | KY853452                  | KY853513             | KT278689             | MN704308              | MN704331               |
|                           |                         | —                         | —                    | —                    | —                      | —                      |
| **N. limnetica**          | CBS 126792              | KY853453                  | KY853514             | KT278690             | MN704309              | MN704332               |
|                           |                         | —                         | —                    | —                    | —                      | —                      |
| **N. terrestris**         | CBS 144402              | MN699405                  | MN699434             | MN699386             | MN704310              | MN704333               |
|                           |                         | —                         | —                    | —                    | —                      | —                      |
| **Parafuscospora moniliformis** | MFLUCC 15-0628T         | MG388219                  | XX50895              | XX50899              | —                      | —                      |
| **Phaeoisaria aquatica**  | MFLUCC 16-1298T         | MF399237                  | MF398254             | —                    | MF401406              | —                      |
| **P. clematidis**         | DAOMC 226789            | JQ429155                  | JQ429231             | JQ429243             | JQ429262              | —                      |
| **P. fasciculata**        | CBS 127885T             | KT278719                  | KT278705             | KT278693             | KT278741              | —                      |
| **P. pseudoclematidis**   | MFLUCC 11-0393T         | KP744457                  | KP744501             | KP753962             | —                      | —                      |
| **Phragmocephala stemphylioides** | DAOM 673211           | KT278730                  | KT278717             | —                    | —                      | —                      |
| **Plagiascoma frondosum** | CBS 139031T             | —                         | KT278713             | KT278701             | KT278749              | —                      |
| **Pleurothecia aquatica** | MFLUCC 17-0464T         | MF399236                  | MF398253             | MF399220             | MF401405              | —                      |
| **P. centenaria**         | DAOMC 229631T           | JQ429151                  | JQ429234             | JQ429246             | JQ429265              | —                      |
| **P. erumpens**           | CBS 142291T             | KY853454                  | KY853515             | KY853547             | —                      | —                      |
| **P. fusiformis**         | MFLUCC 17-0113T         | MF399233                  | MF398250             | MF398218             | MF401403              | —                      |
| **P. guttulata**          | KUMCC 15-0296T          | MF399240                  | MF399257             | MF399223             | MF401409              | —                      |
| **P. krabii**             | MFLUCC 16-0852T         | MG837018                  | MG837013             | MG837023             | —                      | —                      |
| **P. lunata**             | MFLUCC 17-0111T         | MF399238                  | MF399255             | MF399221             | MF401407              | —                      |
| **P. rivulata**           | CBS 125238T             | JQ429160                  | JQ429232             | JQ429244             | JQ429263              | —                      |
| **P. saprophytica**       | MFLUCC 16-1251T         | MF399241                  | MF399258             | MF399224             | MF401410              | —                      |
| **P. submersa**           | MFLUCC 17-1709T         | MF399243                  | MF399260             | MF399226             | MF401412              | —                      |
| **P. tropica**            | MFLUCC 16-0867T         | MG837020                  | MG837015             | MG837025             | —                      | —                      |
| **P. uniseptata**         | DAOMC 673210T           | KT278729                  | KT278716             | —                    | —                      | —                      |
| **P. aquaticum**          | MFLUCC 17-1331T         | MF399245                  | MF399263             | —                    | —                      | —                      |
| **P. floriforme**         | MFLUCC 15-1163T         | KY697281                  | KY697277             | KY697279             | —                      | —                      |
| **P. pulneyense**         | MFLUCC 16-1293T         | —                         | MF398262             | MF398228             | MF401414              | —                      |
| **P. recurvatum**         | CBS 101581              | JQ429148                  | AF261070             | JQ429248             | JQ429266              | —                      |

(continued on next page)
| Taxon                        | Source                  | GenBank accession numbers | Reference                        |
|-----------------------------|-------------------------|---------------------------|-----------------------------------|
|                            |                         | ITS | LSU | SSU | rpb2 | tef1-a       |                                   |
| *P. semifecundum*           | CBS 131271T             | JQ429159 | JQ429240 | JQ429254 | JQ429270 | —            | Reblova et al. (2012)            |
| *Pseudosclerococcum golindoi*| CBS 143732T             | MK759885 | MK759890 | MK759887 | —        | —            | Olariaga et al. (2019)           |
| *Rhopalophora clavispora*   | CBS 129.74              | KX537751 | KX537755 | —      | KX537767 | —            | Reblova et al. (2016b)           |
| *R. clavispora*             | CBS 281.75              | KX537752 | KX537756 | KX537771 | KX537768 | —            | Reblova et al. (2016b)           |
| *R. clavispora*             | CBS 637.73T             | KX537753 | KX537757 | KX537772 | KX537769 | —            | Reblova 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 | HQ446338     | 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. uniseptata*             | NTOU 4002T              | —      | KC692153 | KC692152 | KC692154 | —            | Pang et al. (2014)               |
| *Stenigmatobotrys macrocarpa*| PRM 915682, CBS 113468  | JQ429153 | GU017317 | JQ429255 | JQ429271 | —            | Reblova et al. (2012)            |
| *S. rudis*                  | DAO MC 229638           | JQ429152 | JQ429241 | JQ429256 | JQ429272 | —            | Reblova et al. (2012)            |
| *S. viridiflavus*           | FMR 11937               | —      | HF677178 | —      | —        | —            | Hernández-Restrepo et al. (2017) |
| *Tolypocladium capitatum*   | OSC 71233               | —      | AY489721 | AY489689 | DSQ22421 | AY489615     | Castlebury et al. (2004), Spatafora et al. (2007) |
| *T. japonicum*              | OSC 110991              | —      | DG518761 | DG522547 | DG522428 | DG522330     | 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 4511J             | 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.
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, 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

**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
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. 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. Conidium 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.
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 1000 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 1000 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.

**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–Q.** 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** 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.**
RESULTS

Phylogenetic analyses

Phylogenetic relationships of *B. abruptum*, *B. diversum*, *B. leptopus*, *B. obovatum*, *B. pallidum* and *B. spilomeum*, and three undescribed species of *Ascotaia wania*, *Helioascusotaia wania* and *Pleurothecia wia* were resolved by conducting two analyses of the combined ITS, LSU, SSU, rpb2 and tef1-α sequences with homologous sequences of representatives of four orders (*Coniosphycyales*, *Fuscosporales*, *Pleurotheciales* and *Savorcellales*) of the *Hypocreomycetidae*. In total, 86 isolates were studied and divided into two subsets. Evolutionary relationships of *B. longisporum* and *B. stiltoides* 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 *Tnichoma conopha* (Euridiales), *Tolypodium capitatum* and *T. japonicum* (Hypocreales), *Botrytonia fackeliana* and *Sclerotinia sclerotiorum* (Sclerotiniaceae) and the new species of *Helioascusotaia wania* and *Pleurothecia wia* and *Melanotrigram 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 (*Savorcellales*), 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 consistently 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 *Coniosphycyales* (100% ML BS/1.0 BI PP), *Fuscosporales* (100/1.0), *Pleurotheciales* (91/1.0) and *Savorcellales* (100/1.0). In the ML analysis, *Ascotaia wania* is shown monophyletic, but the clade is statistically unsupported; *Bactrodesmium* and *Neascootaia wania* are inferred as strongly supported monophyletic genera. In the BI, the *Ascotaia wania* 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. sawadiae* is a sister clade to the remaining genera of the *Savorcellales*. The unknown *Heliococcusotaia wania* is positioned as a sister to *H. farinosa* in a strongly supported clade (100/1.0), and the unknown *Pleurothecia wia* is nested in the *Pleurothecia lineae* (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 *Savorcellales* 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 *Ascootaia wania* 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 *Neascootaia wania* (100/1.0) with three species, are resolved as monophyletic, well-supported clades. *Ascootaia wania* fusiformis is nested within *Neascootaia wania*, and a new combination is proposed in the latter genus. The remaining *Ascootaia wania* form a statistically unsupported clade. The unknown *Ascootaia wania* with a monodictys-like asexual morph is closely related to *A. lignicola*. *Dematiosporium* is positioned in the *Savorcellales*, unrelated to *Ascootaia wania* with a monodictys-like asexual morphs; it resides on a single branch as a sister taxon to the strongly supported *Canalisporium* and *Savorcella* clade (100/1.0). The tree topologies of the *Savorcellales* 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 *Ascootaia wania* 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 gabyrin* is resolved in an *incertae sedis* lineage as a sister taxon to *Aquapotomum pinicola* ATCC MYA-4213 and *Unigulciara unigulciula* NK 322.

In the fourth analysis of the combined ITS-LSU-SSU-rpb2 sequences, we assessed relationships of *B. longisporum* and *B. stiltoides* 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 *Pseudosclerococcus golinio*). The ML tree is shown in Fig. 4. The *Sclerococcales* encompass four genera, namely *Cylindoconidiis*, *Pseudosclerococcus*, *Rhopalopora*, *Sclerococcus*, 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. stiltoides* 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, mononematous to semi-macronematous, simple or sparsely or penicillately branched, sometimes moniloid 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, monon- or polyplastic, rarely sympodially elongating, hyaline to subhy- aline, conidial secession rheolytic. 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 con- spicuous 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, 1983, 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 monophylet in the Savoryellas in the combined five-genus 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 conidiogenous cells and euseptate vs distoseptate conidia following the evidence provided by DNA sequence data (Koukol & Kolárová 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 rheolytic, 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 blastic or polyblastic, usually in a chain to form monilioid secession patterns (Fig. 5). The conidial secession of some species is referred to as rhexolytic, exhibiting multiple secession patterns (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 & Kuthubuthen 1989), Cancelli- dium 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. pitioideum
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. oblignum

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

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 penicillate 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. ramosus

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: obvoid to pyriform, light brown, (14–) 17–26 μm wide or subglobose to lacrymose, 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 obvoid, 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 obvoid, 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, obvoid to subglobose, brown.........................B. novageronense

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

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

20b. Conidia 10.5–15 × 5.5–7.5 μm, ellipsoidal to obvoid, brown..................B. escheri

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. ellipsiodeum

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, obvoid 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 obvoid, 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
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.
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, pellucida, 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.

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 = 1000 μm, H = 200 μm, N = 1 cm.
Conidiogenous cells terminal, integrated, monoblastic, 3–5.5 μm wide, oblong to short-cylindrical, often broadening towards the apex, hyaline, thin-walled. Conidia (36.5–42.5–65.5–70) × (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 moniloid. Conidiomata sporodochial-like, usually developed as clusters of fasciculate conidiophores. Conidiophores macroconidial, semi-macroconidial, mostly simple or sparsely branched, or macroconidial often reduced to conidiogenous cells, hyaline, arising from aerial or submerged hyphae. Conidiogenous cells terminal, intercalary, integrated, monoblastic, 3–5 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, Betulae nigra tawa, Fraxinus excelsior, Quercus sp., Robinia pseudoacacia 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 J.F. 18064 (PRA-00016128, culture CBS 145966). England, Bodewyddan, on decaying wood, Mar. 1864, Bloxam (holotype IMI 6833); ibid., St. Catrines, Barheaton, Apr. 1867, C.E. Broome, in Rabenhorst, Fungi europaei Exs. No. 1163 (IMI 6833). 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 obovate, 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.: 13–16 mm, B. o.: 13–14 mm). The appearance of the darker

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, Bodewyddan, on decaying wood, Mar. 1864, Bloxam (holotype IMI 6833); ibid., St. Catrines, Barheaton, Apr. 1867, C.E. Broome, in Rabenhorst, Fungi europaei Exs. No. 1163 (IMI 6833).
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,
polyblastic, 3–4.5 μm wide, oblong to cylindrical, often broadening towards the apex, thin-walled. Conidia (27–30–48(–52.5) × (14–20.5) 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

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.
ag, 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 subglobeose 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 fimbritate, 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 Malle 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 CBS 142450); Fraxinus excelsior, 19 Jun. 2017, J. Fournier J.F. 17037, MBT390478 (epitype designated here, PRA-00016137, culture CBS 142451); Alnus glutinosa, 18 Jul. 2017, N. Mar-IGNY 17042, MBT390480 (epitype designated here, PRA-00016138, culture CBS 142452).
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.
Bactrodesmium and its Allies

Specimens 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. Riebövá M.R. 3933 (PRA-00016190, 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 sporodochial-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 × 15–18 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 micromematous 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 145530; 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 sylvestria, 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. Riebövá M.R. 3938 (PRA-00016145, culture CBS 144407). France, Ariège, Rimont, La Maile brook, 550 m a.s.l., on submerged wood of Corylus avellana, 19 Jun. 2017, J. Fournier J.F. 17031 (PRA-00016143, culture CBS 144407); 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-00016144, culture CBS 144408); ibid., on submerged wood, 14 Mar. 2018 (incubated in moist chamber until 7 Apr. 2018), J. Fournier J.F. 18006A (PRA-00016145, culture CBS 145530).

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

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.
B. arnaudi 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, punc-tiform, 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) × 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, subcyllindrical 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, floc-cose 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, floc-cose, 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, 16 Nov. 2017, J. Fourrier J.F. 17030 (PRA-00016148); ibid., Las Muros, Peyrua brook, 400 m a.s.l., on submerged wood of Fraxinus excelsior, 15 Sep. 2016, J. Fourrier J.F. 16057 (PRA-00016146, culture CBS 142449); ibid., on submerged wood of Robinia pseudoacacia, 17 Jun. 2017, J. Fourrier 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) 7 United Kingdom, England, Yorkshire, Kingtonhe Woods, on bark of Fraxinus excelsior, Nov. 1945, E.W. Mason & S.J. Hughes (holotype of B. pallidum IMI 1555b).

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 pseudoacacia 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 ellipsioideum 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. ellipsioideum differs from it by shorter (30–42 μm), ellipsoidal conidia which are illustrated as somehow narrowed at the apex. Bactrodesmium diversum, B. ellipsioideum, 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. Co-nidiophores 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 = 32 ± 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 subhyaline. Conidia secede rhexolytically. Conidiogenous cell monoblastic, 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 (6-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.

**Description on OA:** Vegetative hyphae hyaline 2–3.5 μm, sometimes monilioid 5–9.5 μm wide. Colonies effuse, conidiodoma not observed. *Conidiophores* semi-macronematous, sometimes sparsely fasciculate, or micronematous, hyaline, occasionally monilioid and formed by inflated cells. *Conidiogenous cells* terminal, integrated, rarely intercalary, monoclonial, 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 (6-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. Colonies effuse with sporodochium-like clusters in vitro. *Conidiophores* semi-macronematous or micronematous, loosely fasciculate, branched, sometimes swollen, hyaline. *Conidiogenous cell* monoclonial, integrated, terminal. *Conidia* dry, solitary, ellipsoidal to obvoid, distoseptate with transverse and oblique septa, pigmented, basal cell hyaline to pale brown. Conidia secede rhexolytically. **Sexual morph:** unknown.

**Specimens examined:** *France*, Ariege, Rimont, Las Muros, Peyrrou 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 europæi 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**

*Anaphodesmium* 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:** *Anaphodesmium gabretae* (Koukol & Kolárová) 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* monoclonial, integrated, terminal. *Conidia* dry, solitary, ellipsoidal to obvoid, distoseptate with transverse and oblique septa, pigmented, basal cell hyaline to pale brown. Conidia secede rhexolytically. **Sexual morph:** unknown.

*Anaphodesmium gabretae* (Koukol & Kolárová) Réblová & Hern.-Restr., comb. nov. MycoBank MB832923

**Basionym:** Bactrodesmium gabretae Koukol & Kolárová, Nova Hedwigia 91: 244. 2010.

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

**Habitat and distribution:** *Anaphodesmium 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 & Kolárová 2010).

**Notes:** Given the morphology of sporodochia, fasciculate conidiophores, monoblastic conidiogenous cells and pigmented, distoseptate and dicystoseptate 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 & Kolárová 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. *Aqualpoterium pinicola* (strain ATCC MYA-4213, Raja et al. 2008) and...
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.

*Aphoticaniwania* Sivan. & H.S. Chang, Mycol. Res. 96: 481. 1992. **Type species**: *Aphoticaniwania 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 1989) and characterised by non-stromatic ascomata with a lateral neck lying horizontally or obliquely on the host, transversely septate ascii 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 Rélová 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), Neaoascotaiwania (Herández-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. wula) conform to the sexual diagnostic morphological traits of Ascotaiwania and only two of them, A. latericolla and A. lignicola, produce dictyosporia. 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; conidigenous 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, monodictyspora-like asexual morph..................................A. mitriformis
5b. Ascospores 62 μm or shorter........................................6
6a. Ascospores 14 μm or wider, 53–62 × 14–16 μm...A. wula
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–)3–5–7-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. licaule
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, ascis shorter than 150 μm........A. pennisetorum

Ascotaiwania latericolla Rélová, 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. Rélová 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: Ascocoma perithecial, non-stromatic, solitary to aggregated, immersed to semi-immersed becoming erumpent, black, flask-shaped, glabrous with sparse 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 peripheras. 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. Asc 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 (25.4–)25.5–32.5(−35) × 7.5–8.5(−9) μm (mean ± SD = 29 ± 2.5 × 8 ± 0.4 μm), fusiform, inulegitudinal, 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 sepathe hyphae ca. 1.5–2.5 μm wide. Conidiophores micromenatus, reduced to undifferentiated hyphal branches; conidial secession probably schizolytic. Conidigenous 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
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, slightly convex centrally, 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, ascii, ascocarps 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 ascocarps on the host likely represents the asexual morph of A. latericolla. Conidigenous cells were not preserved on the natural substrate. Ascotaiwania lignicola differs from the present species by larger (42–55 x 8–13 μm) 7-septate ascospores, and larger (234–290 x 13–19 μm) ascii and (29.5–42.75 x 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 x 12.3–13.4 μm) ascii and a trichoderm-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 micromonotomous, reduced to undifferenitated hyphal branches; conidial succession 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 conidigenous 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 blastid conidigenesis, when conidia are born in cyathiform to doliiform blastid conidigenous 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, conidigenous cells and conidiophores, however, such morphology is rather non-descriptive; 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 micromonotomous, reduced to undifferenitated 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) x (18–)19.5–26–(30) μm (mean ± SD = 26.2 ± 2.5 x 23.1 ± 2.7 μm), sometimes obpyriform, 33.5–38 × (18–)19–25(–29.5) μm (mean ± SD = 35.6 ± 2.1 x 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-monoclonatous or micromonotomous, often reduced to undifferenitated hyphal branches. Conidiogenous cells terminal, integrated, monoblastic, either indistinguishable from other cells, hyaline, oblong to subcylindrical or pale brown and lageniform, 9–9.5 x 4 μm. Conidia dry, terminal, intercalary, subcylindrical to ellipsoidal, 18–25 x 15–20.5 μm (mean ± SD = 20.8 ± 2.8 x 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 x 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, Peyrou 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-
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. *Dematiaceum aquaticum* can also be compared to the monodictys-like asexual morphs of two *Ascostaia*; *A. lignicola* differs by larger (29.5–42.75 × 17.25–44.5 μm), dark reddish-brown dictyoconidia (*Chang 2001*), while *A. latericolla*...
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. & Rébelová, 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. & Rébelová

**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.

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**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.
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 (*Eurolotremycetes*), 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 sporodochial 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 sporodochial 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: Conidiomata sporodochial or synnematus, scattered, superficial, dark brown, synnemata 74–305 μm long and 18.5–35 μm wide. Conidiophores macronematous, fasciculate, unbranched or branch, subhyaline or pale brown, septate. Conidiogenous cells terminal, integrated, monoblastic, 4.5–13 × 2–4 μm, subcylinindrical, 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 5–7.5 diam, (6–)14–25-septate, smooth, pale brown to brownish 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.

**Habitat and distribution**: *Gamsomyces longisporus* occurs on decaying wood, timber and bamboo stems; it has been collected so far on *Ainus* sp., *Beilschmiedia tarai*, *Olea 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. 2019).

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. longisporus* conspecific with morphologically similar but synnematus *B. stilboideus* 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 synnematus 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, culture CBS 240.89).

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 synnematus 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
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.

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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.
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 rheolytic secession (Matsushima 1993).

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

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

*Description on the natural substrate: Asexual morph: Conidiomata synnematous, scattered, superficial, 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, 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 capitellate 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 *Calytrix plumero*.*. 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 *Calytrix plumero* 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 (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) Rébélová, Hern.-Restr. & J. Fourn.

**Notes:** *Helicoascotaiwania* is a member of the *Pleurotheciales* and accommodates saprobic freshwater species morphologically reminiscent of *Ascostaiwania* (*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-amylid ring in the ascal apex, early deliquescent paraphyses, transversely septate ascospores with middle cells brown and end cells hyaline to subhyaline and a helicosporous asexual morph, which has
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*

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**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:* Asco*taiwania 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.

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*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-00018153, N CBS 145963. Bars: A = 500 μm, B–D = 250 μm, E–M = 20 μm, N = 1 cm.
**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 Ascotaia w Hughesii ILLS 53605).

**Notes**: Asotaia w Hughesii was experimentally linked with the Helicocon fariniosum 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 Réblóvá et al. (2012). The species was positioned in the well-resolved Pleurothecium clade, unrelated to the Savoryellales, where other Ascotaia species resided (Boonyuen et al. 2011). Later, the order Pleurotheciales was introduced for this robust clade containing *He. Hughesii* and its relatives (Réblóvá et al. 2016a). At that time, the generic placement of Helicocon 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. lutoeurobellula (Orbiliomycetes). However, its ITS1-5.8S sequence (UT72605, Pfister 1997) shows 99% similarity with the ITS sequences of numerous strains of Saraciadium kilense 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).

Dayarathe et al. (2019) proposed the generic name Helicoascotaia w Hughesii typified by *A. Hughesii*. However, the correct epithet for the type species of Helicoascotaia 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. lacostris*.

**Helicoascotaia w Hughesii** Réblóvá & J. Fourn., sp. nov. MycoBank MB832930. Fig. 19.

**Typification**: France, Haute-Garonne, Carbone, SW of route du Laçon, 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, chitinous, 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, versicolor, 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 sepioid or 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 PDA 12–14 mm after 4 wk, circular, flat, margin undulate to fimbriate, mucoid, smooth centrally, pale sepioid-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., Carbone, SW of route du Laçon, artificial lake in a
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 ascii, 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 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 ascii 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 (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 sporochial 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 uvifera* 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 *telf-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 *Massartinae* 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 uvifera* 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.

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

**Type species:** *Neoscataiwania 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 *Neoscataiwania* 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. *Neoscataiwania* 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 *Neoscataiwania***

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

2a. Conidia (3–)5–6-septate, (30–)33–41 × 15–17.5 μm... *N. limnetica*
2b. Conidia (2–)3–4(–5)-septate, 25.5–44.5 × 13–22 μm

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
**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 subbaccate..........................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-subcylindrical..........................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 subcylindrical...........................................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 obvoid...........................................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 subbaccate...........................................P. fusiformis

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

**Typification:** France, Anière, 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 ascocoma that become gradually erumpent.

**Description on the natural substrate:** Sexual morph: Ascomata perithelial, 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 prismatic a, inner layer of light brown, thin-walled elongated cells with 0.5–1 μm thick wall of textura prismatic, inwardly becoming subhyaline. Paraphyses abundant, septate, hyaline, thin-walled, 3.5–4.5(–6) μm wide, tapering apically to ca. 2 μm, longer than the asc. Asc (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, unilunate, 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 funiculate 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: Pleurothecia erumpens occurs on submerged decaying wood of various deciduous or coniferous trees such as Abies alba, Alnus glutinosa, Alnus incana, Fraxinus excisior, 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 1400 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 Pujo brook along D 119 road, 400 m a.s.l., on submerged wood of a branch of Fraxinus excisior; 31 Jul. 2009, J. Fournier J.F. 09220 (PRA-00016164); ibid., Illier, Laramade, Vicedessos 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., Montsegur, 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., Ortu, Jasse de Justuniac, Onègle stream, 1200 m a.s.l., on submerged wood of a branch of Fraxinus excisior; 29 Sep. 2015, J. Fournier J.F. 15133 (PRA-00016169); ibid., Rimont, Combolongue, Le Baup brook along D 18b road, 480 m a.s.l., on submerged wood of a branch of Fraxinus excisior; 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 Cagatelle, small stream, 1150 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 excisior, 29 May 2009, J. Fournier J.F. 09130 (PRA-00016162); ibid., Puy-de-Dôme, St Alyre d’Arliac, 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 Pralongnan stream, Pont de Pierra, 1207 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, Carbonea, 1400 m a.s.l., on submerged wood of a branch of Abies alba, 31 Aug. 2009, J. Fournier J.F. 17034 (PRA-00016171).

Notes: Pleurothecia rivularia (Réblóvá 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) \times (5–)5.5–6(-6.5) \text{μm}

ascospores and narrower (9–9.5 μm) asci. Pleurothecia 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-oblung 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.

Pleurothecia 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 Bactrodesmi um 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 exist 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.

Bactrodesmi ella 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 conidigenous cells. Based on these diagnostic characters, Ellis (1959) introduced a new genus Bactrodesmi ella 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
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 conidio- 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 synnematous hyphomycete currently placed in the Pleosporales (Su et al. 2015, Hernández-Restrepo et al. 2017) and Pleurotheciales (Réblóvá 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 Parasporaria 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. 20: 19. 1959.

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

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 current name type | Current name type | Current ordinal position | Reference |
|------------------------|--------------------------------------------------|-------------------|-------------------------|-----------|
| Bactrodesmium gabretae  | S needles of Picea abies                          | Aphanodesmium gabretae | Helotiales              | Koukol & Kolářová (2010), This study |
| B. caulincola var. caulincola | E herbageous stem of the Apiaceae                        | Clasterosporium caulincola | Magnaporthales               | Saccardo (1886) |
| B. caulincola var. pellucidum | E herbageous stem                                          | Camposporium pellucidum | Pleosporales              | Hughes (1951) |
| B. coryphae            | E/S fallen leaves of Coccoloba uvifera               | B. coryphae                                       | Unknown                  | Sydow & Sydow (1920) |
| B. clavulatum          | E bark of Eucalyptus sp.                             | Polychema clavulatum                              | Pleosporales             | Ellis (1976) |
| B. fasciculare         | E wood of Betula alba                                 | Pleotrichochlamium 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 Achnosp. sp.                           | Gamsomyces longisporus                            | Sclerococcales           | This study |
| B. masonii             | S cupule of Fagus sylvatica                          | Bactrodesmiella masonii                           | Unknown                  | Ellis (1959) |
| B. mastigophorum       | E living leaves of Parasporaria plicata              | B. mastigophorum                                   | Unknown                  | Sydow & Sydow (1920) |
| B. microleucurum       | E dead culms of Chusquea cunningii                   | B. microleucurum                                   | Unknown                  | Ellis (1965) |
| B. obliquum var. suttonii | S bark of Pseudosuga menziesii                     | Stuardella 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. stiboioides         | SYN/S fallen leaves of Calyptronoma plumeriana      | Gamsomyces stiboioides                             | Sclerococcales           | This study |

Remark: Species names given in bold are taxonomic novelties.
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 dark 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. sitchensis* in Canada (Hughes & White 1983). 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 dissopteate 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*: Bactrodesmium 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*: Bactrodesmium 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: 7. 2015.

_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.

_Stigmatina clavulata* (Cooke & Harkn.) Pound & Clem., Minn. bot. Stud. 1(Bulletin 9): 681. 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 monoblastic conidiogenous cells. Based on these morphological traits, Ellis (1976) excluded *B. clavulatum* from the genus and proposed a combination in *Polyschema*.

*Stigmatina 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* spp. 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. obvatum*, *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, Casañeda-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. obvatum*; 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, Studer 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-a*, could distinguish among all six Bactrodesmium. The *tef1-a* locus is relatively easy to amplify, which makes it slightly superior to *rpb2*, which in turn may be difficult to amplify. Thus, the *tef1-a* 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. obvatum*, *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 rheolytic 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 rheolytic. 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 rheolytic 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. moentum*, *B. nothofagi*, *B. obvatum*, *B. pithoideum*, *B. plurisepatum*, and *B. pusillum* (Palm & Stewart 1982; Hughes & White 1983a, f, g, Hughes 1984, Rêvay 1993, Cooper 2005, Markovskaja 2006). Moreover, Hughes & White (1983a) considered the basal frill in conidia of *B. obvatum* as a result of the mechanical rupture of the conidiogenous cell rather than an indication of rheolytic 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 rheolytic. 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 rheolytic 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 rheolytic. 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 Bactrodesmiastrium, Bactrodesmiella, Janetia, Listeromyces and VANAKIPA. Bactrodesmiastrium (Fuscosporidales) 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 phragmoconia. 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 dis-toseptate conidia and phialide synanamorph in vitro (Goos 1971, Ellis 1976). Vanakipa 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 rheolytic 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, Aphanosdesmium (Helotiales), Garnomyces (Sclerococcales) and Kaseiferta (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 Phragmoccephala, 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 pseudo-parenchymatous 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 Tuber- cularia 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 Dematosporium 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 Dematosporium 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 saprobones 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 brasi-
ienensis (Samuels 1980), and seven other species (M. aershanensis, M. arctica, M. austriana, M. capensis, M. castaneae, M. nigrosporum, 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 (Microscales, Sordariomycetes) (Mouzouras & Jones 1985) and several other monodictys-like fungi were reported as asexual morphs of Aquastroma magnistiolata (Pleosporales) (Tanaka et al. 2015), Ascotaiwania latericolla and A. lignicola (Savoryellales) (Chang 2001, this study), Hyaloaspora monodictys (Helotiales, Leotio-
mycetes) (Hosoya & Huhntien 2002, see also Han et al. 2014, Fehrer et al. 2019) and Tubaflia amazonesis and T. cf. paludosa (Tubafliales, Dothideomycetes) (Samuels et al. 1978). A phialidic synana-
morph was reported for M. levii (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 polyphylectic 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, Dematosporium, Neo-
ascotaiwania 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 syn-
onymy with Ascotaiwania and accepted Bactrodesmium (based on B. pallidum) in the latter genus by analysing the combined LSU-SSU-rpb2-tef1-a data. However, the nested position of a single species of Bactrodesmium in the Ascotaiwania clade clearly 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 trichochlamid-like asexual morphs with phragmoconidia, i.e. A. asilio (Chang 2001), A. nitroformis (Ranghoo & Hyde 1998), A. sawadae (Sivichai et al. 1998), and A. uniseptata (Rébelová 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. nitroformis), 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 (Ascotai-
wania, Dematosporium, Neoascotaiwania and Savoryella) are generic diagnostic characters.

Pleurotheciella endamps 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 holo-
blastic denticulate conidiogenous cells seceding schizolytically, non-stromatic dark brown ascomata, cylindrical-clavate ascii with a distinct apical annulus and hyaline, ellipsoid 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 con-
idogenous cells (Rébelová et al. 2012), species subsequently added to the genus were confirmed to produce macronematous, brown or hyaline conidiophores on the natural substrate (Rébelová et al. 2016a, Luo et al. 2018).

Helicoascotaiwania, typified by H. farinosa, was segregated from Ascotaiwania (Savoryellales) by coiled conidia of the Heli-
cocin-type and DNA sequence data (Campbell & Shearer 2004, Boonyuen et al. 2011, Rébelová 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 distin-
guished from other genera of the order by versicolorous, septate ascospores, and ascii with a prominent ascal plug obscuring the apical ring. Our new species H. lacustris is the first member of the genus reported from Europe.

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