Newly recognised lineages of perithecial ascomycetes: the new orders Conioscyphales and Pleurotheciales

M. Réblová¹, K.A. Seifert², J. Fournier³, V. Štěpánek⁴

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multigene analysis
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Abstract  Phylogenetic analyses of DNA sequences from nuclear ribosomal and protein-coding loci support the placement of several perithelial ascomycetes and dematiaceous hyphomycetes from freshwater and terrestrial environments in two monophyletic clades closely related to the Savoryellales. One clade formed by five species of Conioscypha and a second clade containing several genera of uncertain taxonomic status centred on Pleurothecium, represent two distinct taxonomic groups at the ordinal systematic rank. They are proposed as new orders, the Conioscyphales and Pleurotheciales. Several taxonomic novelties are introduced in the Pleurotheciales, i.e. two new genera (Adelosphaeria and Melanotrigonum), three novel species (A. catenata, M. ovale, Phaeoisaria fasiculata) and a new combination (Pleurothecilla uniseptata). A new combination is proposed for Savoryella limnetica in Ascothecania s.str. based on molecular data and culture characters. A strongly supported lineage containing a new genus Plagiascoma, species of Bactrodeosmium and Ascothecania personii, was identified as a sister to the Conioscyphales/Pleurotheciales/Savoryellales clade in our multilocus phylogeny. Together, they are nested in a monophly in the Hypocreomycetidae, significantly supported by Bayesian inference and Maximum Likelihood analyses. Members of this clade share a few morphological characters, such as the absence of stromatic tissue or clypeus, similar anatomies of the 2-layered ascomatal walls, thin-walled uniloculate asci with a distinct, non-amyloid apical annulus, symmetrical, transversely septate ascospores and holoblastic conidiogenesis. They represent the only fungi in the Hypocreomycetidae with apically free, filiform to cylindrical, persistent or partially disintegrating paraphyses. The systematic placement of two other dematiaceous hyphomycetes was resolved based on DNA sequences; Phragmocephala stemphylioides is a member of the Pleurotheciales and Triadelphia uniseptata is within the Savoryellales.

INTRODUCTION

The subclass Hypocreomycetidae (Sordariomycetes) includes non-lichenised ascomycetes with perithelial and cleistothecial ascomata. Many species are parasitic on plants, insects and other fungi. Some are endophytes in plants or saprobes on decaying wood and herbs, and some involved in associative mutualism with wood-boring beetles. Based on DNA sequences from nuclear ribosomal and protein-coding loci, the Hypocreomycetidae was recognised as a strongly supported monophyletic clade encompassing five orders (Spatafora et al. 2007, Zhang et al. 2007), i.e. the Coronophorales, Halosphaeriales, Hypocreales, Melanosporales, Microascales, and one family not then placed in an order, the Glomerellaceae. The absence of paraphyses was used to delimit this subclass (Zhang et al. 2007). In the more recent classification, the Hypocreomycetidae comprises eight orders, i.e. the Coronophorales, Falcocladiales, Glomerellales including the Plectosphaerellaceae (Zare et al. 2007, Réblová et al. 2011), Hypocreales, Melanosporales, a revised Microascales (De Beer et al. 2013), Savoryellales (Boonyuen et al. 2011) and Torpedosporales (Schoch et al. 2007, Jones et al. 2014, 2015). Hamathelial elements in the Hypocreomycetidae comprise several types, i.e. apical, centripetal and lateral paraphyses, catenophyses, a reticulate network of filiform filaments attached at the top and bottom of the ascomatal cavity; sometimes interthecal filaments are lacking. The only group characterised by paraphyses, i.e. sterile filiform, apically free filaments emerging from the hymenium among asci and growing upwards, is the Savoryellales, placed in this subclass based on a combined analysis of six nuclear loci (Boonyuen et al. 2011).

The Savoryellales comprises three genera, Ascothecania, Canalisporium and Savoryella from freshwater, brackish, marine and terrestrial habitats. They share a set of characters including non-stromatic, immersed, semi-immersed to superficial, dark, coriaceous ascomata, often lying horizontally to the host, uniloculate asci with a non-amyloid apical annulus, partly disintegrating paraphyses and fusiform to ellipsoidal, transversely septate ascospores with hyaline polar cells and brown middle cells. Asexual morphs were experimentally proven for two species of Ascothecania (as Montosporella, Ranghoo & Hyde 1998, Sivichai et al. 1998) and one species of Canalisporium (with Ascothailand sexual morph; Sri-indrasutdhi et al. 2010). The distant placement of Helicoön farinosus, the asexual morph of Ascothecania Hughesii (Fallah et al. 1999), from members of the Savoryellales was revealed by rDNA data (Boonyuen et al. 2011, Réblová et al. 2012). The asexual morphs linked to the Savoryellales are dematiaceous hyphomycetes characterised by semi-macronematous conidiophores and monoblastic conidiogenesis in the Hymenomycetidae, with the exception of Phaeoisaria which was placed in the Hypocreomycetidae by Boonyuen et al. (2011). In the cladistic analyses, the Savoryellales were placed in the Family Canaliellaceae, although their affinities with the monoblastic conidiophores of this family are not clear.
diogenous cells producing brown, thick-walled, transversely septate or cheiroid, dictyoseptate macroconidia, rare characters in the Hypocreomycetidae. Although the asexual morphs of Savoryella are unknown (Boonyuen et al. 2011), dark brown, 3–5-septate macroconidia were obtained in living cultures derived from ascospore isolates of two of our specimens of *S. limnetica* (Chang et al. 1998) collected on wood submerged in freshwater in France. Identical conidia were also observed scattered among ascomata on the host.

Previous phylogenies inferred from sequences of the small and large subunit of nuclear ribosomal DNA (nuc18S and nuc28S rDNA) and the second largest subunit of RNA polymerase II (rpb2) revealed a close relationship among members of the *Savoryellales* and several terrestrial and freshwater genera of uncertain taxonomic status forming two clades, i.e. *Conioscypha* and a clade comprising *Phaeosaria, Pleurotheciella, Pleurothecium* and *Sterigmatobotrys* (Rébllová et al. 2012). However, relationships among these genera remained largely unresolved. They are characterised by non-stromatic, semi-immersed to superficial, brown, subhyaline to pale orange perithecial ascomata, paraphyses, uniloculate asci with a non-amyloid apical annulus and ellipsoidal to fusiform, hyaline to subhyaline, septate ascospores (Fernández et al. 1999, Rébllová & Seifert 2004, 2011, Rébllová et al. 2012). Their asexual morphs are hyphomycetes with dematiaceous or hyaline conidiophores, holoblastic, sympodial conidiogenous cells and conidia that are often formed on a short rachis on denticles. The conidogenesis of *Conioscypha* is unique; brown, non-septate conidia are born in cyathiform to doliiform blastic conidiogenous cells surrounded by hyaline, cup-like collyarettes with a multinuclear plasmalemma (Shearer & Motta 1973).

Preliminary analysis of DNA sequences of nuclear ribosomal and protein-coding loci of four undescribed ascomycetes revealed their close relationship with members of the *Savoryellales* and the clade mentioned above centred around *Pleurothecium*. Three of these unidentified fungi are perithecial ascomycetes that share with members of the *Pleurothecium* clade characters of ascomata, asc, paraphyses and ascospores. Five specimens of the first undescribed fungus were found on strongly decaying wood of *Quercus cerris* in the Czech Republic. Although no conidiophores were formed on the host, cultures derived from ascospore isolates yielded identical asexual morphs with oval to oblong, filamentous, hyaline to brown, ellipsoidal to fusiform, hyaline to subhyaline, septate ascospores (Fernández et al. 1999, Rébllová & Seifert 2004, 2011, Rébllová et al. 2012). Their asexual morphs are hyphomycetes with dematiaceous or hyaline conidiophores, holoblastic, sympodial conidiogenous cells and conidia that are often formed on a short rachis on denticles. The conidogenesis of *Conioscypha* is unique; brown, non-septate conidia are born in cyathiform to doliiform blastic conidiogenous cells surrounded by hyaline, cup-like collyarettes with a multinuclear plasmalemma (Shearer & Motta 1973).

Herbarium material and fungal strains

Dry ascomata were rehydrated with water; material was examined with an Olympus SXZ12 dissecting microscope and hand-sectioned centrum material (including asc, ascospores and paraphyses) was mounted in Melzer’s reagent, Lugol, 90 % lactic acid, aqueous cotton-blue (1 mg/mL), Pelikan ink and blue or black Waterman ink. Hand sections of the ascomatal wall were studied in 3 % KOH or heated chloral-lactophenol. All measurements were made in Melzer’s reagent. Means ± standard deviation (SD) based on 20–25 measurements are given for dimensions of asc and ascospores. Images were captured by differential interference (DIC) or phase contrast (PC) microscopy using an Olympus DP70 camera operated by Imaging Software Cell on an Olympus BX51 compound microscope. Conidia and conidiogenous cells were photographed in the living state using an FEI Quanta 200 Environmental Scanning Electron Microscope (ESEM). A c. 2 x 2 mm cube of agar with mycelium was observed at 20 kV after the sample chamber achieved local thermodynamic equilibrium: chamber pressure 200 Pa, sample temperature from -15 °C to -16 °C. A Gaseous Secondary Electron Detector (GSED) was used for signal detection. Cooling of the specimen in the chamber was achieved using a PC controlled Peltier cooling stage with external water chiller (made by JT Manufacturing, USA).

Multi-ascospore and multi-conidial isolates were obtained from fresh material with the aid of a spore isolator (Meopta, Prague, Czech Republic). Ascospores and asc were spread on water agar, ascospores and conidia germinated within 48 h. Germinating ascospores were transferred and isolated were grown on water agar, CMA (Difco), potato dextrose agar (PDA, Oxoid) and potato-carrot agar (PCA, Gams et al. 1998). Colonies were examined after 7, 21 and 30 d incubated at 25 °C in the dark. Ex-type and other cultures are maintained at the CBS-KNAW Fungal Biodiversity Centre, Utrecht, The Netherlands (CBS) and Canadian Collection of Fungal Cultures, Agriculture and Agri-Food Canada, Ottawa, Canada (DAOMC). Type and other herbarium material is deposited in the Mycological Herbarium in the National Museum in Prague, Czech Republic (PRM) and Canadian National Mycological Herbarium, Ottawa, Canada (DAOM). The Online Auction Colour Chart (2004) was used as the colour standard.

DNA extraction, amplification and sequence alignment

Cultures used for DNA isolations were grown as previously described by Rébllová et al. (2011) and DNA was extracted following the protocols of Lee & Taylor (1990). Procedures for amplifying and sequencing the internal transcribed spacer rDNA (ITS rDNA), small and large subunit nuclear ribosomal DNA (nuc18S rDNA, nuc28S rDNA), second largest subunit of
RNA polymerase II (rpb2) and DNA replication licensing factor (mcm7?) were performed as described in Réblová et al. (2011, 2013). A fragment of the 5'-end of the β-tubulin gene region (exons 3 to 6) was amplified and sequenced using primers B2a/benA1and B2b (Glass & Donaldson 1996, Geiser et al. 1998). Sequences were edited using Sequencer v. 5.0 (Gene Codes Corp., Ann Arbor, MI, USA).

| Taxon                          | Source         | ex-type | GenBank accession numbers |
|-------------------------------|----------------|---------|----------------------------|
|                               |                |         | ITS | nuc28S | nuc18S | RPB2 | MCM7 | TUB2 |
| Adelosphaeria catenata        | CBS 138679     | T       | KT278721 | KT278707 | KT278692 | KT278743 | KT278733 | KT278754 |
| Ascoaitania ligicola          | NIL 00005      | –       | –        | –        | –        | –        | –        | –        |
| Ascotaiainia limnetica        | CBS 126576     | –       | –        | –        | –        | –        | –        | –        |
| Ascotaiainia mitsuriformis    | HKUC 3706      | –       | –        | –        | –        | –        | –        | –        |
| Ascotaiainia sawadiae         | SS 00051       | –       | –        | –        | –        | –        | –        | –        |
| Ascotaiainia persooni         | ASY-14C        | –       | –        | –        | –        | –        | –        | –        |
| Bactrodesmastrum obovatum     | FMR 6482       | –       | –        | –        | –        | –        | –        | –        |
| Brachysporiella setosa        | FMR 10576      | –       | –        | –        | –        | –        | –        | –        |
| Canalisporium caribense       | CBS 113653     | T       | KT278722 | KT278704 | KT278691 | KT278740 | –        | –        |
| Canalisporium elegans         | CBS 227889     | –       | –        | –        | –        | –        | –        | –        |
| Canalisporium minitinispora   | CBS 137263     | –       | –        | –        | –        | –        | –        | –        |
| Canalisporium granadoideum    | CBS 20507      | T       | KT278724 | KT278709 | KT278696 | KT278740 | –        | –        |
| Canalisporium pulchrum        | SS 03962       | –       | –        | –        | –        | –        | –        | –        |
| Canispora japonica            | CBS 387.84     | T       | KT278725 | KT278710 | KT278697 | KT278740 | –        | –        |
| Canispora ligicola            | CBS 335.93     | T       | KT278724 | KT278709 | KT278696 | KT278740 | –        | –        |
| Conioscypha minitisporella     | CBS 137263     | T       | KT278724 | KT278709 | KT278696 | KT278740 | –        | –        |
| Conioscypha pvenusia           | ILL 41202      | –       | –        | –        | –        | –        | –        | –        |
| Conioscypha varia             | CBS 113653     | T       | KT278722 | KT278704 | KT278691 | KT278740 | –        | –        |
| Flammisspora boletica          | ILL 13367     | T       | KT278722 | KT278704 | KT278691 | KT278740 | –        | –        |
| Helicocan farinosum           | DAOM 241947    | –       | –        | –        | –        | –        | –        | –        |
| ILLS 53605                    | –              | –       | –        | –        | –        | –        | –        | –        |
| Magnolithra stevemossago       | CBS 139776     | –       | –        | –        | –        | –        | –        | –        |
| Melanorotnigone ovale          | CBS 138742     | –       | –        | –        | –        | –        | –        | –        |
| Phaeosaria clematidis          | CBS 138743     | T       | KT278724 | KT278709 | KT278696 | KT278740 | –        | –        |
| Phaeosaria fasciculata         | CBS 138744     | T       | KT278724 | KT278709 | KT278696 | KT278740 | –        | –        |
| Phaeosaria sediminticola       |CBS 138815      | –       | –        | –        | –        | –        | –        | –        |
| Phaeosaria sp.                 | unknown        | –       | –        | –        | –        | –        | –        | –        |
| Phragnocephala stemphylocoides | DAOM 673211    | –       | –        | –        | –        | –        | –        | –        |
| Phlorisporium cimbiforme       | CBS 127888     | –       | –        | –        | –        | –        | –        | –        |
| Phlagaecoma frondosum          | CBS 139031     | T       | KT278729 | KT278716 | KT278712 | KT278748 | KT278758 | –        |
| Pleurothecia centenaria        | DAOM 229631    | T       | KT278729 | KT278716 | KT278712 | KT278748 | KT278758 | –        |
| Pleurothecia rivulata          | CBS 125237     | –       | –        | –        | –        | –        | –        | –        |
| Pleurothecia unisepata         | DAOM 673210    | T       | KT278729 | KT278716 | KT278712 | KT278748 | KT278758 | –        |
| Pleurothecia boveboideum       | CBS 209.95     | T       | KT278729 | KT278716 | KT278712 | KT278748 | KT278758 | –        |
| Pleurothecium recurvatum       | CBS 101581     | –       | –        | –        | –        | –        | –        | –        |
| Pleurothecium semicolumnatum   | DAOM 131482    | –       | –        | –        | –        | –        | –        | –        |
| Savyrella appendiculata        | NF 00206       | –       | –        | –        | –        | –        | –        | –        |
| Savyrella aquatica             | SS 03801       | –       | –        | –        | –        | –        | –        | –        |
| Savyrella ligicola             | NF 00204       | –       | –        | –        | –        | –        | –        | –        |
| Savyrella longispora           | SAT 0022       | –       | –        | –        | –        | –        | –        | –        |
| Savyrella paucispora           | SAT 0056       | –       | –        | –        | –        | –        | –        | –        |
| Savyrella verrucosa            | SS 00052       | –       | –        | –        | –        | –        | –        | –        |
| Sterigmatobrya macrocarpa      | PRM 951662     | –       | –        | –        | –        | –        | –        | –        |
| Sterigmatobrya unisepata       | FMR 11337      | –       | –        | –        | –        | –        | –        | –        |
| Sterigmatobrya unisepata       | DAOM 229838    | –       | –        | –        | –        | –        | –        | –        |
| Triadelphia unisepata          | DAOM 250376    | –       | –        | –        | –        | –        | –        | –        |

A fragment of the 5'-end of the β-tubulin gene region (exons 3 to 6) was amplified and sequenced using primers B2a/benA1and B2b (Glass & Donaldson 1996, Geiser et al. 1998). Sequences were edited using Sequencer v. 5.0 (Gene Codes Corp., Ann Arbor, MI, USA).

GenBank accession numbers for newly sequenced taxa and other homologous sequences of members of the Savoryellales and two new orders described in this study retrieved from GenBank are listed in Table 1. For detailed investigation of phylogenetic relationships within the Sordariomycetes, sequences of the three loci nuc28S, nuc18S and rp22 included in Réblová et al. (2015) were downloaded from GenBank and combined with those generated during the present study.

Table 1 A list of members of the Conioscyphales, Pleurotheciales, Savoryellales and other fungi, their isolate information and new sequences determined for this study and those retrieved from GenBank. Sequences with GenBank accession numbers in bold were generated for this study. Sequence nuc28S* published in Chew et al. (2010).
Sequences were manually aligned in BioEdit v. 7.1.8 (Hall 1999). Nuclear ribosomal loci were aligned according to the secondary structure of Saccharomyces cerevisiae to improve the decisions on homologous characters and introduction of gaps (Gutell 1993, Gutell et al. 1993, www.ma.ccbu.utexas.edu). These procedures and alignment of the sequences of protein-encoding genes were performed as described in Réblová & Růžičková (2013).

The single-locus datasets were examined for topological incongruence among loci (ITS: 26 sequences and 616 characters; \( \beta \)-tubulin: 11 sequences and 500 characters; nuc28S: 126 sequences and 1,947 characters; nuc18S: 104 sequences and 1,792 characters; rpb2 segments 5–7: 77 sequences and 216 characters; mcm7: eight sequences and 659 characters). The ITS and \( \beta \)-tubulin loci were generated only for members of the new order Pleurotheciales. Because only a few mcm7 sequences were generated, they were not tested for topological conflicts among clades at familial or ordinal rank in the Sordariomycetes. For each individual partition, 500 bootstrap replicates were generated with RAxML-HPC v. 7.0.3 (Stamatakis et al. 2005, Stamatakis 2006) and compared visually for topological conflict among supported clades in phylogenetic trees. A conflict between two loci was assumed to occur when a clade appeared monophyletic with bootstrap support of \( \geq 75 \% \) in one tree, but was not supported as monophyletic in another (Mason-Gamer & Kellogg 1996). Individual, conflict-free alignments were concatenated to combine sequences for two subsequent phylogenetic analyses. The multiple sequence alignments are deposited in TreeBASE (Study no. 18187).

**Phylogenetic analyses**

Phylogenetic relationships of the unidentified fungi and other ascomycetes were resolved by two combined analyses of ITS, nuc18S, nuc28S, \( \beta \)-tubulin, mcm7 and rpb2 sequences of representatives of the Sordariomycetes. We analysed the whole ITS rDNA barcode, the first 2/3 of the 5’ half of the nuc28S, the entire nuc18S, partial mcm7, exons 3–6 of \( \beta \)-tubulin and segments 5–7 of rpb2. Bases 1–155 of the nuc18S, 1–85 of the nuc28S and 1–58 of the rpb2 alignments at the 5’-end and 1470–1947 of the nuc28S alignment at the 3’-end were excluded from analysis because of incompleteness of the majority of the available sequences. The coding regions (exons) 3, 4, 5 and partly 6 of the \( \beta \)-tubulin with a total length of 291 nucleotides were analysed, non-coding regions were excluded. The combined datasets were partitioned into several subsets of nucleotide sites, i.e., ITS, nuc28S, nuc18S, and first, second and third codon positions of \( \beta \)-tubulin, mcm7 and rpb2. Two members of the Leotiomycetes, Leotia lubrica and Microglossum rufum, were used to root the two multilocus phylogenies.

The program MrModeltest2 v. 2.3 (Nylander 2008) was used to infer the appropriate substitution model that would best fit the model of DNA evolution for each sequence dataset and each partition of the combined datasets. Maximum likelihood (ML) and Bayesian inference (BI) analyses were used to estimate phylogenetic relationships. ML analysis was performed with RAxML-HPC v. 7.0.3 with a GTRCAT model of evolution. Nodal support was determined by non-parametric bootstrapping (BS) with 1,000 replicates.

Bayesian inference analysis was performed in a likelihood framework as implemented in MrBayes v. 3.0b4 to reconstruct phylogenetic trees (Huelsenbeck & Ronquist 2001). For the ITS, nuc18S, nuc28S, and rpb2 dataset, we used for each partition the GTR+G+I substitution model. For \( \beta \)-tubulin we used HKY+G, F81 and SYM+G for the first, second and third codon position, and for mcm7 we used HKY+G, GTR+G and GTR for the first, second and third codon position. Two Bayesian searches were performed using the default parameters. Analyses were run for 10 million generations, with trees sampled every 1,000 generations. Tracer v. 1.6.0. (Rambaut et al. 2013) was used to confirm convergence of trees and burn-in. The first 50,000 trees, which represented the burn-in phase of the analysis, were discarded. The remaining trees were used for calculating posterior probabilities (PP) of recovered branches (Larget & Simon 1999).

**PHYLOGENETIC RESULTS**

In the first analysis, 134 combined nuc18S, nuc28S and rpb2 sequences were assessed for 120 species in 20 orders in the Sordariomycetes: The alignment had 2,767 distinct alignment patterns (ML analysis). In the ML tree shown in Fig. 1, a strongly supported monophyletic clade was resolved (100 ML BS/1.0 PP) in the Hypocreomycetidae with three nested clades. The Savoryellales (100/1.0) was associated with the Conioscyphales clade (100/1.0) comprising eight genera and three other undescribed ascomycetes. They represent two new lineages of freshwater and terrestrial fungi and are introduced below as the orders Conioscyphales and Pleurotheciales. A strongly supported monophyletic lineage (100/1.0) containing Ascotaiawania persoonii, two species of the dematiaceous hyphomycetous genus Bactrodesmiastrum and one unidentified ascomycete is positioned as a sister to a clade containing Conioscyphales, Pleurotheciales and Savoryellales. Together they form a robust monophylum (100/1.0) in the Hypocreomycetidae, including Flammospora biotecta (BCC 13367) in a basal position.

Two undescribed perithecial fungi were nested within the Pleurotheciales and are described here as new genera, Melanotrigonum and Adelosphaeria. Two strains of Phaeoisaria sp. with fasiculate conidiophores were positioned in the strongly supported Phaeoisaria clade (100/1.0) of the Pleurotheciales as the sister taxon to Phaeoisaria sparsa. They are introduced as a new species. The third unidentified perithecial ascomycete from freshwater habitat was nested within the Bactrodesmiastrum clade on a separate branch and it is described as a new monotypic genus Plagiastoma.

Two strains of Savoryella limnetica and Triadelphia unisepitata were positioned in the Ascotaiawania clade (79/0.91) in the Savoryellales. The genus Ascotaiawania is polyphyletic in our phylogeny. Helicoön farinosum, the asexual state of A. Hughesii is grouped within the Pleurotheciales. Ascotaiawania lignicola, the type species, and three other species are members of the Savoryellales, while A. persoonii is nested in the Bactrodesmiastrum clade. Two dematiaceous hyphomycetes, Phragmoccephala stemphylioides and Dactylaria unisepitata, were grouped among members of the Pleurotheciales; the latter is transferred to Pleurotheciella below.

In the second phylogenetic analysis (Fig. 2), the combined ITS, nuc18S, nuc28S, \( \beta \)-tubulin, mcm7 and rpb2 dataset consisted of 60 sequences representing 18 species of the Pleurotheciales, five of the Conioscyphales, 15 species of the Savoryellales and four species of the Bactrodesmiastrum clade. The alignment had 2,370 distinct alignment patterns (ML analysis). The robust clade containing the three orders and the Bactrodesmiastrum clade (100/1.0) has identical topologies in the three- and six-gene phylogenies. Six terminal clades were identified in the Pleurotheciales and are labelled as Clade I to VI on Fig. 2. Clades I, V and VI are strongly supported monophyletic lineages representing genera Melanotrigonum (100/1.0), Phaeoisaria (100/1.0) and Pleurothecium s.s.t. (100/1.0). Clade II (72/0.97) is morphologically heterogeneous containing Brachysporiella setosa, Helicoön farinosum, Phragmoccephala stemphylioides
Fig. 1  Multilocus phylogenetic analysis of the nuc18S-nuc28S-rpb2 sequences of the Sordariomycetes showing majority of the recognized ordinal lineages. Phylogram was inferred from the ML analysis with RAxML using a GTRCAT model of evolution. Only high branch support is shown at the nodes, maximum likelihood bootstrap support (ML BS) ≥ 70 % and Bayesian posterior probability (PP) ≥ 0.95. Symbol ● indicates nodes with 100 % ML BS and 1.0 PP. Taxa written in bold represent taxonomic novelties.
Fig. 2  Multilocus phylogenetic analysis of the ITS-nuc18S-nuc28S-β-tubulin-rpb2-mcm7 sequences of the CPS (Conioscyphales, Pleurotheciales, Savoryellales) and Bactrodesmiatrum clades. Phylogram inferred from the ML analysis with RAxML using a GTRCAT model of evolution. Only high branch support is shown at the nodes, ML BS ≥ 70 %, PP ≥ 0.95. Taxa written in bold represent taxonomic novelties.
and Pleurothecium obovatum. Clade III (100/1.0) includes Sterigmatobotrys and Taeniolella rudis. Clade IV (92/1.0) includes the monophyletic Pleurotheciellia (100/1.0) and Adelosphaeria catenata.

**TAXONOMY**

**Conioscyphales** Réblová & Seifert, ord. nov. — MycoBank MB813226

Type family. Conioscyphaceae Réblová & Seifert.

Ascomata perithelial, non-stromatic. Ostiole periphysate. Hamathecium of paraphyses. Asci unitunicate, with a non-amyloid apical annulus. Ascospores hyaline, transversely multisepitate. Conidiophores micronematous, mononematous. Conidiogenous cells blastic, percurrently regenerating. Conidia brown, variable in shape; sessile or secession schizolytic. Saprobic on wood.

**Conioscyphaceae** Réblová & Seifert, fam. nov. — MycoBank MB813227

Type genus. Conioscypha Höhn., Ann. Mycol. 2: 58. 1904, emend. Shearer, Mycologia 65: 128. 1973.

= Conioscyphacus Réblová & Seifert, Stud. Mycol. 50: 100. 2004.

Ascomata perithelial, immersed to superficial, papillate or with elongated neck. Ascomatal wall leathery, waxy, comprising two layers. Paraphyses filiform, unbranched, longer than the asci. Asci unitunicate, persistent, 8-spored, with a pronounced non-amyloid apical annulus, cylindrical-clavate, stipitate. Ascospores fusiform to fusiform-navicular, hyaline, transversely multiseptate.

**Conioscyphales** Réblová & Seifert, Stud. Mycol. 50: 100. 2004.

= Conioscyphagus Réblová & Seifert, MycoBank MB813228

**Pleurotheciaceae** Réblová & Seifert, ord. nov. — MycoBank MB813229

Type family. Pleurotheciaceae Réblová & Seifert.

Ascomata perithelial, non-stromatic. Ostiole periphysate. Hamathecium of paraphyses. Asci unitunicate, with a non-amyloid apical ring. Ascospores hyaline or versicolor with polar cells hyaline and middle cells brown, transversely multisepitate. Conidiophores micronematous or semi-macronematous, loosely fasciculate or aggregated in indeterminate synnemata. Conidiogenous cells producing conidia holoblastically, monoblastic or with sympodial extension, conidial secession rhexolytic or schizolytic on monoblastic or solitary thallic conidiogenous cells. Conidia hyaline, sometimes with protracted maturation of the middle cells, which turn brown, or brown or versicolor, septate or non-septate.

**Adelosphaeria** Réblová, gen. nov. — MycoBank MB813230

Type species. Adelosphaeria catenata Réblová.

Etymology. Adelo- (Gk), meaning unclear, referring to the difficulty of recognizing this taxon among other morphologically similar fungi; sphaera (L) meaning globe, referring to ascoma.

Ascomata perithelial, non-stromatic, semi-immersed becoming superficial, subglobose, dark brown, papillate. Ostiole periphysate. Ascomatal wall leathery to fragile, 2-layered. Paraphyses abundant, persistent, septate. Asci unitunicate, cylindrical-clavate, stipitate, 8-spored, apex with a non-amyloid apical annulus. Ascospores ellipsoidal, slightly curved, hyaline, transversely septate. Asexual morph unknown.

**Adelosphaeria catenata** Réblová, sp. nov. — MycoBank MB813231; Fig. 3, 4

Etymology. Cateniformis (L), meaning chain-shaped, referring to the dark brown cells arranged in chains formed on vegetative hyphae in the axenic culture.

Ascomata perithelial, non-stromatic, semi-immersed, becoming superficial, solitary or in small groups; venter 200–280 µm diam, 300–360 µm high, subglobose, dark brown, glabrous, papillate, opening by a rounded pore. Ostiole periphysate. Ascomatal wall leathery to fragile, 20–30 µm thick, 2-layered; outer layer consisting of brown, polyhedral cells of textura prismatica with opaque walls, inner layer consisting of several rows of thin-walled, hyaline, flattened cells. Paraphyses abundant, persistent, septate, hyaline, sparsely branched, anastomosing, c. 3.5–5.0 µm wide, tapering to c. 2.5 µm. Asci (85–)93–105 µm long in the sporiferous part, 12.5–14.5 µm wide (mean ± SD = 199.7 ± 5.4 µm), with a stipe 20–35(–50) µm long; cylindrical-clavate, broadly rounded apically to obtuse, 8-spored, apex with a flattened, non-amyloid apical annulus 3.0–3.5 µm wide, about 2.0 µm high. Ascospores 16.5–19.5(–20) × 5.0–5.5(–5.8) µm (mean ± SD = 17.8 ± 1.3 × 5.4 ± 0.2 µm), ellipsoidal, straight or slightly curved, hyaline, smooth, 3-septate, non-constricted at the septa, arranged 1–2-seriately in the sporiferous part.

Culture characteristics — Colonies slow growing reaching 12–15 mm diam on PDA after 21 d at 25 °C. Aerial mycelium dark brown (aoc735), paler brown (aoc723) towards the margin. Mainly flat, felt, reverse brown (aoc734), with a marginal zone of dark brown (aoc734) submerged mycelium. Aerial and submerged hyphae 1.5–2.0 µm wide, smooth, subhyaline to pale brown, thin-walled, unbranched or sparsely branched. Sporulation absent. On vegetative hyphae are formed brown, globose to ellipsoidal cells 5.0–14.5 µm diam (mean ± SD = 10.3 ± 2.9 µm), with thick, often opaque walls, arranged in chains or arising laterally on another cell.

Specimen examined. CZECH REPUBLIC, Southern Bohemia, Novohradské hory Mts, Dobrá voda, Hodiná voda National nature monument, decorticated wood of a trunk of Fagus sylvatica, 4 Oct. 2012, M. Réblová M.R. 3755 (holotype PRM 933853, culture ex-type CBS 138679).
Fig. 3  *Adelosphaeria catenata*. a, b. Ascomata; c. vertical section of the ascomatal wall; d–f. asci with ascospores; g, h. apical annulus; i. paraphyses (a–i. PRM 933853 holotype); d–f, h: DIC; g, i: PC. — Scale bars: a, b = 250 µm; c = 30 µm; d–f, i = 10 µm; g, h = 5 µm.
**Notes** — *Adelosphaeria catenata* resembles species of *Pleurothecium* and *Pleurotheciella* because of its hyaline, 3-septate ascospores, cylindrical-clavate asci and brown semi-immersed ascomata. *Pleurothecium recurvatum* is easily distinguishable from *A. catenata* by its slender ascospores, pronounced apical annulus, setose ascomata and macronematous conidiophores bearing hyaline, polyblastic, denticulate conidiogenous cells elongating in a sympodial pattern and 3-septate, hyaline conidia with protracted maturation of the middle cells, which turn brown. It is more difficult to separate *Adelosphaeria* from *Pleurotheciella*, because species of both genera share similar morphological characters of ascospores, asci and ascomata. The only conspicuous difference lies in morphology of their asexual states; *Pleurotheciella* can be easily distinguished by *Dactylaria*-like, hyaline to subhyaline conidiophores and conidia.

**Melanotrigonum Réblová, gen. nov.** — MycoBank MB813232

*Type species.* Melanotrigonum ovale Réblová.

**Etymology.** *Melas*- (Gk), meaning dark, referring to the brown conidia; *Trigonon* (Gk) meaning triangle, referring to conspicuous triangle-like conidiogenous cells of the asexual morph.

**Ascomata** perithecial, non-stromatic, immersed to semi-immersed, subglobose to broadly conical, dark brown, papillate. *Ostiole* periphysate. Ascomatal wall leathery to fragile, 23–30 µm thick, 2-layered; outer layer consisting of brown, polyhedral cells of *textura prismatica* with opaque walls; towards the interior grading into polygonal to angular cells of *textura angularis*; towards the interior grading into pale-brown, elongated cells. Inner layer consisting of several rows of thin-walled, hyaline, flattened cells. *Paraphyses* abundant, persistent, septate, anastomosing, hyaline, sparsely branched, c. 3.0–4.5 µm wide, tapering to c. 3.0 µm, longer than the asci. *Asci* (105–115–128(–142) µm long in the sporiferous part, (8.5–)9.0–11.5 µm wide (mean ± SD = 122.8 ± 7.4 × 11.0 ± 5.2 µm) with a stipe 32–50 µm long; cylindrical, obtuse apically, 8-spored, apex with a large, conspicuous non-amyloid apical annulus 4.5–5.0 µm wide, 3.5–4.0 µm high. *Ascospores* (17–18–21(–21.5) µm in diameter (mean ± SD = 19.4 ± 1.5 × 5.8 ± 0.3 µm), ellipsoidal, straight to slightly curved, hyaline, smooth, 3-septate, non-constricted at the septa, arranged obliquely uniseriate, sometimes 2-seriate only in the upper part of the ascus.

**Culture characteristics** — Colonies slow growing, reaching 8–10 mm diam on PDA after 21 d at 25 °C. Aerial mycelium beige in the centre of the colony and on the inoculum block, white towards the margin, felty, centre elevated, later with a moist appearance, bent into deep folds, reverse dark beige.

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**Melanotrigonum ovale** Réblová, sp. nov. — MycoBank MB813233; Fig. 5, 6

**Etymology.** *Ovalis* (L), referring to the oval shape of conidia.

**Ascomata** perithecial, non-stromatic, immersed to semi-immersed, gregarious, occurring in small to large groups; venter 320–480 µm diam, 400–500 µm high, subglobose to broadly conical, brown, glabrous, papillate, opening by a rounded pore. *Ostiole* periphysate. Ascomatal wall leathery to fragile, 23–30 µm thick, 2-layered; outer layer consisting of brown, polyhedral cells of *textura prismatica* with opaque walls; towards the exterior grading into polygonal to angular cells of *textura angularis*; towards the interior grading into pale-brown, elongated cells. Inner layer consisting of several rows of thin-walled, hyaline, flattened cells. *Paraphyses* abundant, persistent, septate, anastomosing, hyaline, sparsely branched, c. 3.0–4.5 µm wide, tapering to c. 3.0 µm, longer than the asci. *Asci* (105–115–128(–142) µm long in the sporiferous part, (8.5–)9.0–11.5 µm wide (mean ± SD = 122.8 ± 7.4 × 11.0 ± 5.2 µm) with a stipe 32–50 µm long; cylindrical, obtuse apically, 8-spored, apex with a large, conspicuous non-amyloid apical annulus 4.5–5.0 µm wide, 3.5–4.0 µm high. *Ascospores* (17–18–21(–21.5) µm in diameter (mean ± SD = 19.4 ± 1.5 × 5.8 ± 0.3 µm), ellipsoidal, straight to slightly curved, hyaline, smooth, 3-septate, non-constricted at the septa, arranged obliquely uniseriate, sometimes 2-seriate only in the upper part of the ascus.

**Culture characteristics** — Colonies slow growing, reaching 8–10 mm diam on PDA after 21 d at 25 °C. Aerial mycelium beige in the centre of the colony and on the inoculum block, white towards the margin, felty, centre elevated, later with a moist appearance, bent into deep folds, reverse dark beige.
Fig. 5 Melanotrigonum ovale. a. Ascomata; b, c. vertical sections of the ascomatal wall; d–f. asci with ascospores; g. apical annulus; h. ascospores; i. paraphyses (a–i. PRM 933852 holotype); b–h: DIC; i: PC. — Scale bars: a = 250 μm; b, c = 25 μm; d–f, i = 20 μm; g, h = 10 μm.
Fig. 6 Asexual morph of Melanotrigonum ovale. a, b. Colony on PDA (5 mo, 25 °C); c, d. colony on PDA (1 mo, 25 °C); e, f, h, i. conidiogenous cells on PCA: g, j. conidiogenous cells with conidia borne on a denticle on PCA; k–n. conidia (a, b, g–i, k–n. M.R. 3685; c, d–f, j. CBS 138742; e–j. 21 d, 25 °C); e–n: DIC. — Scale bars: a = 2.5 mm; b = 5 mm; c, d = 10 mm; e–n = 5 µm.
**Fig. 7** *Plagiascoma frondosum.* a. Ascomata; b. vertical section of the ascomatal wall; c, d. germinating ascospores; e. ascospores; f. paraphyses; g. asci in freshly collected material in Pelikan ink; h, i. asci from air dried herbarium material, arrow indicates apical annulus; j. apical annulus; k, l. pigmented cells formed in vitro on vegetative hyphae on PCA (a–j. PRM 933854 holotype; k, l. CBS 139031, 21 d, 25 °C); c–e, h–l. DIC; f, g. PC. — Scale bars: a = 500 µm; b = 250 µm; c–f, j = 10 µm; g = 25 µm; h, i, k, l = 20 µm.
Aerial hyphae 2.0–3.0 µm wide, smooth, hyaline, thin-walled, sparsely branched. Submerged hyphae 2.0–2.5 µm wide, smooth, hyaline. Sporulation appears later on the youngest aerial hyphae at the margin of the colony. Conidiophores semi-micronematous, reduced to a conidiogenous cell, arising vertically from hyphae, unbranched, smooth, tapering towards the apex. Conidiogenous cell 4.5–8.0(–10.0) µm long, 2.0–3.0 µm wide in the broadest point (mean ± SD = 6.9 ± 1.1 × 2.8 ± 0.4 µm), integrated, intercalary, almost triangular to ampulliform, tapering towards the apex, pale brown, with a single, rarely two, pale brown to subhyaline denticle 1.0–2.0 µm long. Conidia (10–)15.5–13.5(–15) × 5.0–6.0 µm (mean ± SD = 12.3 ± 0.6 × 5.4 ± 0.5 µm), 1-septate, oval to bean-shaped, straight or slightly curved, leaving a pore when detached, smooth, rounded at both ends or slightly tapering towards the base, brown, darker at the ends, or slightly tapering towards the base, pale brown to subhyaline denticle 1.0–2.0 µm long.

Notes — Five strains of M. ovale were collected on soft, strongly decaying wood of several fallen trunks of *Quercus cerris*, the remains of old growth trees that were more than hundred years old. Specimen M.R. 3685 has ascii shorter in the sporiferous part (100–105 µm long) and generally smaller ascospores, (15–)16–17.5(–19.5) × 4.5–5.5 µm.

*Melanotrigonum ovale* is similar to *Pleurotheciella rivularia* in characters of ascospores, asci and ascocarps, but differs in the ascospore arrangement of ascospores changes and they became biseriate revealed asci over 200 µm long and 13–15 µm wide, with uniseriate ascospores arranged obliquely (Fig. 7g). Upon drying, the arrangement of ascospores changes and they became biseriate within the ascus. The asci in dry herbarium material are shorter in the sporiferous part, 100–160 µm long, and wider 15–20 µm with almost twice the stipe length (Fig. 7h, i). No sheath or appendages were observed on immature or mature ascospores. Freshwater perithecial ascomycetes often have ascospores enclosed in a hyaline sheath or have appendages to facilitate their attachment on moist woody substrates. Interestingly, this is largely true for species from Asia, America and Australia but not in Europe, where many of the most widespread freshwater species lack these structures.

The fusiform, hyaline, 3–5-septate ascospores of *P. frondosum* resemble multisepulate ascospores of some species of *Annuilactatus*, e.g. *A. nilensis* (Abdel-Wahab et al. 2011) and *A. tropicallis* (Tsu et al. 2002). In our multilocus phylogeny, *P. frondosum* is positioned in the strongly supported *Bactrodiesniastrium* clade.

*Phaeoisaria fasciculata* Réblová & Seifert, sp. nov. — MycoBank MB813236; Fig. 8

Etymology. *Fasciculus* (L), meaning fascicle or bundle, referring to conidiophores arranged in fascicles and lacking a distinct stipe.

Colonies in vivo effuse, dark grey, whitish to beige when sporulating. *Sexual morph* not observed. *Synnemata* absent, conidiophores forming fascicles. *Conidiophores* 25–65 × 3.0–3.5 µm (mean ± SD = 41.7 ± 14.2 × 3.3 ± 0.3 µm), macronematous, arising from brown, thick-walled cells, cylindrical, pale brown, subhyaline towards the apex, unbranched, smooth-walled. *Conidiogenous cells* 10–29(–36) × 2.5–3.5 µm (mean ± SD = 20.2 ± 6.7 × 3.1 ± 0.5 µm), integrated, terminal, cylindrical, tapering towards tip, pale brown to subhyaline near base, hyaline towards apex, smooth-walled, polyblastic, forming conidia sympodially on conspicuous denticles 1.0–1.5 µm long, about 0.5 µm wide, scattered or clustered in the apical region. *Conidia*
Fig. 8  *Phaeoisaria fasciculata*. a. Colony on PCA; b. conidiophores in vivo; c. conidia in vivo; d, f, g–i. conidiophores on PCA; e. conidia on PCA (a, d–f. CBS 127885; b, c. PRM 933855 holotype; g–i. DAOM 230055; a, d–i. 21 d, 25 °C); b–f. DIC; g–i. ESEM. — Scale bars: a = 50 µm; b = 250 µm; b, d, f = 20 µm; c, e = 10 µm; g–i = 10 µm.
6.0–8.0(–9.0) µm long, about 2.0 µm wide (mean ± SD = 7.3 ± 1.2 ± 2.0 ± 0.1 µm), ellipsoidal to obovoid, straight, rounded at the apex, obtuse and tapering towards base, hyaline, non-septate, smooth-walled.

Culture characteristics — Colonies reaching 12–18 mm diam on PCA after 21 d at 25 °C. Aerial mycelium beige to pale brown (oac682), at first smooth, later cottony, reverse brown (oac640). Aerial and submerged hyphae 2.0–3.0 µm wide, hyaline to pale brown, sparsely branched, smooth-walled. Sporulation appears first in the centre of the colony, later present over the whole colony or in isolated patches; sporulating colony beige (oac809) with a powdery appearance. Synnemata first in the centre of the colony, later present over the whole colony with a papilla or short neck, broadly conical or cylindrical, slightly tapering towards the apex, pale brown, subhyaline towards the apex, unbranched, smooth-walled. Conidiogenous cell 10–29(–36) × 2.5–3.5(–4.0) µm (mean ± SD = 20.2 ± 6.7 ± 3.1 ± 0.5 µm), integrated, terminal and intercalary, cylindrical, tapering towards tip, pale brown to subhyaline, hyaline towards apex, smooth-walled, polypastic, with numerous conspicuous denticles 1.0–1.5 µm long, 0.5 µm wide, scattered along the whole length of intercalary conidiogenous cell and clustered in the apical region. Conidia 5.5–7.5(–8.5) × 2.0–2.5(–3.0) µm (mean ± SD = 6.7 ± 0.9 ± 2.5 ± 0.3 µm), ellipsoidal to obovoid, straight, rounded at the apex, obtuse and tapering towards base, hyaline, non-septate, smooth-walled.

Specimens examined. Canada, Ontario, Goulbourn Twp., Stittsville, bark on branch on ground, 23 Oct. 2008, Keith A. Seifert, K.A.S. 1433 (DAOM 230055). Czech Republic, Southern Moravia, Břeclav distr., Milovice, Milovická stráň Nature Reserve, north slopes of Mt Špičák, 293 m asl, decorticated wood of Sambucus nigra, 22 May 2009, M. Réblová M.R. 3084 (holotype PRM 933855, culture ex-type CBS 127885).

Notes — Phaeoisaria fasciculata is easily distinguished from other species of the genus by its conidiophores, which grow in fascicles on the host, while typical indeterminate synnemata are not formed. The ellipsoidal to obovoid, non-septate conidia of Ph. fasciculata resemble those of Ph. caffera, the Ph. clematidis species complex and Ph. magnifica. Phaeoisaria caffera differs from the new species by longer, pale yellowish brown conidia.

Ascothaiwania limnetica (H.S. Chang & S.Y. Hsieh) Réblová & J. Fourn., comb. nov. — MycoBank MB813237; Fig. 9, 10

Basionym. Savoryella limnetica H.S. Chang & S.Y. Hsieh, Mycol. Res. 102: 715. 1998.

Ascomata perithecial, non-stromatic, semi-immersed, gradually erumpent to almost superficial, scattered or clustered in small groups of 2–3, upright, obliquely oriented or lying horizontally on the host; venter 210–260 µm diam, 220–250(–300) µm high, black, subglobose with a flattened base and a broadly conical apex, often laterally flattened, flask-shaped when lying horizontally, with a papilla or short neck, broadly conical or cylindrical, apically truncate, central, eccentric or lateral, oriented upwards when ascomata lie horizontally. Ostiolo periphysate. Ascomatal wall fragile, 9–15 µm thick, thicker at the apex up to 20 µm, 2-layered; outer layer consisting of dark brown, polygonal, flattened cells of textura prismatica with opaque walls and sparse pores, outwards grading into small protruding cells, inner layer consisting of several rows of thin-walled, hyaline, flattened cells. Asci 125–150 × 11–14 µm (mean ± SD = 137 ± 9.4 ± 12.6 ± 1.2 µm), cylindrical, short-stipitate, broadly rounded apically to obtuse, with a non-amyloid, discord apical annulus 4.5–5.5 µm wide, 1.0–2.0 µm high. Paraphyses sparse, partially disintegrating at maturity, septate, branching, anastomosing, 4.0–9.5 µm wide. Ascospores (17.5–)19.5–23.5(–24) × (6.3–)7.0–8.5 µm, (mean ± SD = 21.4 ± 1.4 × 7.7 ± 0.5 µm), ellipsoidal, equilateral, straight, versicolorous, middle cells olivaceous brown to brown, containing numerous small guttules, polar cells smaller, hyaline, smooth, unequally 3-septate, slightly constricted at the septa, without prothall or appendages, arranged obliquely uniseriately in the ascus. Colonies in vivo diffuse, visible only as single scattered macroconidia arising from short, hyaline conidigenous cells on vegetative mycelium near ascomata. Conidia (30–)33–41 × 15–17.5 µm, ellipsoidal, broadly rounded at the apex, tapering basally, dark brown, opaque, basal cell subhyaline to pale brown, (3–)5–6-septate, septa obscured by a darker band.

Culture characteristics — Colonies slow growing, reaching c. 8–10 mm diam on PDA after 21 d at 25 °C. Aerial mycelium brown (oac639), pale brown (oac661) in the centre of the colony and on inoculum block, velvety, reverse brown (oac733). Aerial hyphae smooth, thin-walled, sparsely branched, hyaline to subhyaline 1.5–2.0 µm, submerged hyphae sometimes pale brown 2.0–3.0 µm wide. Conidiophores reduced to a monoblastic conidigenous cell. Conidiogenous cells 4.5–7.0 × 5.0–8.0 µm, usually with several subtending cells, integrated, hyaline to subhyaline with a single conidigenous locus. Conidia 32–36(–39) × (14.5–)16–17.5(–18.5) µm (mean ± SD = 34.5 ± 2.2 × 17.0 ± 1.0 µm), ellipsoidal to obovoid, straight or slightly curved, smooth, dark brown, 3–5-septate, with darker bands obscuring the septa, non-constricted at the septa, basal cell subhyaline 3.0–4.5 µm wide tapering to 2.5–3.0 µm.

Specimens examined. France, Midi-Pyrénées, Ariège, Rimont, valley of the Peyrou brook, c. 400 m asl, 23 Feb. 2008, on submerged wood, J. Fournier J.F. 08011 (PRM 933849, culture CBS 126792); ibid., 22 May 2009, submerged wood of Alnus glutinosa, J. Fournier J.F. 09127 (PRM 933851, culture CBS 126576); ibid., 19 Apr. 2010, submerged wood of Fraxinus excelsior, J. Fournier J.F. 10014; ibid., Vernajoul, Vernajoul brook, Pont Fagé, c. 350 m asl, on unidentified submerged wood, 2 July 2007, J. Fournier J.F. 07123 (PRM 933850).

Notes — Savoryella limnetica was originally collected on decaying wood submerged in freshwater in Taiwan and assigned to the genus based on its 3-septate ascospores and flattened apical apparatus (Chang et al. 1998). This species was recently repeatedly collected on submerged deciduous wood in southern France. Two living cultures were successfully obtained from isolated ascospores from fresh material. Savoryella and Ascothaiwania are closely related, morphologically similar genera and their delimitation is based primarily on ascospore septation, morphology of the apical apparatus of theascus and width of the paraphyses (see Discussion). The transfer of S. limnetica to Ascothaiwania is supported by molecular data and culture characters. The majority of Ascothaiwania species have 5–7-septate ascospores and only few are characterised by ascospores with three septa, i.e. A. Hughesii, A. Palmicola and A. Sawadae. Helicoon farinosum and its sexual morph described as A. Hughesii (Fallah et al. 1999), is a member of the Pleurotheciales. Ascothaiwania palmicola differs from A. Limnetica by terrestrial habitat and affiliation to palm wood, asci with a conspicuous apical apparatus 4 × 5 µm and slender ascospores, 17.5–20 × 5.0–6.5 µm with polar mucilaginous appendages (Hyde 1995). Ascothaiwania sawadae can be compared to A. Limnetica by ascomatal morphology, but differs by asci with a less flattened apical apparatus and larger and inequilateral ascospores 25–30 × 7.5–10 µm (Sivichai et al. 1998).

When observed in Congo red, the asci of A. Limnetica revealed a conspicuous flattened apical annulus that stains deep red (Fig. 9k).
Fig. 9  Ascotaiwania limnetica. a, b. Ascomata, arrow indicates ascospores aggregated at the top of the neck; c, d. vertical sections of the ascomatal wall; e. asci with ascospores in Pelikan ink; f. asci with ascospores; g–i. paraphyses; j. apical annulus, arrow indicates the tip of ascal apex, when ascospore is released through the annulus; k. asci with apical annulus in Congo red (a–e. k. PRM 933850; f, g, i, j. PRM 933851; h. PRM 933849); c–f, j, k: DIC; g–i: PC. — Scale bars: a, b = 150 µm; c, j = 10 µm; d = 100 µm; c, e = 10 µm; e, f, k = 50 µm.
Fig. 10  Asexual morph of *Ascotaiwania limnetica*. a. Conidia in vivo; b. ascoma with macroconidia scattered on wood surface; c–h. conidia and conidiogenous cells on PDA; i. colony on PCA; j–m. conidia on PCA (a, c–h. CBS 126576; b. PRM 933850; j–m. CBS 126792; a, c–m. 21 d, 25 °C); a, c–h, j, k: DIC; i, m: ESEM. — Scale bars: a, c–h, j, k, l = 20 µm; b = 250 µm; i = 5 mm; m = 10 µm.
**Pleurotheciella uniseptata** (Matsush.) Seifert, comb. nov. — MycoBank MB813238; Fig. 11

*Basionym. Dactylaria uniseptata* Matsush., *Microfungi of the Solomon Islands and Papua-New Guinea*: 19. 1971.

Colonies in vivo effuse, visible as solitary to 4–5 caespitose dark brown conidiophores with dry, whitish to greyish conidia. *Sexual morph* not observed. *Conidiophores* mostly 100–150 µm tall, 4.5–5.0 µm wide at the base, tapering to 3.0–4.0 µm wide, macronematous, unbranched, straight or sinuous, dark brown at the base, with walls up to 1.0 µm thick near the base, thinner towards the apex, cylindrical, smooth-walled or slightly granular or roughened, usually with a terminal node of denticles, but rarely extending through the original node with a new extension of the conidiophore. *Conidiogenous cell* 15–32 µm long, 2.5–3.5 µm wide at the base, 2.0–3.0 µm wide below the fertile zone, integrated, terminal, cylindrical or tapering towards tip, pale brown to subhyaline near base, hyaline towards apex, smooth-walled or slightly granular, polyblastic, forming conidia sympodially on conspicuous denticles 1.0–2.0 µm long, about 0.5 µm wide, sometimes slightly broader at base, occluded, fertile zone at first just a few denticles, but can expand into a node-like zone that is cylindrical to ellipsoidal in outline, usually with compact clusters of 4–15 denticles but sometimes extended, rarely geniculate, up to 5.0–9.0 × 3.0 µm, wide, or be constricted down to 1.5 µm, up to 15 denticles seen. *Conidia* 12.5–16.5 × 2.0–4.0 µm (mean ± SD = 14.1 ± 0.9 × 2.9 ± 0.5 µm), fusoid or slightly clavate, straight, rounded at the apex, obtuse and tapering towards base, hyaline, 1-septate with an inconspicuous central septum, often with 1–2 large guttules in each cell, smooth-walled, remains of denticle sometimes attached to seceded conidium.

*Culture characteristics* — Colonies reaching 8–10 mm diam on CMA after 21 d at 25 °C. Aerial mycelium absent, colony and reverse inconspicuous to white. Submerged hyphae 1.5–2.0 µm wide, hyaline, smooth-walled. Sporulation appears first on the inoculum of the colony, and later is sparsely present on the older parts of the new growth. Conidiophores 50–85 × 3.5–4.0 µm wide, slightly swollen at base to about 4 µm, semi-macronematous, pale brown, subhyaline towards the apex, unbranched, smooth-walled. Conidiogenous cells and conidia similar to those produced in vivo.

*Specimen examined.* Canada, Ontario, Arnprior, MacNamara Trail, on decaying wet wood, 12 Oct. 2011, K.A. Seifert & G. White K.A.S. 4459 (DAOM 673210, culture DAOMC 250294).

*Notes* — *Pleurotheciella uniseptata* is known only from its asexual morph. Its occurrence on water saturated decayed wood is consistent with the ecology of the other two species now classified in this genus. Its conidia are of a similar length...
and septation to those of *P. rivularia*, but narrower and more uniformly fusiform rather than the often obovoidal shape of the latter species. The conidia of *P. centenaria* are also fusoid, but longer than the other two species and consistently 3-septate. Our specimen from Canada fits the description and illustration of *Dactylaria uniseptata* by Matsushima (1971) well, considering that the protologue was based on a culture grown on banana leaf agar. We note that De Hoog (1985) failed to obtain the holotype of *D. uniseptata* and we did not attempt to obtain it here. We have resisted the temptation to epitypify a Japanese species with a Canadian specimen and culture. Lectotypification with the drawings from the protologue would be a precondition to epitypification if the holotype is truly unavailable.

This is the first species of *Pleurothecia* for which the conidiophores have been observed on the natural substrate. The protologue of the genus suggested that the conidiophores were dactylaria-like, but in *P. uniseptata* the conidiophores are macronematous and much more similar to those of *Pleurothecium* species. However, the conidiophores of *P. uniseptata* produced in culture lack dark basal cells and are rather similar to those produced by *P. rivularia* and *P. centenaria* in vitro (Fig. 11d). It seems possible that the conidiophores or all *Pleurothecia* species would be macronematous in vivo. Morphologically, there are few if any characters to distinguish between the asexual morphs of *Pleurothecia uniseptata* and some species classified in the hyphomycete genus *Pleurophragmium*. The two genera are clearly phylogenetically distinct, with *Pleurophragmium parvisporum*, the type of that genus, classified in the *Papulosaceae*, *Sordariomycetes* by Réblóvá (2009). A great morphological diversity of species are classified in *Pleurophragmium* (see key in D’Souza & Bhat 2012) and it is unlikely to be phylogenetically homogeneous.

**DISCUSSION**

**The CPS (Conioscyphales/Pleurotheciales/Savoryellales) clade**

The combined three- and six-gene phylogenetic analyses of the newly described genera *Melanotrigonum* and *Adelosphaeria* with members of the *Savoryellales* and other taxa related to *Conioscypha* and *Pleurothecium* revealed a robust monophylum in the *Hypocreomycetidae* (Fig. 1). It contains three nested monophyletic clades significantly supported by BI and ML methods, namely i) the *Savoryellales*; ii) a clade containing five species of *Conioscypha*; and iii) another clade that comprises several genera centred around *Pleurothecium*. The two latter clades represent distinct taxonomic groups at the ordinal systematic level and are introduced as the *Conioscyphales* and *Pleurotheciales* above. A sister relationship was revealed between the CPS (Conioscyphales/Pleurotheciales/Savoryellales) clade and a monophyletic strongly supported lineage of uncertain systematic position containing *Ascotaiwania persoonii*, *Bactrodesmiastrum* and the new genus *Plagiocoma*. Members of the CPS and *Bactrodesmiastrum* clades share a few morphological features such as the absence of stromatic tissue or clypeus, similar anatomies of the ascomatal walls, thin-walled unistromatic asci with a distinct, non-amyloid apical annulus, paraphyses and symmetrical, transversely septate ascospores. The known asexual morphs are dematiaceous hyphomycetes with holoblastic conidiogenesis. Although the morphology of sexual morphs is more or less uniform and rather non-descriptive within each order, the observed variability in extension of conidiogenous cells and conidial morphology is characteristic of each order. In the CPS clade, pleomorphism is commonly observed, i.e. the ability of fungi to reproduce sexually and asexually and form independent spore-stages in the life cycle. All known life-histories discussed here were established experimentally, i.e. *Ascotaiwania* (Ranghoo & Hyde 1998, Sivichai et al. 1998, this study), *Canalisporium* (Tri-indrasudhi et al. 2010), *Conioscypha* (Réblóvá & Seifert 2004, Zelski et al. 2014), *Helicóon farinosum* (Fallah et al. 1999), *Pleurothecium* (Fernández et al. 1999), *Pleurothecia* (Réblóvá et al. 2012), *Sterigmatobotrys* (Réblóvá & Seifert 2011) and the new genera described in this study.

At the base of the monophyletic clade with the nested CPS and *Bactrodesmiastrum* clades, *Flammispora biotica* is positioned on a separate branch (Fig. 1, 2). This species was collected on submersed leaves of the peat swamp palm *Licuala longecalyx* and is characterised by non-stromatic, black, immersed ascomata, clavate deliquescent asci without an apical annulus, subcylindrical to elongate-fusiform ascospores with a polar appendage and absence of paraphyses (Pinrnua et al. 2004). Its asexual morph is unknown.

**The Bactrodesmiastrum clade**

*Bactrodesmiastrum*, based on *B. obscurum*, was described by Holubová-Jechová (1984) for dematiaceous hyphomycetes characterised by schizolytic conidal secession and a formation of conidiogenous cells related to the maturation of brown, septate conidia. When the conidium matures at the tip of the conidiogenous cell, a new monoblastic conidiogenous cell is borne near the previous one on repent basal hyphae, followed by formation of other conidiogenous cells in the same manner. No DNA sequences are available of the type species *Bactrodesmiastrum*. The sexual state of *Bactrodesmiastrum* is unknown (Holubová-Jechová 1984, Hernández-Restrepo et al. 2013, 2015) and no conidia or conidiogenous cells were observed on the type and other herbarium material of its closest ascoma-producing sibling *A. persoonii* (Fallah et al. 1999). We prefer to avoid proposing a new genus for *A. persoonii* or its new combination in *Bactrodesmiastrum*, based on current DNA sequence data, until similarities in the life histories of these two taxa are proven or disproven experimentally.

**Conioscyphales**

The *Conioscyphales* comprises a single genus *Conioscypha* with 12 species from freshwater and terrestrial habitats. *Conioscyphus* was originally proposed for fungi with *Conioscypha* asexual morphs by Réblóvá & Seifert (2004). *Conioscypha* exhibits a unique mode of conidiogenesis with multiple, conspicuous collarettes forming a multilamellar structure around the blastic conidiogenous locus of the intercalary conidiogenous cells (Shearer & Motta 1973). It is characterised by inconspicuous perithecial ascomata that are typically immersed to semi-immersed, hyaline, subhyaline to pale orange with a papilla or long upright neck, coriaceous, waxly ascomatal wall, cylindrical-clavate stipitate asci with a pronounced non-amyloid apical annulus, filiform paraphyses and fusiform to fusiform-navicular, septe, hyaline ascospores. Nine species are known as apparently asexual (Von Höhnel 1904, Shearer 1973, Matsushima 1975, 1993, 1996, Kirk 1984, Udagawa & Toyazaki 1983, Chen & Tzean 2000, Crous et al. 2014) and only two have experimentally proven link between the sexual and asexual morphs, i.e. *C. varia* (Réblóvá & Seifert 2004) and *C. peruviana* (Zelski et al. 2014). A third sexually reproducing species, *Conioscyphus gracilis*, was recently transferred to *Conioscypha* (Zelski et al. 2014).

**Pleurotheciales**

Six monophyletic clades that include species of eleven genera were nested in the clade that we describe above as the *Pleurotheciales* (Fig. 2). Members of the *Pleurotheciales* share dark,
papillate, glabrous or sparsely setose peritrich, upright or lying horizontally to the host, asci with a distinct non-amyloid apical annulus, filiform paraphyses that disintegrate partially at maturity and fusiform to ellipsoidal, septate, hyaline ascospores. Only ascospores of the sexual morph of Helicóon farinosum are versicolorous with brown middle cells and hyaline polar cells. The variation in the details of holoblastic conidiogenesis correlates with clades recovered within the order. Rhexolytic conidial secession either on short denticles or rachis on sympodially proliferating conidigenous cells occurs in Helicóon farinosum, Phaeoisaria, Melanotrigonum, Pleurothecium, Pleurotheciella and Sterigmatobotrys. This type of conidiogenesis is characteristic of Clades I, IV, V, VI and partially occurs in Clades II and III. Schizolytic conidial secession on a single locus on percurrently regenerating conidigenous cells is characteristic of Brachysporiella sensu Ellis (Ellis 1959). The same type of secession but on monoblastic or solitary thallic conidigenous cells is typical of Phragmocephala. Both latter genera are positioned in Clade II. In Taeniolella, a sister of Sterigmatobotrys in Clade III, the dark brown macroconidia are formed on monoblastic conidigenous cells in dry, acropetal chains, while the apex of the conidium may develop into a fertile penicillus head with sympodially elongating conidigenous cells similar to Sterigmatobotrys (see further under Taeniolella).

The nondescript morphology of sexual characters of members of the Pleurotheciales makes their correct placement in the Sordariomycetes difficult and significantly hinders their identification and even distinction from each other. Without cultivation and/or molecular data their correct systematic placement is challenging. The presence of conspicuous asexual morphs in intimate juxtaposition to ascomata on the natural substratum helps identification of several genera only. Some species of Pleurotheciella do not form conidiophores in vivo, only reduced, hyaline to subhyaline conidiophores in the axenic culture. Genera like Adelosphaeria and Plagiisma, the latter is positioned in the Bactrodesmiastrum clade outside the Bactrodesmiastrum and three other species of Pleurotheciales, do not even form typical asexual morphs. They produce brown, ellipsoidal to globose, non-septate cells arising basally from vegetative hyphae or other cells in the axenic culture. Members of Chaetosphaeria (Chaetosphaeriales) are morphologically similar to Pleurothecium, Pleurotheciella and Sterigmatobotrys of the Pleurotheciales, especially species with Menispora asexual morphs, e.g. C. ciliata, C. ovoidea, C. pulviscula or C. tortuosa (Holubová-Jechová 1973, Réblová et al. 2006, Réblová & Seifert 2008). They possess brown, upright, papillate ascomata, fusiform, 3-septate, hyaline ascospores in cylindrical-clavate asci with distinct apical annulus and their phialidic asexual morphs are often absent on the host. Several freshwater genera such as Aquaticola, Annulatascus and Annulatusmus (Ho et al. 1999, Hyde 1992a, Campbell & Shearer 2004) can be compared with Adelosphaeria, Melanotrigonum, Pleurothecium, Pleurotheciella and Sterigmatobotrys based on morphology of ascomata, asci, ascospores and paraphyses. Species of Aquaticola have miniature, coriaceous ascomata lying horizontally to the host, asci with in conspicuously non-amyloid apical annulus and septate or non-septate, hyaline ascospores (Ho et al. 1999, Tsui et al. 2003). Annulatascus and Annulatusmus are easily distinguished by asci with a conspicuous, non-amyloid apical annulus and relatively large, septate, fusiform ascospores with a sheath or appendages in the former taxon, arranged 1-seriately or obliquely 1-seriately in the ascus. Their asexual morphs are unknown and when isolated from ascospores, sterile mycelium, or in the case of Annulatusmus triseptatus abundant fertile ascomata (M. Réblová, pers. obs.) are formed in vitro. Phomatospora, whose taxonomic placement in the Sordariomycetes is uncertain (Lumbsch & Huhndorf 2010), is another perithelial ascmycete that can be compared with genera of the Pleurotheciales. Its species are distinguishable by occurrence primarily on submerged herbaceous stems, rarely on wood in freshwater and marine habitats, immersed ascomata with thickened wall surrounding the ostiolum and hyaline, longitudinally striate non-septate ascospores enclosed in mucilaginous sheath or with bipolar appendages (e.g. Hyde 1988, 1992b, Fallah & Shearer 1998, Fournier & Lechat 2010). Only Phomatospora berkeleyi, the type species, and P. arenaria produce sporothrix-like asexual morphs with holoblastic denticulate conidiogenesis in axenic culture (Rappaz 1992).

Savoryellales

The Savoryellales was placed in the Hypocreomycetidae based on DNA sequences of six ribosomal and protein-coding loci (Boonwyn et al. 2011). It forms a well-supported lineage that includes saprobic, lichenicolous species from terrestrial, marine, brackish and freshwater environments and water-cooling towers (e.g. Jones & Eaton 1969, Minoura & Muroi 1978, Hyde & Jones 1988, Chang et al. 1998, Ranghoo & Hyde 1998). Although Ranghoo (1998) introduced the family Savoryellaceae as a member of the Halosphaeriales in her PhD Thesis, a valid description was never published. The family was formally introduced recently as Savoryellaceae (Jaklitsch & Réblová 2015).

As now delimited, the Savoryellales comprises three genera, Ascostaiwania, Canalisporium and Savoryella. Ascostaiwania is polyphyletic in our analyses, although the genus appeared monophyletic in three previous studies (Campbell & Shearer 2004, Hernández-Restrepo et al. 2013, 2015). The latter results were inadvertently distorted by the inclusion of species of Ascostaiwania that only represent the CPS and Bactrodesmiastrum clades on a small scale. In our multilocus phylogenies (Fig. 1, 2) the core of Ascostaiwania in the Savoryellales is centred around the type species A. lignicola (Sivanesan & Chang 1992) and three other species. Helicóon farinosum (as A. Hughesii, Fallah et al. 1999) is nested in the Pleurotheciales, while A. peronii (Fallah et al. 1999) is in a strongly supported monophyletic clade with Bactrodesmiastrum and Plagiisma basal to the CPS clade.

Genera of the Savoryellales share a similar morphology of dark, minute perithecial ascomata with elongated, dark or subhyaline neck, often oblique or lying horizontally on the host with the neck facing upwards, asci with a non-amyloid apical annulus, partly deliquescent paraphyses and ellipsoidal to fusiform, transversely septate, versicolorous ascospores. The generic delimitation of Ascostaiwania and Savoryella is narrow and for two decades was based predominantly on ascospore septation, and the morphologies of paraphyses and the ascal apex, i.e. size and shape of the apical annulus and presence or absence of apical thickening. The ascal apex of Savoryella was variously interpreted in different studies, by authors studying different species. In the protologue of the type species S. lignicola, the ascal apex was described as apically thickened with a pore (Jones & Eaton 1969). Sivanesan & Chang (1992) separated Ascostaiwania from Savoryella by an unthickened ascus apex with a distinct apical annulus and ascospores with more than three septa, while delimiting Savoryella for species lacking an apical ring and having 3-septate ascospores. Later, several other species were introduced to the genus, e.g. S. aquatica (Hyde 1993) and S. limnetica (Chang et al. 1998), characterised by a thickened ascus apex containing apical annulus with a pore. Read et al. (1993) based their distinction of Ascostaiwania and Savoryella on ultrastructural observations and used the term ‘apical apparatus’ to describe the complex structure of the ascus apex of these fungi. They characterised species of Ascostaiwania by ascal apical apparatus comprising an annulus with a protrusion (pendant) and plugged pore, whereas in species of
Savoryella the ascus apex was described as thickened with a pore, but lacking a pendant-like protrusion. Chang et al. (1998) also used characters of paraphyses to delimit the genera, i.e. narrow, filiform, early deliquescent filaments up to 2 μm wide in Ascotaiwania vs. filaments consisting of broad, partially disintegrating cells up to 8 μm wide in Savoryella. Sri-indrasutdhi et al. (2010) introduced another morphologically similar genus, Ascothailandia, as the sexual state of Canalispernum and distinguished it from Savoryella by its conspicuous apical annulus. Recently, Boonyuen et al. (2011) modified the generic concept of Savoryella and accepted species with 3-septate ascospores and comparatively flattened apical ring.

The transfer of S. limnetica to Ascotaiwania proposed above is based on molecular evidence and an experimentally proven life history. The micromorphological characters of S. limnetica, i.e. flattened apical annulus, cylindrical, septic, disintegrating paraphyses 4.0–9.5 μm wide and 3-septate ascospores, do not fit well with the long-held morphology-based concepts of either genus. Stable delimitation of Ascotaiwania and Savoryella will require re-evaluation of all sexual and asexual morphological characters and concentrated sampling filtered through the optics of multigene phylogenetics.

Asexual morphs associated with the Savoryellales were described for Canalispernum grenadoideum (as Ascothailandia grenadoidea) sexual morph, Sri-indrasutdhi et al. 2010) and three species of Ascotaiwania were linked with Brachysporiellalelike dematiaceous hyphomycetes, A. nitriformis and A. sawadae (as Monotosporella, Ranghoo & Hyde 1998, Sivichai et al. 1998) and A. limnetica (this study). With some reservations Acarocybiopsis was suggested as another suitable genus for asexual morphs of Ascotaiwania (Réblová & Seifert 2004). They are characterised by semi-macromaternal conidiophores often reduced to conidiogenous cells with a single locus and brown macroconidia. Conidia are either cheiroid, dicystopectate with pores between cells and conidiogenous cells arise from sporodochia in Canalispernum. The asexual morphs of Ascotaiwania produce aleuroconidium-like, transversely septate macroconidia with darker bands around septa and a few rhizoids arising from subtending cells beneath the monoblastic conidiogenous cell.

In our analysis, the dematiaceous hyphomycete Triadelphia uniseptata nested within the monophyletic Ascotaiwania clade as a sister to A. nitriformis. Triadelphia, based on T. heterospora, was introduced for fungi from freshwater and brackish environments and characterised by conidiophores reduced to subglobule, subhyaline to dematiaceous conidiogenous cells, schizolytic conidial secession and conidia produced blastically from a single locus (Shearer & Crane 1971). Conidia of species of Triadelphia are brown or versicolorous often with one or two polar cells paler than the middle ones, septate, usually with darker bands obscuring several septa. Although T. heterospora was described with two morphologically distinct types of conidia, currently eight types are known (Constantinescu & Samson 1982), but these other asexual morphs have never been formally named. The gregarious to caespitose, globose to subglobose to ampulliform conidiogenous cells borne directly on vegetative hyphae are the hallmark of Triadelphia. They are also remarkably similar to cylindrical to lageniform aggregated conidiogenous cells of Bactrodesmiastrum. The morphology of larger, broad to ellipsoidal, brown, septate conidia of T. heterospora and their conidio genesis illustrated in the protologue (Shearer & Crane 1971: f. 9c, f, g) resembles conidia and conidio genesis of A. limnetica (Fig. 10c–h) that we observed in axenic culture on PDA. The ampulliform conidiogenous cells are absent and conidia arise directly from mycelium or a small monoblastic conidiogenous cell with several supporting cells. Triadelphia comprises 17 species, but phylogenetic placement of its type is unknown. The only available ITS and nuc28S rDNA sequences in the GenBank belong to T. pulvinata and they show affinity with members of the Microascales (Edathodu et al. 2013). The position of T. uniseptata in the Savoryellales shown here demonstrates that the present concept of Triadelphia is polyphyletic, and that the application of this generic name, and the redisposition of its species, requires much improved sampling.

The ascoma centrum in the Hypocreomycetidae

In members of the Hypocreomycetidae, the centrum consists of several types of interthecal filaments. The other two subclasses of the Sordariomycetes, Sordariomycetidae and Xylariomycetidae include either only paraphyses and periphyses in the ostiolum or paraphyses are lacking in some groups. Apical, lateral and centripetal paraphyses occur in members of the Hypocreales (e.g. Samuels 1973, Mhasker & Rao 1976, Jaklitsch 2009, Jaklitsch & Voglmayr 2014). Filaments consisting of wide, inflated, early disintegrating cells interspersed among the asci occur in the Bertiellaceae and Chaetosphaerellaceae of the Coronophorales (Réblová 1999, Huhndorf et al. 2004). A hamathecium consisting of catenophyses, i.e. pseudoparenchymatous cells that break up to form chains of large, thin-walled, early dissolving cells interspersed among asci or the pseudoparenchyma may completely disappear in mature ascoma, is typical of members of the Halosphaeriaceae of the Microascales (Spatafora et al. 1998, Sakayaraj et al. 2011). A pseudoparenchymatous centrum occurs in the Melanosporales (Goh & Hanlin 1994, Samuels & Blackwell 2001). A reticulate network of filiform, branching and anastomosing filaments attached to the top and bottom of the cavity uniquely characterises the Reticulascaceae of the Glomerellales while in members of other two families, Australascaceae and Glomerellaceae, sparse septeate filaments occur (Samuels & Müller 1978, Sivanesan & Alcom 2002, Réblová et al. 2011). Numerous unbranched filaments attached to the top and bottom of the ascomatal cavity occur in members of the Torpedosporales except for Marinkuklati chaetosa, where the filaments are apically free (Jones et al. 2014, 2015). In some groups, a hamathecium is lacking, e.g. in the Scortechiniaceae and Nitschkaia of the Coronophorales (Huhndorf et al. 2004) or in some members with cleistothecial ascomata of the Microascales. The presence of periphyses in genera of the Coronophorales is variable and depends on how the apex of ascomata is formed, whether it contains a Quellkoper (Nannfeldt 1975) and whether it is ostiolate or non-ostiolate (Huhndorf et al. 2004).

Members of the CPS clade represent the only three orders in the Hypocreomycetidae defined by the presence of apically free paraphyses in the ascomatal centrum. These sterile, filiform, septeate filaments emerge from the subhymenium either interspersed among the asci, e.g. in Ascothaiawia, Conioscypha, Melanotirginiun, Pleurothecilla, Savoryella and Sterigmatobryts, or form separate tuft-like structures, e.g. Pleurothecium. Paraphyses are usually longer than the asci and may disintegrate at maturity; for example in some species of Savoryella or Ascothaiawia they disintegrate rapidly and are difficult to observe.

Recently, the new order Pirisoriporales was introduced for predominantly aquatic fungi, which morphologically mimic members of the Annulatascales in ascus and ascomospore characters, and the Amphipholiaceae in a conspicuous, tayloid apical annulus and non-stromatic ascobatha (Réblová et al. 2015). The order is isolated on a separate branch as a sister to the Hypocreomycetidae but without statistical support. The Pirisoriporales represents another group related to this subclass and classifies by filiform, septate, partly disintegrating paraphyses interspersed among ascii, but densely branching
and anastomosing above their apices in the ascma cavity. Although the two species of Pisorisporum, P. cymbiforme and P. glaucum, were described from wood submerged in freshwater, several recent collections of P. cymbiforme were made in terrestrial habitats in the Czech Republic, suggesting that the fungus might be widespread. The new nuc18S rDNA and rpb2 sequences of terrestrial strains are listed in Table 1.

Pleurotheciales: The polyphyletic genera Helicoön, Phaeoisaria, Pleurothecium and Taeniolella

Helicoön

Several genera now classified in the Pleurotheciales appear polyphyletic based on molecular phylogenies. Helicoön farinosum, which has hyaline, coiled, septate conidia formed holo- blastsically on short denticles, is the only representative with helicosporous conidia in the Pleurotheciales and in the whole CPS clade. It was experimentally linked with its sexual state Ascostaionia hughesii (Fallah et al. 1999) and in our phylogeny it is nested in Clade I as a sister to Brachysporiella setosa. We confirmed the phylogenetic position of H. farinosum (DAOM 241947) with collections, cultures and sequences made in Canada (Réblová et al. 2012). Although the correct species epithet for this holomorphic fungus would be ‘farinosum’, whether the generic assignment should be Helicoön is unclear pending confirmation of the phylogenetic placement and classification of the type species H. sessile. The genus Helicoön sensu Goos et al. (1986) was shown to be polyphyletic with DNA sequences of two nuc rDNA loci by Tsui & Berbee (2006), but H. sessile was not included. The only available ITS rDNA sequence of this species (UTZ2605, Pfister et al. 1997) shows 99 % similarity with the ITS sequence of Sarocladium kilienne of the Hypocreales (KP132606, Trinj et al. 2015), an unlikely relationship suggestive of a mislabelled or contaminated culture. Other species of Helicoön were placed in the Pleosporales, Tubuffiales and Venturiales of the Dothideomycetes (Tsui & Berbee 2006).

Phaeoisaria

Phaeoisaria is a dematiaceous hyphomycete genus with species producing indeterminate synnemata with septate or non-septate ellipsoidal, obvoidal, fusiform-cylindrical or falcate conidia formed on a sympodially extending rachis, occurring on decaying wood, plant debris or soil sediments (e.g. Sutton 1973, Deighton 1974, Castañeda et al. 2002, Seifert et al. 2011, Melnik 2012, Cheng et al. 2014, Crous et al. 2015). The genus was proposed by Von Höhnel (1909) with the only species Ph. bambusae. It was originally described as an assexual state of Neo- peckia bambusae, inferred from the intimate juxtaposition of synnemata and ascomata. Based on his revision of type and herbarium material, Deighton (1974) considered Ph. bambusae a synonym of Ph. clematidis. It compiled an extensive synonomy of the latter species, distinguishing it from morphologically similar Ph. magnifica, which has broader conidia. Deighton’s concept of Ph. clematidis seems to represent a complex of several phylogenetic species.

Phaeoisaria now includes 19 species, five of which were analysed in our study. The sampled species form a strongly supported monophyletic clade in the Pleurotheciales that includes species with synnemata and conidiophores formed in fascicles. In our analysis, P. clematidis is represented by two strains isolated from bark and senescent flower heads of Protea.

Phaeoisaria curvata is the only described mononematous species; it was isolated from leaves of Parinari capense and its wild type is unknown (De Hoog & Papendorf 1976). The nuc28S sequence of the ex-type strain CBS 153.72 (sequence in the CBS strain database) shows affinity with taxa of the Sordariomycetidae.

Although all species of Phaeoisaria species are asexual, including all species in our analyses, several perithecial ascoc- mycetes have been linked with Phaeoisaria-like asexual states. In the Sordariomycetes, Lentomitella and Rhamphoria produce sparsely branched, mononematous conidiophores with aseptate conidia borne on a short rachis in culture (Müller & Samuels 1982, Réblová 2006). Two genera of the Diatrypaceae, Eutypella (as Peroneutypella, Deighton 1974) and Pareutypella (Ju & Rogers 1995), were linked with Phaeoisaria-like synnema- tous asexual states. For these connections, the morphologi- cally similar synnematous genus Harpographium, typified by the asexual state of Eutypella scoparia, should be considered.

Although Phaeoisaria is usually considered non-pathogenic to human beings, two cases of inflammation of the eye’s cornea called keratitis were attributed to Phaeoisaria sp. (Chew et al. 2010) and Ph. clematidis (Guarro et al. 2000). The former pathogenic strain Phaeoisaria sp. was included in our analysis and is a sister taxon to two saprobic strains of Ph. clematidis with strong branch support.

Pleurothecium

Pleurothecium includes fungi with dematiaceous, macronema- tous, unbranched conidiophores and holoblastic, hyaline to sub- hyaline, sympodially extending conidigenous cells with a con- spicuous rachis of denticles and hyaline, septate conidia. The sexual morph is known only for the very common P. recurvatum, the type species (as Carpoligna pleurothecii, Fernández et al. 1999). Of the eight species assigned to the genus, only three have been studied with DNA sequence data. Pleurothecium recurvatum and P. semifecundum represent the core of the genus and form a strongly supported monophyletic clade in the Pleurotheciales, while P. obovoidicum is nested within another clade and sister to Brachysporiella setosa. The asexual morph of P. semifecundum lacks macronematous conidiophores in culture and sporulates sparsely; whether its wild type would better match the distinctive conidigenous apparatus of P. recurvatum remains unknown.

Pleurothecium obovoidicum, originally described in Ramichlo- ridium, is known only from culture and it was isolated from a dead leaf of Pasania edulis (Matsushima 1975). It is character- ised by reduced, septate conidiophores, sympodially proliferating conidigenous cells with a short rachis giving rise to 2–3 denticles and ellipsoidal to obovate, pale brown, non-septate conidia formed singly or in short chains. The morphology is rather nondescript and we prefer to avoid introducing a new genus for this species, until either the wild type is collected or relationship with other morphologically similar taxa is revealed. Based on its morphology, P. obovoidicum is similar to Rhinocla- diella mackenziei (Chaetothyriales), a pathogen causing severe cerebral phaeohyphomycosis in humans (Sutton et al. 1998). It also resembles members of Subramaniomyces (Xylariales, Crous et al. 2007) and Pterygosporopsis (Kirk 1983), whose phylogenetic placement is unknown.

Taeniolella

Taeniolella exilis, the type of the genus, is commonly found on decaying wood and bark of Betula (Hughes 1958, Ellis 1971). During a revision of the type material of T. exilis by Jones et al. (2002), a penicillately branched conidiophore was observed as an extension of the terminal macroconidia. A similar penicillate conidiophore was observed in two other species, T. longisima and T. rudis (Hughes 1980, Jones et al. 2002). The latter taxon was shown to be closely related to Sterigmatobotrys macarocarpa of the Pleurotheciales, whose asexual state is characterised by similar penicillate conidiophores with several series of branches and metulae terminating macronematous conidiophores (Réblová & Seifert 2011). However, brown, sep-
tate *Taeniella* macroconidia were not observed in axenic cultures obtained from conidia or ascospores of *S. macrocarpa*. Several other species of *Taeniella* are positioned in distantly related groups. *Taeniella*-like conidia were obtained in a culture derived from ascospores of the freshwater ascomycete *Chaetorostrum quincemilensis*, tentatively placed in the *Annulatacaceae* (*Zelkis et al. 2011*). Shearer et al. (2009) showed the strain of *T. alta* (CBS 488.80) nested in a clade with *Dia- porthe angeliniae* and *Phomopsis* sp., and the ex-type strain of *T. typoides* (CCM F-10198) in the *Lingdomycetaceae* of the *Pleosporales*. A *Taeniella*-like fungus was isolated from the rhizosphere soil of strawberry, producing a phialophora-like asexual state on vegetative hyphae or directly on macroconidia in vitro, and described as *T. phialosperma* (Watanabe 1989, in vitro, and described as rhizosphere soil of strawberry, producing a phialophora-like asexual state on vegetative hyphae or directly on macroconidia in vitro, and described as *T. phialosperma* (Watanabe 1989, 1992). The ITS sequences of two non-ex-type strains of *T. phialosperma* (Cheng 2014. *Phaeoisaria* from inter-

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REFERENCES

Abdel-Wahab MA, Abdel-Azz FMA, Mohamed SS, et al. 2011. Annulatacaceae nilesis sp. nov., a new freshwater ascomycete from the river Nile, Egypt. IMA Fungus 2: 1–6.

Alonso i Tarrés C, Heures JK, Gutdo E, et al. 1993. Subcutaneous phaeohyphomycosis caused by *T. exilis* species was reported by Alonso et al. (1993). While the pathogentic strain of *T. exilis* isolated from a human skin lesion (strain IP 2199,93) was shown closely related to *Ochrocladosporium etatum* (CBS 146.33) of the *Pleosporales* by Masclaux et al. (1995), the placement of the wood-inhabiting strain of *T. exilis* resembling *T. rudis* (*Phaeothecaeteles*) has yet to be confirmed with molecular sequence data.

Cousin PW, Chuntherak RK, Wingfield MJ, et al. 2015. Fungal Systematics and Evolution: FUSE 1. Sydowia 67: 81–118.

Cousin PW, Shivas RG, Quaadflieg W, et al. 2014. Fungal Planet description sheets: 214–280. Persoonia 32: 184–306.

De Beer ZW, Seifert KA, Wingfield MJ. 2013. The ophiostomatales fungi: their dual position in the Sordariomycetes. In: Ophiostomatales fungi: expanding frontiers. CBS Biodiversity Series 12: 1–19. CBS-KNAW Fungal Biodiversity Centre, Utrecht, Netherlands.

De Hoog GS. 1985. Taxonomy of the Dactylaria complex IV. Dactylaria, Neta Subulispora and Scleobasidium. Studies in Mycology 26: 1–60.

De Hoog GS, Papendorf MC. 1976. The genus *Pheoisaria*. Persoonia 8: 407–414.

Deighton FC. 1974. Four synnematous hyphomycetes. Transactions of British Mycological Society 62: 243–252.

D’Souza MA, Bhat DJ. 2012. A new species of *Pleurophragmium* from India. Mycoting 119: 477–482.

Edathodhu J, Al-Abdeli HM, Alhawadi S, et al. 2013. Invasive fungal infec-
tion due to *Triadelphia pulvinata* in a patient with acute myeloid leukemia. Journal of Clinical Microbiology 51: 3426–3429.

Ellis MB. 1959. Clasterosporium and some allied dematiace-phragmo-
sporae. II. Mycological Papers 72: 1–75.

Ellis MB. 1971. Dematiaceous hyphomycetes. CAB Commonwealth Myco-

Eurasian Ascomycete Collection of the National Fungal Herbarium, Kew, England.

Fallah PM, Cranle CA. 1999. Freshwater ascomycetes: two new species of *Ascotheca* from North America. Canadian Journal of Botany 77: 87–92.

Fallah PM, Shearer CA. 1998. Freshwater ascomycetes: *Phomatospora* sp. from lakes in Wisconsin. Mycologia 90: 323–329.

Fernández FA, Lützoni FM, Huhndorf SM. 1999. Teleomorph-anamorph con-

Fournier J, Lechat C. 2010. *Phomatospora* *luteotingens* sp. nov., a new aquatic species of *Phomatospora* from France and Spain. Mycosphere 1: 39–43.

Gams W, Hockstra ES, Aproot A. 1998. CBS course of mycology, 4th edn. Baarn, The Netherlands: Centraalbureau voor Schimmelcultures.

Geiser DM, Friszad JC, Taylor JW. 1998. Evolutionary relationships in As-
pendiculata section Fundiglum from several *β*-tubulin and hydropbinobin DNA sequences. Mycologia 91: 831–845.

Glass NL, Donaldson GC. 1995. Development of primer sets designed for use with the PCR to amplify conserved genes from filamentous ascomycetes. Applied and Environmental Microbiology 61: 1323–1330.

Goh TK, Hanlin RT. 1994. Ascomata development in *Melanospora zamiae*. Mycologia 86: 357–370.

Goes RD, Abdullah SK, Fisher PJ, et al. 1986. The anamorph genus Helicoc. Transactions of British Mycological Society 87: 115–122.

Guarro J, Vieira LA, De Freitas D, et al. 2000. Phaeoisaria clematidis as a cause of Keratomycosis. Journal of Clinical Microbiology 38: 2434–2437.

Gutell RR, Gray MW, Schnare MN. 1993. A compilation of large subunit (23S) rDNA sequences. Mycologia 95: 831–845.

Hall TA. 1999. BioEdit 5.0.9: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Fungal Hyphomycetes*, New York: Columbia University Press, pp. 3055–3074.

Hall TA. 1999. BioEdit 5.0.9: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Fungal Hyphomycetes*, New York: Columbia University Press, pp. 3055–3074.

Hermández-Restrepo M, Gené J, Castañeda-Ruíz RF, et al. 2015. Emen-
da of the genus Bactrodesmiastrium (Sordariomycetes) and description of Bactrodesmiastrium monilicoides sp. nov. from plant debris in Spain. Mycological Progress: doi 10.1007/s11557-015-1067-6.

Hermández-Restrepo M, Mena-Portales J, Gené J, et al. 2013. New Bact-

Honegger D. 1995. BioEdit 5.0.9: an user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Fungal Hyphomycetes*, New York: Columbia University Press, pp. 3055–3074.

Ho WW, Tsui CKM, Hodgkiss LJ, et al. 1999. Aquaticola, a new genus of *Annulatacaceae* from freshwater habitats. Fungal Diversity 3: 87–97.

Holubová-Jechová V. 1984. Lignicolous hyphomycetes from *Czechoslovakia*. 4. Menispora. Folia Geobotanica et Phytotaxonomica 19: 103–106.

Hulsenbeck JP, Ronquist F. 2001. MrBayes: Bayesian inference of phy-
genetic trees. Bioinformatics 17: 754–755.

Hughes SJ. 1958. Revisions Hyphomycetum aliquot cum appendice de genetic trees. Bioinformatics 17: 754–755.

Hughes SJ. 1958. Revisions Hyphomycetum aliquot cum appendice de genetic trees. Bioinformatics 17: 754–755.

Hughes SJ. 1958. Revisions Hyphomycetum aliquot cum appendice de genetic trees. Bioinformatics 17: 754–755.
Hyde KD. 1988. Phomatospora acrostichii sp. nov., a marine fungus on pinniae of Acrostichum speciosum. Transactions of the British Mycological Society 90: 135–138.

Hyde KD. 1992a. Tropical Australian freshwater fungi I. Annulatuscas tus velatissp. gen. et sp. nov. A. biolaris sp. nov. and Nais aquaticola sp. nov. (Ascomycetes). Australian Systematic Botany 5: 117–124.

Hyde KD. 1992b. Interdigital fungi from Candelia candeli including Phomatospora candeloides sp. nov. Transactions of the Mycological Society of Japan 33: 313–316.

Hyde KD. 1993. Tropical Australian freshwater fungi. V. Bombardia sp., Jahnula australiensis sp. nov., Savoryella aquatica sp. nov. and S. lignicola sp. nov. Australian Systematic Botany 6: 161–167.

Hyde KD. 1995. Fungi from palms. XXI. A new species of Ascostawania. Sydowia 47: 213–216.

Hyde KD. Jones EBG. 1988. Marine mangrove fungi. P.S.Z.N.I. Marine Ecology 9: 15–33.

Iriñy L, Serena C, García-Hermoso D, et al. 2015. International Society of Human and Animal Mycology (ISHAM)-ITS reference DNA barcoding database – the quality controlled standard tool for routine identification of human and animal pathogenic fungi. Medical Mycology 53: 313–337.

Jaklitsch WM. 2009. European species of Hypocrea. Part I. The green-spored taxa. Mycotaxon 104: 1–91.

Jaklitsch WM, Réblová M. 2015. Savoryellaceae Jaklitsch & Réblová. Index Fungorum 209: 1.

Kirk PM. 1983. New or interesting microfungi X. Hyphomycetes on Laurus nobilis leaf litter. Mycotaxon 18: 259–298.

Kirk PM. 1984. New or interesting microfungi XII. A new species of Coniocypha (Hyphomycetes). Transactions of British Mycological Society 82: 177–178.

Kirk PM. 1985. New or interesting microfungi X. Hyphomycetes on Laurus nobilis leaf litter. Mycotaxon 18: 259–298.

Kirk PM. 1987. New or interesting microfungi XII. A new species of Coniocypha (Hyphomycetes). Transactions of British Mycological Society 82: 177–178.

Kirk PM. 1988. New or interesting microfungi X. Hyphomycetes on Laurus nobilis leaf litter. Mycotaxon 18: 259–298.

Kirk PM. 1987. New or interesting microfungi XII. A new species of Coniocypha (Hyphomycetes). Transactions of British Mycological Society 82: 177–178.

Kirk PM. 1988. New or interesting microfungi X. Hyphomycetes on Laurus nobilis leaf litter. Mycotaxon 18: 259–298.

Kirk PM. 1987. New or interesting microfungi XII. A new species of Coniocypha (Hyphomycetes). Transactions of British Mycological Society 82: 177–178.

Kirk PM. 1988. New or interesting microfungi X. Hyphomycetes on Laurus nobilis leaf litter. Mycotaxon 18: 259–298.

Kirk PM. 1987. New or interesting microfungi XII. A new species of Coniocypha (Hyphomycetes). Transactions of British Mycological Society 82: 177–178.

Kirk PM. 1987. New or interesting microfungi X. Hyphomycetes on Laurus nobilis leaf litter. Mycotaxon 18: 259–298.

Kirk PM. 1987. New or interesting microfungi XII. A new species of Coniocypha (Hyphomycetes). Transactions of British Mycological Society 82: 177–178.

Kirk PM. 1987. New or interesting microfungi X. Hyphomycetes on Laurus nobilis leaf litter. Mycotaxon 18: 259–298.

Kirk PM. 1987. New or interesting microfungi XII. A new species of Coniocypha (Hyphomycetes). Transactions of British Mycological Society 82: 177–178.

Kirk PM. 1987. New or interesting microfungi X. Hyphomycetes on Laurus nobilis leaf litter. Mycotaxon 18: 259–298.

Kirk PM. 1987. New or interesting microfungi XII. A new species of Coniocypha (Hyphomycetes). Transactions of British Mycological Society 82: 177–178.

Kirk PM. 1987. New or interesting microfungi X. Hyphomycetes on Laurus nobilis leaf litter. Mycotaxon 18: 259–298.

Kirk PM. 1987. New or interesting microfungi XII. A new species of Coniocypha (Hyphomycetes). Transactions of British Mycological Society 82: 177–178.

Kirk PM. 1987. New or interesting microfungi X. Hyphomycetes on Laurus nobilis leaf litter. Mycotaxon 18: 259–298.

Kirk PM. 1987. New or interesting microfungi XII. A new species of Coniocypha (Hyphomycetes). Transactions of British Mycological Society 82: 177–178.

Kirk PM. 1987. New or interesting microfungi X. Hyphomycetes on Laurus nobilis leaf litter. Mycotaxon 18: 259–298.

Kirk PM. 1987. New or interesting microfungi XII. A new species of Coniocypha (Hyphomycetes). Transactions of British Mycological Society 82: 177–178.

Kirk PM. 1987. New or interesting microfungi X. Hyphomycetes on Laurus nobilis leaf litter. Mycotaxon 18: 259–298.

Kirk PM. 1987. New or interesting microfungi XII. A new species of Coniocypha (Hyphomycetes). Transactions of British Mycological Society 82: 177–178.

Kirk PM. 1987. New or interesting microfungi X. Hyphomycetes on Laurus nobilis leaf litter. Mycotaxon 18: 259–298.

Kirk PM. 1987. New or interesting microfungi XII. A new species of Coniocypha (Hyphomycetes). Transactions of British Mycological Society 82: 177–178.

Kirk PM. 1987. New or interesting microfungi X. Hyphomycetes on Laurus nobilis leaf litter. Mycotaxon 18: 259–298.

Kirk PM. 1987. New or interesting microfungi XII. A new species of Coniocypha (Hyphomycetes). Transactions of British Mycological Society 82: 177–178.

Kirk PM. 1987. New or interesting microfungi X. Hyphomycetes on Laurus nobilis leaf litter. Mycotaxon 18: 259–298.

Kirk PM. 1987. New or interesting microfungi XII. A new species of Coniocypha (Hyphomycetes). Transactions of British Mycological Society 82: 177–178.
Shearer CA. 1973. Fungi of Chesapeake Bay and its tributaries. II. The genus Conioscypha. Mycologia 65: 128–136.
Shearer CA, Crane JL. 1971. Fungi of the Chesapeake Bay and its tributaries. I. Patuxent River. Mycologia 63: 237–260.
Shearer CA, Motta JJ. 1973. Ultrastructure and conidiogenesis in Conioscypha (Hyphomycetes). Canadian Journal of Botany 51: 1747–1751.
Shearer CA, Raja HA, Miller AN, et al. 2009. The molecular phylogeny of freshwater Dothideomycetes. Studies in Mycology 64: 145–153.
Sivanesan A, Alcorn JL. 2002. Australiasca queenslandica gen. et sp. nov. (Chaetosphaeriacae: Ascomycota) and its anamorph Dischloridium cameliae sp. nov. from Australia. Australian Systematic Botany 15: 741–747.
Sivanesan A, Chang HS. 1992. Ascostaiwania, a new amphisphaeriacous ascomycete genus on wood from Taiwan. Mycological Research 96: 481–484.
Sivichai S, Hywel-Jones N, Jones EBG. 1998. Lignicolous freshwater Ascomycota from Thailand: 1. Ascostaiwania sawadae and its anamorph state Monotosporella. Mycoscience 39: 307–311.
Spatafora JW, Johnson D, Sung G-H, et al. 2007, ‘2006’. A five-gene phylogenetic analysis of the Pezizomycotina. Mycologia 98: 1020–1030.
Spatafora JW, Volkmann-Kohlmeier B, Kohlmeyer J. 1998. Independent terrestrial origins of the Halosphaereales (marine Ascomycota). American Journal of Botany 85: 1569–1580.
Sri-indrasutdhi V, Boonyuen N, Suetrong S, et al. 2010. Wood-inhabiting freshwater fungi from Thailand: Ascothailandia granadoidia gen. et sp. nov., Canalisporium granadoidia sp. nov. with a key to Canalisporium species (Sordariomycetes, Ascomycota). Mycoscience 51: 411–420.
Stamatakis A. 2006. RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. Bioinformatics 22: 2688–2690.
Stamatakis A, Ludwig T, Meier H. 2005. RaxML-III: a fast program for maximum likelihood-based inference of large phylogenetic trees. Bioinformatics 21: 456–463.
Sutton BC. 1973. Hyphomycetes from Manitoba and Saskatchewan, Canada. Mycological Papers 132: 1–143.
Sutton DA, Slifkin M, Yakulis R, et al. 1998. U.S. case report of cerebral phaeohyphomycosis caused by Ramichloridium obovoidum (R. mackenziei): Criteria for identification, therapy, and review of other known dematiaceous neurotropic taxa. Journal of Clinical Microbiology 36: 708–715.
Tsui CKM, Berbee ML. 2006. Phylogenetic relationships and convergence of helicosporous fungi inferred from ribosomal DNA sequences. Molecular Phylogenetics and Evolution 39: 587–597.
Tsui CKM, Hodgkiss LJ, Hyde KD. 2003. Three new species of Aquaticola (Ascomycetes) from tropical freshwater habitats. Nova Hedwigia 77: 161–168.
Tsui CKM, Ranghoo VM, Hodgkiss LJ, et al. 2002. Three new species of Annulatacusc (Ascomycetes) from Hong Kong freshwater habitats. Mycoscience 43: 383–389.
Udagawa SI, Toyazaki N. 1983. A new species of Conioscypha. Mycotaxon 18: 131–137.
Von Höhnel FXR. 1904. Mykologische Fragmente. Annales Mycologici 2: 38–60.
Von Höhnel FXR. 1909. Fragmente zur Mykologie (VI. Mitteilung, Nr. 182 bis 288). Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften in Wien. Mathematisch-Naturwissenschaftliche Klasse, Abt. 1, 118: 275–452.
Watanabe T. 1989. Soil fungal flora in Hachijo-jima island. Transactions of Mycological Society of Japan 30: 427–435.
Watanabe T. 1992. Taenirolella phialosperma sp. nov. from Japan. Mycologia 84: 478–483.
Zare R, Gams W, Starink-Willemsen M, et al. 2007. Gibellulopsis, a suitable genus for Verticillium nigrescens, and Musicillium, a new genus for V. theobromae. Nova Hedwigia 85: 463–469.
Zelski SE, Raja HA, Miller AN, et al. 2011. Chaetorostrum quinunciiilenis, gen. et sp. nov., a new freshwater ascomycete and its Taenirolella-like anamorph from Peru. Mycosphere 2: 593–600.
Zelski SE, Raja HA, Miller AN, et al. 2014. Conioscypha peruviana sp. nov., its phylogenetic placement based on 28S rRNA gene, and a report of Conioscypha gracilis comb. nov. from Peru. Mycoscience 56: 319–325.
Zhang N, Castelbury LA, Miller AN, et al. 2007, ’2006’. An overview of the systematics of the Sordariomycetes based on a four-gene phylogeny. Mycologia 98: 1076–1108.