

Phylogenetic classification and generic delineation of *Calyptosphaeria* gen. nov., *Lentomitella*, *Spadicoides* and *Torrentispora* (Sordariomycetes)

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Abstract: The genus *Ceratostomella* has a long history of taxonomic confusion. While species with evanescent asci have been transferred to the *Microascales* and *Ophiostomatales*, the taxonomic status of species with persistent asci has not been completely resolved. In previous studies using DNA sequence data, cultures and morphology, several *Ceratostomella* spp. were allocated in 13 genera in the *Eurotiomycetes* and *Sordariomycetes*. In our study, the systematics of the remaining *Ceratostomella* spp. with persistent asci is revisited with new collection data, cultures and phylogeny based on novel DNA sequences from six nuclear loci. Bayesian inference and Maximum Likelihood analyses support the monophyly of several wood-inhabiting species formerly classified in *Ceratostomella* and other unknown morphologically similar taxa and their division into four genera, i.e. *Lentomitella*, *Spadicoides*, *Torrentispora* and the newly described *Calyptosphaeria*. This robust clade represents the order *Xenospadicoidales* in the *Sordariomycetidae*. Comparative analysis of the ITS2 secondary structure revealed a genetic variation among *Lentomitella* isolates; 11 species were recognised, of which five are newly introduced and two are new combinations. Other taxonomic novelties include four new species and eight new combinations in *Calyptosphaeria*, *Spadicoides*, and *Torrentispora*. Molecular data suggest that *Spadicoides* is polyphyletic. The core of the genus is positioned in the *Xenospadicoidales*; *Spadicoides* s. str. is experimentally linked with sexual morphs for the first time. Based on DNA sequence data, the monotypic genera *Xenospadicoides* and *Pseudodiplococcium* are reduced to synonymy under *Spadicoides*, while *Fusoidispora* and *Pseudoannulatuscus* are synonymised with *Torrentispora*. Members of the *Xenospadicoidales* inhabit decaying wood in terrestrial and freshwater environments and share a few morphological characters such as the absence of stromatic tissue, ascomata with a cylindrical or rostrate neck, similar anatomies of the ascomatal walls, thin-walled unitunicate asci with a non-amyloid apical annulus, disintegrating paraphyses, usually ellipsoidal to fusiform ascospores and holoblastic-denticulate or tetric conidiogenesis. Revised *Ceratostomella* spp. with persistent asci are listed and the taxonomic status of each species is re-evaluated based on revision of the holotype and other representative material, published details and available phylogenetic data.

Key words: *Ceratostomella*, Conidiogenesis, Holoblastic-denticulate, Molecular systematics, New taxa, Phaeoisaria-like, Selenosporella-like, Tetric, Taxonomy, *Xenospadicoidales*.

Taxonomic novelties: **New genus:** *Calyptosphaeria* Réblová & A.N. Mill.; **New species:** *Calyptosphaeria collapsa* Réblová & A.N. Mill., *C. tenebrosa* Réblová & A.N. Mill., *Lentomitella magna* Réblová, *L. obscura* Réblová, *L. striatella* Réblová, *L. sulcata* Réblová, *L. tenuirostris* Réblová, *Torrentispora calembola* Réblová & A.N. Mill., *T. novae-zelandiae* Réblová & A.N. Mill.; **New combinations:** *Calyptosphaeria subdenudata* (Peck) Réblová & A.N. Mill., *C. tropica* (Huhndorf et al.) Réblová & A.N. Mill., *Lentomitella conoidea* (Feltg.) Réblová, *L. investita* (Schw.) Réblová, *Spadicoides fuscolutea* (Rehm) Réblová, *S. hyalostoma* (Munk) Réblová, *Spadicoides iberica* (Hern.-Restr. et al.) Réblová & A.N. Mill., *Torrentispora aquatica* (Vijaykr. et al.) Réblová & A.N. Mill., *T. biatriispora* (K.D. Hyde) Réblová & A.N. Mill., *T. dubia* (Sacc.) Réblová & A.N. Mill.

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INTRODUCTION

The perithecial ascomycete genus *Ceratostomella* (Saccardo 1878a) has a long history of taxonomic debate. Although the simple generic diagnosis comprised only hyaline, aseptate ascospores, asci and perithecia, which are similar to those of *Ceratostoma* (Fries 1818), *Ceratostomella* soon became a large, heterogeneous assemblage of fungi for which Index Fungorum lists 110 epithets. Although widely distributed throughout the Northern Hemisphere, members of *Ceratostomella* are inconspicuous and difficult to find due to their small immersed to superficial, long-necked ascomata. The asci are persistent or evanescent containing septate or aseptate, hyaline or brown ascospores, and most of the species are difficult to culture.

The homogeneity of *Ceratostomella* was soon challenged by Kuntze (1898), who transferred 29 species with persistent asci and mostly hyaline ascospores to *Amphitrichum* (Nees & Nees

1818). *Amphitrichum* was emended by Corda (1837) based on *A. olivaceum* (= ? *Cladosporium* sp. fide Hughes 1958), but later it was determined to be a nomen dubium fide Hughes (1958), as no type specimen was given. Kuntze (1898) clearly misinterpreted the generic concept of *Amphitrichum*, which is likely a dematiaceous hyphomycete. Another step towards clarification of the concept of *Ceratostomella* was made by Höhnelt (1906a). *Lentomitella*, originally described as a monotypic genus for *Ceratostomella vestita*, was introduced in order to segregate taxa with ellipsoidal, 1-septate, hyaline, longitudinally striate ascospores from species with similar ascospores containing more than one septum and 2–4 large drops. Höhnelt (1906a) suggested that such taxa should belong to *Ceratospheeria* and *Lentomita*. However, von Arx (1952) did not accept Höhnelt's narrow concept and designated *Ceratostomella* as the correct generic name.

The broadly perceived *Ceratostomella* was redefined by Réblová (2006) based on the lectotype species, *C. rostrata*

(Clements & Shear 1931), and three other accepted species. Using comparative morphology, *Ceratostomella* was confined to taxa with non-stromatic ascomata with a cylindrical neck, ascogonial wall up to 100 µm thick, persistent clavate asci arising from supporting ascogenous cells, broad-celled paraphyses and brown, aseptate, ellipsoidal to reniform ascospores. Based on DNA sequence data of two representative species, *C. cuspidata* and *C. pyrenaica*, the genus was classified as *Sordariomycetidae incertae sedis*. Species with evanescent asci and dark perithecia with filiform necks were recombined and placed in *Ceratocystis*, *Huntia* and *Thielaviopsis* of the *Microascales*, or *Lepographium*, *Ophiostoma* and *Pesotum* of the *Ophiostomatales* (Höhnelt 1918, Elliott 1925, Moreau 1952, Hunt 1956, de Beer et al. 2013a, b, 2014). Based on multigene phylogenetic analyses, the placement of the remaining *Ceratostomella* spp. with persistent asci was partially resolved resulting in the recovery of three robust phylogenetic lineages centred around the *Amplistromatales*, *Calosphaeriales* and *Ophiostomatales*. The genus *Wallrothiella* (Saccardo 1882) (*Amplistromatales*) based on *W. congregata* [= *Ceratostomella sphaerosperma*] was redefined with the aid of DNA sequence data, recently collected material and an acrodontium-like asexual morph (Réblová & Seifert 2004, Huhndorf et al. 2009). Several other *Ceratostomella* species were reclassified in *Jattaea* and *Togniniella* (*Calosphaeriales*) and *Phaeoacremonium* (*Togniniales*) based on the revision of type material, evidence from molecular data and phialophora- or acremonium-like asexual morphs producing phialidic conidia *in vitro* (Réblová et al. 2004, 2015a, Réblová 2011, Gramaje et al. 2015). The “ophiostomataceous” lineage comprised *Ceratostomella* s. str. and also *Barbatosphaeria*, *Lentomitella*, *Natantiella*, and *Xylomelasma* (Höhnelt 1906a, Réblová 2006, 2007, Huhndorf et al. 2008, Marinowitz et al. 2008, Réblová & Štěpánek 2009). The asexual morphs linked with genera of this lineage are dematiaceous hyphomycetes with holoblastic conidia produced on a sympodially extending rachis or on a terminal cluster of denticles. They are part of the life cycle of *Barbatosphaeria* as ramichloridium- and sporothrix-like (Samuels & Candoussau 1996, Réblová 2007, Réblová et al. 2015b) and *Lentomitella* as phaeoisaria-like (Réblová 2006) asexual morphs. Other *Ceratostomella* spp. were dispersed to *Ceratospheeria* (*Magnaporthales*) (Niessl 1876, Huhndorf et al. 2008), *Chaetosphaeria* (*Chaetosphaeriales*) (Booth 1957, Huhndorf & Fernández 2005), *Daruvedia* (*Pyrenulales*) (Dennis 1988) and *Pseudorhynchia* (*Hypocreales*) (Samuels & Barr 1997).

The ongoing taxonomic revision of species of *Ceratostomella* s. lat. with persistent asci revealed for many of them striking morphological similarities with *Lentomitella*. Based on nuLSU and nucSSU rDNA sequence data, comparative morphology and cultures, *Lentomitella* was reinstated in the *Sordariomycetidae* and shown to be distantly related to *Ceratostomella* (Réblová 2006). The generic concept of *Lentomitella* was expanded to include species with 1–3-septate, longitudinally striate, hyaline ascospores, and also aseptate, smooth-walled, hyaline (Réblová 2006) and brown ascospores (Huhndorf et al. 2008). Members of *Lentomitella* bear a certain resemblance to *Torrentispora* (Hyde et al. 2000) and *Pseudoannulatuscus* (Luo et al. 2015) characterised by ascomata with a long-neck, cylindrical asci and fusiform, hyaline, smooth- and thick-walled, usually aseptate ascospores, rarely with delayed formation of septa (Hyde et al. 2000, Fryar & Hyde 2004, Barbosa et al. 2013). A monotypic family, the *Lentomitellaceae*, was introduced by Zhang et al. (2017).

In this study, several species historically treated in *Ceratostomella* were recollected and isolated in axenic culture. Together with other unknown, morphologically similar taxa resembling *Lentomitella* and *Torrentispora* were subjected to phylogenetic analyses. Fungi of this assemblage occur on decaying wood or in bark in terrestrial habitats or on wood submerged in water. They share a simple inconspicuous morphology of non-stromatic ascomata with a cylindrical or rostrate neck, hyaline or brown, aseptate or septate, ornamented or smooth-walled ascospores, persistent asci with a non-amyloid apical annulus and partially disintegrating paraphyses. Little is known about their asexual morphs, which so far include only phaeoisaria-like morphs linked with *Lentomitella*. However, the majority of these fungi are difficult to culture or they produce only sterile mycelium *in vitro*. Recently, we found *Ceratostomella fuscolutea* (Rehm 1908), *Ceratostomella hyalostoma* (Untereiner 1993), and an unknown *lentomitella*-like species to produce *Spadicoides* asexual morphs *in vitro*. This dematiaceous hyphomycete is characterised by polytretic conidiogenous cells, unbranched conidiophores and dark brown septate or aseptate conidia borne singly or in short chains (Hughes 1958, Ellis 1963) and has not yet been linked with any sexually reproducing ascomycetes as a part of their life cycle. DNA sequence data suggest that *Spadicoides* is polyphyletic (Shenoy et al. 2010); *S. atra* was shown closely related to *Lentomitella*. Hernández-Restrepo et al. (2017) confirmed the placement of *S. bina*, the type species, in the *Cordanales* and segregated *S. atra* from *Spadicoides* into a monotypic genus *Xenospadicoides* in the *Xenospadicoidales*.

In order to unravel this part of the fungal tree of life, determine the placement of *Ceratostomella* spp. listed above and other similar taxa in monophyletic genera and resolve their familial and ordinal relationships, we employed a polyphasic approach in this study. We generated a multigene-based phylogeny of six nuclear ribosomal and protein-coding loci of the new isolates and intensively examined morphological characters of specimens and isolates in pure culture. We also investigated intraspecific relationships among members of *Lentomitella* using the Compensatory Base Change (CBC) criterion in the ITS2 secondary (2D) structure in two most conserved helices II and III (Mai & Coleman 1997, Coleman 2009) and also in helix I (Müller et al. 2007). The ITS2 is a fast-evolving part of the nuclear-coded rRNA operon, which has proven useful for formulating molecular taxonomic concepts, and its 2D structure has a potential to predict sexual incompatibility among closely related organisms. The CBC hypothesis is based on occurrence of compensatory base changes, i.e. co-evolution of nucleotides involved in the double-sided substitution in helices of the ITS2 molecule (Coleman 2000, Müller et al. 2007). We performed in-depth comparative analyses of ITS2 2D structures of *Lentomitella* spp. and mapped all existing substitutions among co-evolving nucleotides onto the predicted 2D model of ITS2 of the type species *L. vestita*.

MATERIAL AND METHODS

Herbarium material and fungal strains

Herbarium material was rehydrated with water and examined with an Olympus SZX12 dissecting microscope; hand-sectioned ascomata, centrum material (including asci, ascospores and paraphyses), conidiophores and conidia from living cultures were

mounted in 90 % lactic acid, Melzer's reagent or Lugol's iodine. All measurements were made in Melzer's reagent. Means \pm standard deviation (SD) based on 20–25 measurements are given for dimensions of asci, ascospores, conidiogenous cells and conidia. Microscopic structures were examined using an Olympus BX51 compound microscope (Olympus America, Inc., Melville, USA) with differential interference contrast (DIC) and phase contrast (PC) illumination. Images of microscopic structures were captured with an Olympus DP70 camera operated by Imaging Software Cell[^]D (Olympus). Macroscopic images of colonies were documented using an Olympus C-3030 digital camera with daylight spectrum 5600K 16W LED lights. All images were processed with Adobe Photoshop CS6 (Adobe Systems, San Jose, USA).

Cultures were maintained on Modified Leonian's agar (MLA) (Malloch 1981). For comparative purposes, strains were grown on MLA and potato-carrot agar (PCA) (Gams *et al.* 1998). Descriptions of colonies are based on 28-d-old cultures. Ex-type and other cultures are maintained at the Westerdijk Fungal Biodiversity Institute (CBS), Utrecht, the Netherlands and the International Collection of Microorganisms from Plants (ICMP), Auckland, New Zealand. Type and other herbarium material are deposited in the Herbarium of the Institute of Botany (PRA), Průhonice, Czech Republic, the New Zealand Fungarium (PDD), Auckland, New Zealand, and the Illinois Natural History Survey Fungarium (ILLS), Champaign, Illinois, USA.

DNA extraction, amplification and sequencing

Total genomic DNA was extracted from either mycelium removed from 14-d-old cultures grown on MLA or mature ascomata from herbarium material using the UltraClean Microbial DNA Kit (MoBio Laboratories Inc., Carlsbad, USA). For DNA extracted from herbarium material, an alternative lysis method was incorporated: the gelatinous centrum of 10–15 ascomata was saturated with distilled water, carefully removed with a needle and placed in a 1.9 mL MicroBead tube provided by the manufacturer. After the fungal material was dissolved in 300 μ L of MicroBead Solution and 50 μ L of Solution MD1, the preparations were heated to 65 °C for 10 min. The remaining steps for DNA extraction from cultures and herbarium material followed the manufacturer's protocol for filamentous fungi. All amplifications were carried out in 0.5 mL thin-walled PCR tubes (Eppendorf AG, Hamburg, Germany) using a PTC-200 thermal cycler (MJ Research Inc., Watertown, USA). PCR reactions and primers used for the amplification and sequencing of the internal transcribed spacer (ITS) of the nuclear rRNA cistron, portions of the nuclear ribosomal large subunit (nuLSU) and small subunit (nucSSU) RNA gene, and segments 5–7 of the second largest subunit of RNA polymerase II (*rpb2*) were carried out according to the methods of Réblová *et al.* (2017).

Primers used for the amplification and sequencing of other genes included: 1) ACT-512F and ACT-783R (Carbone & Kohn 1999) for alpha-actin (*act1*) gene and 2) T1 and Bt2a in combination with Bt2b (Glass & Donaldson 1995, O'Donnell & Cigelnik 1997) for exons 2–6 of beta-tubulin (*tub2*) gene. PCR reactions containing 4 mM MgSO₄ were performed using Platinum[®] Taq DNA polymerase High Fidelity (Invitrogen, Carlsbad, USA) in 25 μ L volume reactions. PCR conditions were (*act1*) 2 min at 94 °C, 45–48 cycles of 30 s at 94 °C, 30 s at 54–55 °C and 30 s at 68 °C; (*tub2*) 2 min at 94 °C, 40–48 cycles of 30 s at 94 °C, 30 s at

54–56 °C and 45–60 s at 68 °C, with a final extension of 10 min at 68 °C for all amplifications. Amplicons were either purified directly from PCR solution after amplification or isolated from agarose gel using the High Pure PCR Product Purification Kit (Roche Applied Science, Mannheim, Germany) following the manufacturer's directions. Automated sequencing was carried out by GATC Sequencing Service (Cologne, Germany). Raw sequence data were assembled, examined and edited using Sequencher v. 5.4.1 software (Gene Codes Corp., Ann Arbor, USA).

GenBank accession numbers for *act1*, ITS, nuLSU, nucSSU, *rpb2* and *tub2* sequences generated during this study and homologous sequences of representatives of the *Sordariomycetes* and *Leotiomycetes* retrieved from GenBank are listed in Table 1. Retrievable sequences have been published in various studies, e.g. Suh & Blackwell (1999), Huhndorf *et al.* (2004), Miller & Huhndorf (2004a, 2005), Réblová & Seifert (2004), Réblová (2006, 2013), Arzanlou *et al.* (2007), Spatafora *et al.* (2007), Damm *et al.* (2008), Schoch *et al.* (2009), Shenoy *et al.* (2010), Réblová *et al.* (2011, 2015b, 2016), Jaklitsch *et al.* (2013) Untereiner *et al.* (2013), Hernández-Restrepo *et al.* (2014), Su *et al.* (2016).

Sequence alignment

ITS, nuLSU, nucSSU and *rpb2* sequences were manually aligned in BioEdit v. 7.1.8 (Hall 1999). Alignments of *act1* and *tub2* sequences were generated in MAFFT v. 7 (Katoh & Standley 2013) and manually corrected where necessary. Consensus 2D structure models for the ITS1 and ITS2 were obtained for all members of the *Xenospadicoidales* and used to determine positions of homologous nucleotides in the ITS alignment. Introns occurring in nuLSU and nucSSU were delimited manually and excluded from the alignment; in addition, 438 nucleotides (nt) of nuLSU at the 3'-end and 127 nt of nucSSU at the 5'-end were excluded from the alignment because of the incompleteness in the majority of sequences.

The single-locus data sets were examined for topological incongruence among loci for members of the *Xenospadicoidales* (*act1*: 35 sequences/338 characters including gaps, ITS: 37/757, nuLSU: 39/1 842, nucSSU: 34/1 668, *rpb2*: 29/1 127, *tub2*: 28/966), and members of the *Sordariomycetidae* (nuLSU: 104/1 973, nucSSU: 71/1 787, *rpb2*: 65/1 189). Congruence among the loci was tested using the 70 % reciprocal bootstrap criterion (Mason-Gamer & Kellogg 1996). For each individual partition, 1 000 bootstrap replicates were generated with RAxML-HPC v. 7.0.3 (Stamatakis 2006) and PAUP v. 4.0b10 (Swofford 2002) and compared visually for topological conflict among supported clades in phylogenetic trees. The conflict-free alignments were concatenated into a multi-locus alignment that was subjected to subsequent phylogenetic analyses. The multiple sequence alignment is deposited in TreeBASE (S21034).

Phylogenetic analyses

In order to explore monophyly and infrageneric relationships within *Lentomitella*, *Spadicoides*, *Torrentispora* and other morphologically similar taxa, and to resolve their phylogenetic relationships in a broader context we performed analyses of combined *act1*, ITS, nuLSU, nucSSU, *rpb2* and *tub2* sequences on two datasets: a reduced dataset consisting of members of these genera and a full dataset consisting of these taxa along

Table 1. List of fungi, isolate information and new sequences determined for this study and those retrieved from GenBank. The asterisk (*) denotes ex-type strains of members of the *Xenospadicoidales*. GenBank accession numbers in **bold** were generated for this study.

Classification	Taxon	Source	GenBank accession numbers					References
			nucLSU	nucSSU	<i>rpb2</i>	ITS	<i>act1</i>	
<i>Annulatascales</i>	<i>Annulatascus velatisporus</i>	A 70-18	AY316354	–	–	–	–	Raja <i>et al.</i> (2003)
	<i>Annulusmagnus triseptatus</i>	CBS 131483	GQ996540	JQ429242	JQ429258	–	–	Réblová <i>et al.</i> (2010, 2012)
	<i>Ascitendus austriacus</i>	CBS 131685	GQ996539	GQ996542	JQ429257	–	–	Réblová <i>et al.</i> (2010, 2012)
<i>Atractosporales</i>	<i>Atractospora decumbens</i>	CBS 139032	KT991658	KT991640	KT991647	–	–	Réblová <i>et al.</i> (2016)
	<i>A. ellipsoidea</i>	A 411-3	AY316356	–	–	–	–	Raja <i>et al.</i> (2003)
	<i>A. reticulata</i>	CBS 127884	KT991660	–	KT991649	–	–	Réblová <i>et al.</i> (2016)
	<i>A. verruculosa</i>	CBS 132040	KT991659	KT991641	KT991648	–	–	Réblová <i>et al.</i> (2016)
	<i>Rubellisphaeria abscondita</i>	CBS 132078	KT991666	KT991646	KT991657	–	–	Réblová <i>et al.</i> (2016)
<i>Barbatosphaeriaceae</i>	<i>Barbatosphaeria barbirostris</i>	CBS 121149	EF577059	KM492851	KM492903	–	–	Réblová <i>et al.</i> (2015b)
	<i>B. dryina</i>	CBS 127691	KM492864	KM492852	KM492904	–	–	Réblová <i>et al.</i> (2015b)
<i>Boliniales</i>	<i>Camarops microspora</i>	CBS 649.92	AY083821	DQ471036	DQ470937	–	–	Smith <i>et al.</i> (2003), Spatafora <i>et al.</i> (2007)
	<i>Aporhynchostoma curreyi</i>	UAMH 11088	JX460989	KY931894	KY931926	–	–	Untereiner <i>et al.</i> (2013), this study
	<i>Endoxyla operculata</i>	UAMH 11085	JX460992	KY931895	KY931927	–	–	Untereiner <i>et al.</i> (2013), this study
<i>Calosphaeriales</i>	<i>Calosphaeria pulchella</i>	CBS 115999	AY761075	AY761071	GU180661	–	–	Réblová <i>et al.</i> (2004, 2011)
	<i>Jattaea algeriensis</i>	CBS 120871	EU367457	EU367462	HQ878603	–	–	Damm <i>et al.</i> (2008), Réblová (2011)
	<i>Togniniella acerosa</i>	CBS 113648	AY761076	AY761073	GU180660	–	–	Réblová <i>et al.</i> (2004), Réblová (2011)
<i>Chaetosphaeriales</i>	<i>Chaetosphaeria ciliata</i>	ICMP 18253	GU180637	GU180614	GU180659	–	–	Réblová <i>et al.</i> (2011)
	<i>C. curvispora</i>	ICMP 18255	GU180636	AY502933	GU180655	–	–	Réblová <i>et al.</i> (2011)
	<i>Melanochaeta hemipsila</i>	S.M.H. 2125	AY346292	–	AY780184	–	–	Huhndorf <i>et al.</i> (2004), Miller & Huhndorf (2005)
<i>Coniochaetales</i>	<i>Barrina polyspora</i>	AWR 9560A	AY346261	–	–	–	–	Huhndorf <i>et al.</i> (2004)
	<i>Coniochaeta discoidea</i>	SANK 12878	AY346297	AJ875179	AY780191	–	–	Huhndorf <i>et al.</i> (2004), García <i>et al.</i> (2006)
	<i>C. ostrea</i>	CBS 507.70	DQ470959	DQ471007	DQ470909	–	–	Spatafora <i>et al.</i> (2007)
<i>Cordanales</i>	<i>Cordana terrestris</i>	ICMP 15117	EF063573	–	–	–	–	Réblová & Seifert (2007)
	<i>C. pauciseptata</i>	M.R. 1150	AF178563	–	–	–	–	Réblová & Winka (2000)
	<i>C. pauciseptata</i>	CBS 113708	EF204507	–	EF204490	–	–	Shenoy <i>et al.</i> (2010)
	<i>C. pauciseptata</i>	IMI 102120	HE672158	–	–	–	–	Hernández-Restrepo <i>et al.</i> (2014)
	<i>C. ellipsoidea</i>	IMI 229746	HE672156	–	–	–	–	Hernández-Restrepo <i>et al.</i> (2014)
	<i>C. inaequalis</i>	CBS 508.83	HE672157	–	–	–	–	Hernández-Restrepo <i>et al.</i> (2014)
<i>Diaporthales</i>	<i>Diaporthe phaseolorum</i>	FAU 458, NRRL 13736	U47830	L36985	AY641036	–	–	Spatafora & Blackwell (1993), Reeb <i>et al.</i> (2004)
	<i>Gnomonia gnomon</i>	CBS 199.53	AF408361	DQ471019	DQ470922	–	–	Castlebury <i>et al.</i> (2002), Spatafora <i>et al.</i> (2007)
	<i>Valsa ambiens</i>	AR 3516	AF362564	DQ862056	DQ862025	–	–	Zhang <i>et al.</i> (2007)
<i>Distoseptisporaceae</i>	<i>Distoseptispora fluminicola</i>	MFLUCC 15-0417	KU376270	–	–	–	–	Su <i>et al.</i> (2016)
	<i>D. aquatica</i>	MFLUCC 15-0374	KU376268	–	–	–	–	Su <i>et al.</i> (2016)
	<i>D. adscendens</i>	HKUCC 10820	DQ408561	–	DQ435092	–	–	Shenoy <i>et al.</i> (2006)
	<i>D. leonensis</i>	HKUCC 10822	DQ408566	–	DQ435089	–	–	Shenoy <i>et al.</i> (2006)
<i>Jobellisiales</i>	<i>Jobellisia fraterna</i>	S.M.H. 2863	AY346285	–	–	–	–	Huhndorf <i>et al.</i> (2004)
	<i>J. luteola</i>	S.M.H. 2753	AY346286	–	–	–	–	Huhndorf <i>et al.</i> (2004)
<i>Magnaporthales</i>	<i>Gaeumannomyces graminis</i>	AR 3401, M 57	AF362557	JF414874	–	–	–	Farr <i>et al.</i> (2001), Zhang <i>et al.</i> (2011)
	<i>Macgarvieomyces borealis</i>	CBS 461.65	DQ341511	DQ341489	KM485070	–	–	Thongkantha <i>et al.</i> (2009), Klabauf <i>et al.</i> (2014)

Table 1. (Continued).

Classification	Taxon	Source	GenBank accession numbers						References
			nucLSU	nucSSU	rpb2	ITS	act1	tub2	
	<i>Magnaporthe grisea</i>	Ina168, 70-15	AB026819	DQ493955	–	–	–	–	Sone <i>et al.</i> (2000), Rehmeier <i>et al.</i> (2006)
Myrmecridiales	<i>Myrmecridium flexuosum</i>	CBS 398.76	EU041825	–	–	EU041768	–	–	Arzanlou <i>et al.</i> (2007)
	<i>M. montsegurinum</i>	PRM 934684	KT991664	KT991645	KT991654	KT991674	–	–	Réblová <i>et al.</i> (2016)
	<i>M. schulzeri</i>	CBS 100.54	EU041826	–	–	EU041769	–	–	Arzanlou <i>et al.</i> (2007)
Ophiostomatales	<i>Ceratocystiopsis minuta</i>	UM 1533, WIN(M)1537	EU913657	HQ634854	–	–	–	–	Plattner <i>et al.</i> (2009), Hafez <i>et al.</i> (2012)
	<i>Fragosphaeria purpurea</i>	CBS 133.34	AF096191	AF096176	–	–	–	–	Suh & Blackwell (1999)
	<i>Ophiostoma piliferum</i>	CBS 158.74	DQ470955	DQ471003	DQ470905	–	–	–	Spatafora <i>et al.</i> (2007)
	<i>Raffaelea ambrosiae</i>	CBS 185.64	EU984297	AY497518	–	–	–	–	Gebhardt <i>et al.</i> (2004), Massoumi Alamouti <i>et al.</i> (2009)
Papulosaceae	<i>Brunneosporella aquatica</i>	HKUCC 3708	AF132326	–	–	–	–	–	Ranghoo <i>et al.</i> (1999)
	<i>Fluminicola coronata</i>	HKUCC 3717	AF132332	–	–	–	–	–	Ranghoo <i>et al.</i> (1999)
	<i>Papulosa amerospora</i>	J.K. 5547F	DQ470950	DQ470998	DQ470901	–	–	–	Spatafora <i>et al.</i> (2007)
Phomatosporales	<i>Lanspora coronata</i>	J.K. 4839A	U46889	DQ470996	DQ470899	–	–	–	Spatafora <i>et al.</i> (1998, 2007)
	<i>Phomatospora bellaminuta</i>	J.K. 5543N	FJ176857	FJ176803	FJ238345	–	–	–	Schoch <i>et al.</i> (2009)
Sordariales	<i>Gelasinospora tetrasperma</i>	CBS 178.33	DQ470980	DQ471032	DQ470932	–	–	–	Spatafora <i>et al.</i> (2007)
	<i>Lasiosphaeria ovina</i>	S.M.H. 1538, CBS 958.72	AF064643	AY083799	AY600292	–	–	–	Fernández <i>et al.</i> (1999), Smith <i>et al.</i> (2003), Miller & Huhndorf (2004a)
	<i>Sordaria fimicola</i>	S.M.H. 4106, MUCL 937, CBS 723.96	AY780079	X69851	DQ368647	–	–	–	Miller & Huhndorf (2005), Tang <i>et al.</i> (2007)
Sporidesmiaceae	<i>Sporidesmium parvum</i>	HKUCC 10836	DQ408558	–	–	–	–	–	Shenoy <i>et al.</i> (2006)
	<i>S. minigelatinosa</i>	NN 47497	DQ408567	–	DQ435090	–	–	–	Shenoy <i>et al.</i> (2006)
	<i>S. bambusicola</i>	HKUCC 3578	DQ408562	–	–	–	–	–	Shenoy <i>et al.</i> (2006)
	<i>S. fluminicola</i>	MFLUCC 15-0346	KU376271	–	–	–	–	–	Su <i>et al.</i> (2016)
	<i>S. aquaticum</i>	MFLUCC 15-0420	KU376273	–	–	–	–	–	Su <i>et al.</i> (2016)
	<i>S. submersum</i>	MFLUCC 15-0421	KU376272	–	–	–	–	–	Su <i>et al.</i> (2016)
Togniniales	<i>Phaeoacremonium minimum</i>	CBS 213.31, CBS 111015	AY761082	AY761068	HQ878610	–	–	–	Réblová <i>et al.</i> (2004), Réblová (2011)
	<i>P. fraxinopennsylvanicum</i>	CBS 128920	HQ878595	HQ878600	HQ878609	–	–	–	Réblová (2011)
Woswasiaceae	<i>Woswasia atropurpurea</i>	CBS 133167	JX233658	JX233658	JX233659	–	–	–	Jaklitsch <i>et al.</i> (2013)
	<i>Xylochrysis lucida</i>	CBS 135996	KF539911	KF539912	KF539913	–	–	–	Réblová <i>et al.</i> (2014)
Xenospadicoidales	<i>Calyptosphaeria collapsa</i>	PRA-12743*	KY931834	KY931892	KY931861	KY931808	KY931771	KY931924	This study
	<i>C. subdenudata</i>	S.M.H. 3877*	EU527994	–	–	KY931774	KY931739	–	Huhndorf <i>et al.</i> (2008), this study
	<i>C. subdenudata</i>	S.M.H. 2534	EU527993	–	–	KY931775	KY931740	–	Huhndorf <i>et al.</i> (2008), this study
	<i>C. tenebrosa</i>	PRA-12742	–	–	–	KY931776	KY931741	–	This study
	<i>C. tenebrosa</i>	PRA-12741	KY931809	KY931864	KY931836	KY931777	KY931742	KY931898	This study
	<i>C. tenebrosa</i>	PRA-12740*	KY931810	KY931865	KY931837	KY931778	KY931743	KY931899	This study
	<i>C. tropica</i>	S.M.H. 1797*	EU527992	KY931866	–	KY931779	KY931744	–	Huhndorf <i>et al.</i> (2008), this study
	<i>C. tropica</i>	S.M.H. 3225	EU527999	–	–	–	–	–	Huhndorf <i>et al.</i> (2008), this study
	<i>Lentomitella cirrhosa</i>	ICMP 15131*	AY761085	AY761089	KM492911	KY931780	KY931745	KY931900	Réblová (2006), Réblová <i>et al.</i> (2015b), this study
	<i>L. crinigera</i>	CBS 138678	KY931811	KY931867	–	KY931781	KY931746	KY931901	This study
	<i>L. conoidea</i>	CBS 131481	KT991663	KT991644	KT991653	KY931782	KY931747	–	Réblová <i>et al.</i> (2016), this study
	<i>L. conoidea</i>	CBS 131660	KY931812	KY931868	KY931840	KY931783	KY931748	KY931902	This study
	<i>L. conoidea</i>	CBS 141370	KY931813	KY931869	KY931841	KY931784	KY931749	KY931903	This study

(continued on next page)

Table 1. (Continued).

Classification	Taxon	Source	GenBank accession numbers						References
			nucLSU	nucSSU	<i>rpb2</i>	ITS	<i>act1</i>	<i>tub2</i>	
	<i>L. conoidea</i>	M.R. 3135	KY931814	KY931870	KY931842	KY931785	KY931750	KY931904	This study
	<i>L. magna</i>	ICMP 18371*	KY931815	KY931871	KY931843	KY931786	KY931751	–	This study
	<i>L. obscura</i>	CBS 137799	KY931816	KY931872	KY931844	KY931787	KY931752	KY931905	This study
	<i>L. obscura</i>	CBS 138735	KY931817	KY931873	–	KY931788	KY931753	KY931906	This study
	<i>L. obscura</i>	CBS 138736*	KY931818	KY931874	KY931845	KY931789	KY931754	KY931907	This study
	<i>L. striatella</i>	ICMP 18369*	KY931819	KY931875	KY931846	KY931790	KY931755	KY931908	This study
	<i>L. sulcata</i>	ICMP 15124*	AY761086	KY931876	KY931847	KY931791	KY931756	KY931909	This study
	<i>L. tenuirostris</i>	CBS 138734*	KY931821	KY931877	KY931849	KY931792	KY931758	KY931910	This study
	<i>L. tenuirostris</i>	CBS 141371	KY931822	KY931878	KY931850	KY931793	KY931759	KY931911	This study
	<i>L. vestita</i>	PRA-12739	KY931820	KY931879	KY931848	KY931794	KY931757	–	This study
	<i>Lentomitella sp.</i>	M.R. 2953	KY931823	KY931880	–	KY931795	–	KY931912	This study
	<i>Spadicoides atra</i>	CBS 489.77	EF204506	EF204521	EF204489	–	–	–	Shenoy <i>et al.</i> (2010)
	<i>S. bina</i>	CBS 137794	KY931824	KY931881	KY931851	KY931796	KY931760	KY931913	This study
	<i>S. fuscolutea</i>	CBS 141262	KY931825	KY931882	KY931852	KY931797	KY931761	KY931914	This study
	<i>S. fuscolutea</i>	CBS 141263	KY931826	KY931883	KY931853	KY931798	KY931762	KY931915	This study
	<i>S. hyalostoma</i>	CBS 131268	KY931827	KY931884	KY931854	KY931799	KY931763	KY931916	This study
	<i>S. hyalostoma</i>	CBS 137793	KY931828	KY931885	KY931855	KY931800	KY931764	KY931917	This study
	<i>S. hyalostoma</i>	CBS 138688	KY931829	KY931886	KY931856	KY931801	KY931765	KY931918	This study
	<i>S. hyalostoma</i>	CBS 139771	KY931830	KY931887	KY931857	KY931802	KY931766	KY931919	This study
	<i>S. iberica</i>	CBS 127864*	KY853527	–	–	–	–	–	Hernández-Restrepo <i>et al.</i> (2017)
	<i>Torrentispora aquatica</i>	HKU(M) 17484*	AY780365	–	–	–	–	–	Vijaykrishna <i>et al.</i> (2005)
	<i>T. biatriispora</i>	A 464-3	AY316352	–	KY931858	KY931803	KY931767	KY931920	Raja <i>et al.</i> (2003), this study
	<i>T. calembola</i>	PRA-12744*	KY931831	KY931888	–	KY931804	KY931768	KY931921	This study.
	<i>T. dubia</i>	PRA-12746	KY931832	KY931889	–	KY931805	KY931769	KY931922	This study
	<i>T. fibrosa</i>	ICMP 15147	EF577060	KY931890	KY931859	KY931806	KY931770	KY931923	This study
	<i>T. novae-zelandiae</i>	ICMP 18368*	KY931833	KY931891	KY931860	KY931807	–	–	This study
Genera incertae sedis	<i>Brachysporium nigrum</i>	M.R. 1346	KT991662	KT991643	KT991652	–	–	–	Réblová <i>et al.</i> (2016)
	<i>B. polyseptatum</i>	DAOM 231136	AY281102	–	–	–	–	–	Réblová & Seifert (2004)
	<i>Bullimyces communis</i>	AF 281-3	JF775585	JF758617	–	–	–	–	Ferrer <i>et al.</i> (2012)
	<i>Ceratostomella cuspidata</i>	ICMP 17629	FJ617558	KT991642	KT991651	KT991671	KY931772	–	Réblová <i>et al.</i> (2016), this study
	<i>C. pyrenaica</i>	CBS 129343	KY931835	KY931893	KY931863	KT991672	KY931773	–	Réblová <i>et al.</i> (2016), this study
	<i>Ceratolenta caudata</i>	CBS 125234	JX066704	JX066708	JX066699	–	–	–	Réblová (2013)
	<i>Natantiella ligneola</i>	CBS 123470	FJ617556	HQ878598	HQ878605	–	–	–	Réblová <i>et al.</i> (2016)
	<i>Platytrachelon abietis</i>	CBS 125235	JX066703	JX066707	JX066698	–	–	–	Réblová (2013)
	<i>Rhamphoria delicatula</i>	M.R. 1396	AF261068	AF242267	KT991655	–	–	–	Winka (2000), Réblová <i>et al.</i> (2016)
	<i>Rhodoveronaea varioseptata</i>	CBS 123473	FJ617560	JX066710	JX066700	–	–	–	Réblová (2009, 2013)
	<i>Spadicoides verrucosa</i>	CBS 128.86	EF204508	EF204522	–	–	–	–	Shenoy <i>et al.</i> (2010)
	<i>Sporidesmium tropicale</i>	HKUCC 10838	DQ408560	–	–	–	–	–	Shenoy <i>et al.</i> (2006)
	<i>Thyridium vestitum</i>	AR 3872	AY544671	AY544715	DQ470890	–	–	–	Schoch <i>et al.</i> (2009), Spatafora <i>et al.</i> (2007)
	<i>Xylomelasma sordida</i>	CBS 116000	AY761087	AY761090	KY931929	–	–	–	Réblová (2006), this study
Helotiales (outgroup)	<i>Leotia lubrica</i>	AFTOL 1	AY544644	L37536	DQ470876	–	–	–	Gargas & Taylor (1995), Spatafora <i>et al.</i> (2007), Schoch <i>et al.</i> (2009)
	<i>Microglossum rufum</i>	AFTOL 1292	DQ470981	DQ257358	DQ470933	–	–	–	Spatafora <i>et al.</i> (2007)

with homologous sequences of representatives of the subclass *Sordariomycetidae*. In order to resolve relationships among *Pseudodiplococcium*, *Spadicoides* and *Xenospadicoides*, a third analysis was based on a reduced ITS-nucLSU dataset of their representatives, mainly due to the availability of only a nucLSU sequence for *Pseudodiplococcium ibericum*. Two *Ceratostomella* species, *C. cuspidata* and *C. pyrenaica* (*Sordariomycetidae*, *incertae sedis*), and *Leotia lubrica* and *Microglossum rufum* (*Helotiales*, *Leotiomycetes*) were used to root the individual trees in the reduced and full analyses.

The combined datasets were partitioned into several subsets of nucleotide sites, i.e. ITS, nucLSU, nucSSU, *rpb2* and coding and non-coding regions of *act1* and *tub2*. Bayesian Inference (BI) and Maximum Likelihood (ML) analyses were used to estimate phylogenetic relationships. BI analyses were performed in a likelihood framework as implemented in MrBayes v. 3.2.6 (Huelsenbeck & Ronquist 2001) through the CIPRES Science Gateway v. 3.3 (<http://www.phylo.org>). For the BI approach, MrModeltest2 v. 2.3 (Nylander 2008) was used to infer the appropriate substitution model that would best fit the model of DNA evolution. The following models were selected according to the Akaike information criterion for partitions for which we assumed rate heterogeneity: GTR+I+G for ITS, nucLSU, *rpb2* and coding region of *act1*, GTR+G for nucSSU and coding region of *tub2* and HKY+I+G for non-coding regions of *act1* and *tub2*. Two Bayesian searches were performed using default parameters. The B-MCMCMC analyses lasted until the average standard deviation of split frequencies was below 0.01 with trees saved every 1 000 generations. The first 25 % of saved trees, representing the burn-in phase of the analysis, were discarded. The remaining trees were used for calculating posterior probabilities (PP) of recovered branches. ML analyses were performed with RAxML-HPC v. 7.0.3 with a GTRCAT approximation. Nodal support was determined by non-parametric bootstrapping (BS) with 1 000 replicates. Maximum Parsimony (MP) analyses conducted with PAUP v. 4.0b10 (Swofford 2002) were used as supplementary to ML analyses to evaluate congruence among loci and topological variation of single-gene phylogenetic trees. A heuristic search was performed with the stepwise-addition option with 1 000 random taxon addition replicates and TBR branch swapping. All characters were unordered and given equal weight. Gaps were treated as missing data. Branch support was estimated on the recovered topologies by performing a heuristic search of 1 000 bootstrap replicates consisting of ten random-addition replicates for each bootstrap replicate.

Prediction of 2D structure models of ITS of *Lentomitella*

Predicting the 2D structure of the variable and rapidly evolving ITS region is essential for constructing a reliable multiple sequence alignment to compare nucleotides at homologous positions (in helices and loops) while searching for non-conserved co-evolving nucleotides which maintain base pairing. Consensus 2D structure models for the ITS1 and ITS2 were built using the PPfold program v. 3.0 (Sukosd *et al.* 2012) which uses an explicit evolutionary model and a probabilistic model of structures, and relies on multiple sequence alignment of related RNA sequences. The obtained 2D consensus models created for all members of *Xenospadicoidales* were further improved using the program Mfold (Zuker 2003) and then adjusted manually if

necessary, based on comparison of homologous positions in the multiple sequence alignment. The predicted 2D RNA structures were obtained in a dot bracket notation and were visualized and drawn using the program VARNA: Visualization Applet for RNA (Darty *et al.* 2009). The final 2D model of ITS2, which was further utilized in formulating taxonomic hypotheses, was processed with CoreIDRAW Graphics Suite X4.

We performed in-depth comparative analyses of ITS2 2D structures of *Lentomitella* spp. We identified three types of substitutions in the aligned ITS sequences. The compensatory base changes (CBCs) occur when both nucleotides of a paired site mutate, i.e. G=C \leftrightarrow C=G, A-U or U-A, while maintaining a canonical base pair. The hemi-compensatory base changes (hCBCs) inflict the change of a canonical base pair to a near-canonical so called “wobble” base pair, i.e. G=C \rightarrow G/U. The non-compensatory base changes (non-CBC) involve the replacement of a canonical pair or a wobble pair with any non-canonical pair. While the CBCs and hCBCs are responsible for maintaining the RNA helix arrangement, non-CBCs lead to its disruption (Leontis *et al.* 2002). All existing substitutions among *Lentomitella* species identified in the ITS2 were mapped onto the predicted 2D structure of ITS2 of *L. vestita*, the generic type (ITS sequence: KY931794).

RESULTS

Topological variation in single-gene, five- and six-gene phylogenetic trees

We studied molecular phylogenies of the *Xenospadicoidales* based on six nuclear markers in order to compare their phylogenetic utility. Three loci were shown to provide the highest number of distinct alignment patterns (RAxML) and parsimony informative characters (PAUP): *rpb2* (556/459), *tub2* (671/414) and ITS (496/347), which is one or more times as much as provided by nucLSU (318/168), *act1* (255/151) and nucSSU (181/65) loci.

Although topologies of gene trees were generally concordant, there was some incongruence regarding the position of specimen PRA-12743. This specimen is morphologically highly similar to species for which a new genus *Calyptosphaeria* is introduced below. PRA-12743 was shown either nested in the strongly supported *Calyptosphaeria* clade in ITS (100 % ML BS) and nucSSU (99) trees or as sister to *Calyptosphaeria* in the tree based on *tub2* (82). In addition, it was resolved on a separate branch; at the base (100) of the *Xenospadicoidales* clade in the *act1* tree or at the base of the *Lentomitella*/*Calyptosphaeria* clade without support in the nucLSU tree or supported in the *rpb2* tree (not shown). This internode received 92 % and 69 % bootstrap support in the ML and MP analyses, respectively, in the *rpb2* tree. The absence of *tub2* and *rpb2* sequences of *C. subdenudata* and *C. tropica* may affect tree topologies based on these genes. In all single-gene phylogenies, *Lentomitella*, *Spadicoides* and *Torrentispora* were always resolved as strongly supported monophyletic clades except in the nucSSU where *Spadicoides* is paraphyletic with low statistical support.

Two ML and BI phylogenetic analyses were performed for comparison based on a five-gene data set (excluding *rpb2*, results not shown) and a six-gene data set (Fig. 1). In the five-gene tree inferred from ML analysis, PRA-12743 is placed within the

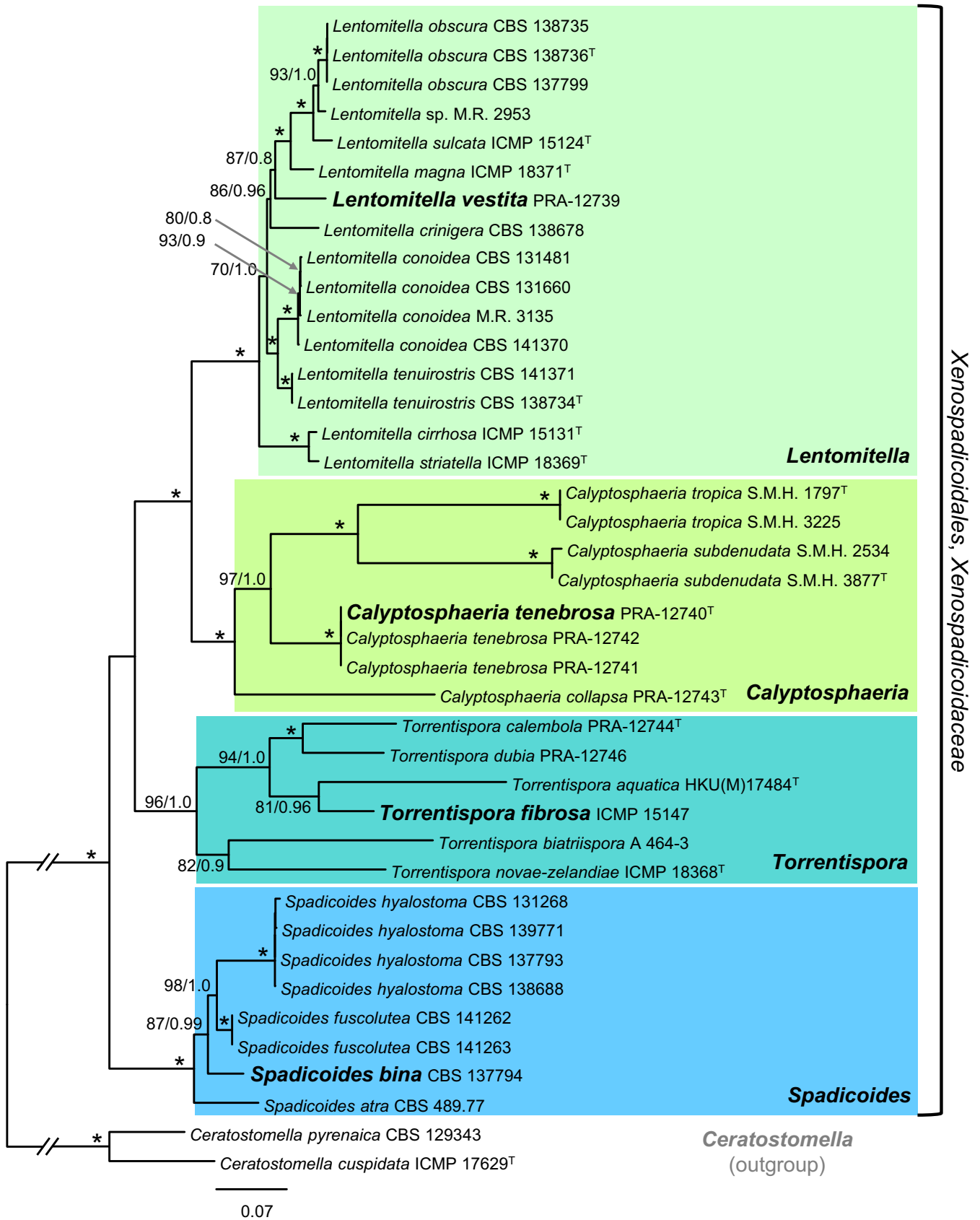


Fig. 1. Phylogenetic analysis of members of the *Xenosporidiales*. Phylogram inferred from the *act1*-ITS-nucLSU-nucSSU-*tub2*-*rpb2* sequences with ML analysis using a GTRCAT model of evolution. An asterisk (*) indicates branches with ML BS = 100 %, PP values = 1.0. Branch support of nodes ≥ 70 % ML BS and ≥ 0.80 PP is indicated above or below branches. 'T' after the name indicates type strain. Taxa given in bold are type species of *Calyptosphaeria*, *Lentomitella*, *Spadicoides* and *Torrentispora*.

Calyptosphaeria clade (100) on a branch next to *C. tenebrosa* without support. In the five-gene tree inferred from BI analysis, PRA-12743 is shown at the basal position within a strongly supported clade (1.0 PP) as sister to *Calyptosphaeria* (0.81). In the combined six-gene analysis, the position of PRA-12743 basal in the *Calyptosphaeria* clade (97/1.0) is strongly supported (100/1.0), and thus this analysis supports its inclusion in *Calyptosphaeria*.

Because the only incongruence among data sets based on individual genes was the placement of PRA-12743 in the *rpb2* tree inferred from ML analysis, the data sets were concatenated. Combination of these six nuclear loci provided robust phylogenetic support for all genera, based on a mixture of the faster evolving ITS region and non-coding regions of *act1* and *tub2* and generally more preserved and slower evolving regions like nucSSU.

The comparison of ITS sequences among the three species of *Calyptosphaeria* and PRA-12743 indicated that the latter taxon has the highest divergence among these species. While the length of the ITS sequences of *Calyptosphaeria* spp. varies between 553–569 nt, the ITS sequence of PRA-12743 (655 nt) is longer by ca. 100 nt with the longest insertion in the helix III of the ITS2.

Phylogeny

In the reduced analysis, 38 combined *act1*, ITS, nuLSU, nucSSU, *rpb2* and *tub2* sequences were assessed for 24 species in four genera of the *Xenospadicoidales*. The alignment consisted of 6 698 characters including gaps and 2 491 distinct alignment patterns (ML analysis). No topological conflicts occurred between trees generated from ML and BI analyses; the ML tree is shown in Fig. 1. The *Xenospadicoidales* (100 % ML BS/1.0 PP) are resolved with four strongly supported subclades that represent *Lentomitella* (100/1.0), *Spadicoides* (100/1.0), *Torrentispora* (96/1.0) and the newly introduced *Calyptosphaeria* (100/1.0). *Lentomitella* comprises 16 strains belonging to nine species, of which five are newly introduced to science. *Ceratostomella fuscolutea* and *Ceratostomella hyalostoma* grouped in the *Spadicoides* clade and therefore these two species are combined in *Spadicoides*. *Xenospadicoides atra*, the type species, formerly described as *Spadicoides atra*, is nested in the *Spadicoides* clade and therefore is accepted in the latter genus. *Ceratostomella dubia*, *Fusoidispora aquatica*, *Pseudoannulatasacus biatriisporus* and two unknown torrentispora-like fungi grouped with *T. fibrosa*, the type species, in a monophyletic clade resulting in two new species and three new combinations in *Torrentispora*. The new genus *Calyptosphaeria* is introduced for *Ceratostomella subdenudata*, *Lentomitella tropica* and two morphologically similar hitherto unknown fungi. They are shown on a separate strongly supported branch unrelated to the core of *Lentomitella*.

The full data set consisted of combined nuLSU, nucSSU and *rpb2* sequences of 102 members of the *Sordariomycetidae*. This alignment consisted of 4 949 characters and 2 280 distinct alignment patterns (ML analysis). The ML tree is shown in Fig. 2. The BI and ML tree topologies differed in the position of *C. collapsa*. In the ML analysis, the *Calyptosphaeria* clade with *C. collapsa* at the basal position is shown to be monophyletic but statistically unsupported, while in the BI analysis *C. collapsa* is shown on a separate branch. Another topological difference lies

in the position of *Sporidesmiaceae* and *Atractosporales* clades as sisters to *Xenospadicoidales* in the BI analysis. The *Sordariomycetidae* contain three major clades (A–C). Clade A (99/1.0) includes orders *Calosphaerales*, *Diaporthales*, *Jobellisiales* and *Togniniales*. Clade B (100/1.0) comprises five orders including the *Boliniales*, *Chaetosphaerales*, *Coniochaetales*, *Cordanales* and *Sordariales*. Clade C (91/0.93) contains orders *Annulatascales*, *Atractosporales*, *Magnaporthales*, *Myrmecridiales*, *Ophiostomatales* and *Phomatosporales*, and five families including *Barbatosphaeriaceae*, *Distoseptisporaceae*, *Papulosaceae*, *Sporidesmiaceae* and *Woswasiaceae*. The *Xenospadicoidales* are shown as a strongly supported monophyletic group (98/1.0) embedded in clade C and distantly related to *Ceratostomella* represented by *C. cuspidata* and *C. pyrenaica* in our phylogeny. Its closest relatives are members of the *Atractosporales*, *Ophiostomatales*, *Papulosaceae* and *Sporidesmiaceae* and several genera of non-stromatic perithecial ascomycetes and dematiaceous hyphomycetes of uncertain positions. The strain CBS 113708 of *Cordana pauciseptata*, formerly misidentified as *Spadicoides bina* (Shenoy *et al.* 2010, Hernández-Restrepo *et al.* 2017), is grouped within the *Cordanales*; for details see Discussion.

The third analysis consisted of combined ITS and nuLSU sequences of representatives of *Pseudodiplococcium*, *Spadicoides* and *Xenospadicoides*. The ITS sequence of ex-type strain CBS 127864 of *P. ibericum* (KY853465, Hernández-Restrepo *et al.* 2017) was excluded from the analysis due to suspected contamination; in the Blast search it shows 91 % similarity with *Cordyceps emeiensis* (AJ309347) and 90 % similarity with *Hirsutella jonesii* (KJ524687) of the *Hypocreales*. The alignment for ML analysis consisted of 2 601 characters and 232 distinct alignment patterns. No topological conflicts occurred between trees generated from ML and BI analyses; the ML tree is shown in the Supplementary Fig. 1. *Spadicoides* is shown as a highly supported clade (100/1.0) including *S. bina*, the type species, *X. atra* (as *S. atra*) and two other *Spadicoides* species. *Pseudodiplococcium ibericum*, the type species, is nested in the *Spadicoides* clade, and therefore is synonymised with the latter genus.

Consensus 2D structure of ITS2 of *Lentomitella*

The predicted consensus 2D structure of ITS2, modelled for the type species *L. vestita* (Figs 3, 4), is folded into the common core structure typical for *Eukaryota*, i.e. a ring structure with four main helices I–IV, of which helices II (35 nt) and III (71 nt) are highly conserved. The folding pattern of the last region corresponding to helix IV is highly variable among *Lentomitella* spp.; in the case of *L. vestita* it adopts a short helix. Therefore, only helices I–III were evaluated.

Three CBCs on 7, 9 and 10th base pairs were identified in helix I but only the CBC on a 10th base pair (C=G → U-A) is unique between *L. crinigera* and other *Lentomitella* species. The other two CBCs show a certain degree of homoplasy and characterise several clades or single branches corresponding to individual species. At the same position, the CBC was accompanied by either hCBC in two cases and by a non-CBC in a single case. In addition, four hCBCs and two non-CBCs were identified in helix I (Fig. 3).

In helix II no CBC was identified, only seven hCBCs and three non-CBCs occur here (Fig. 4). The length of helix II is longer by

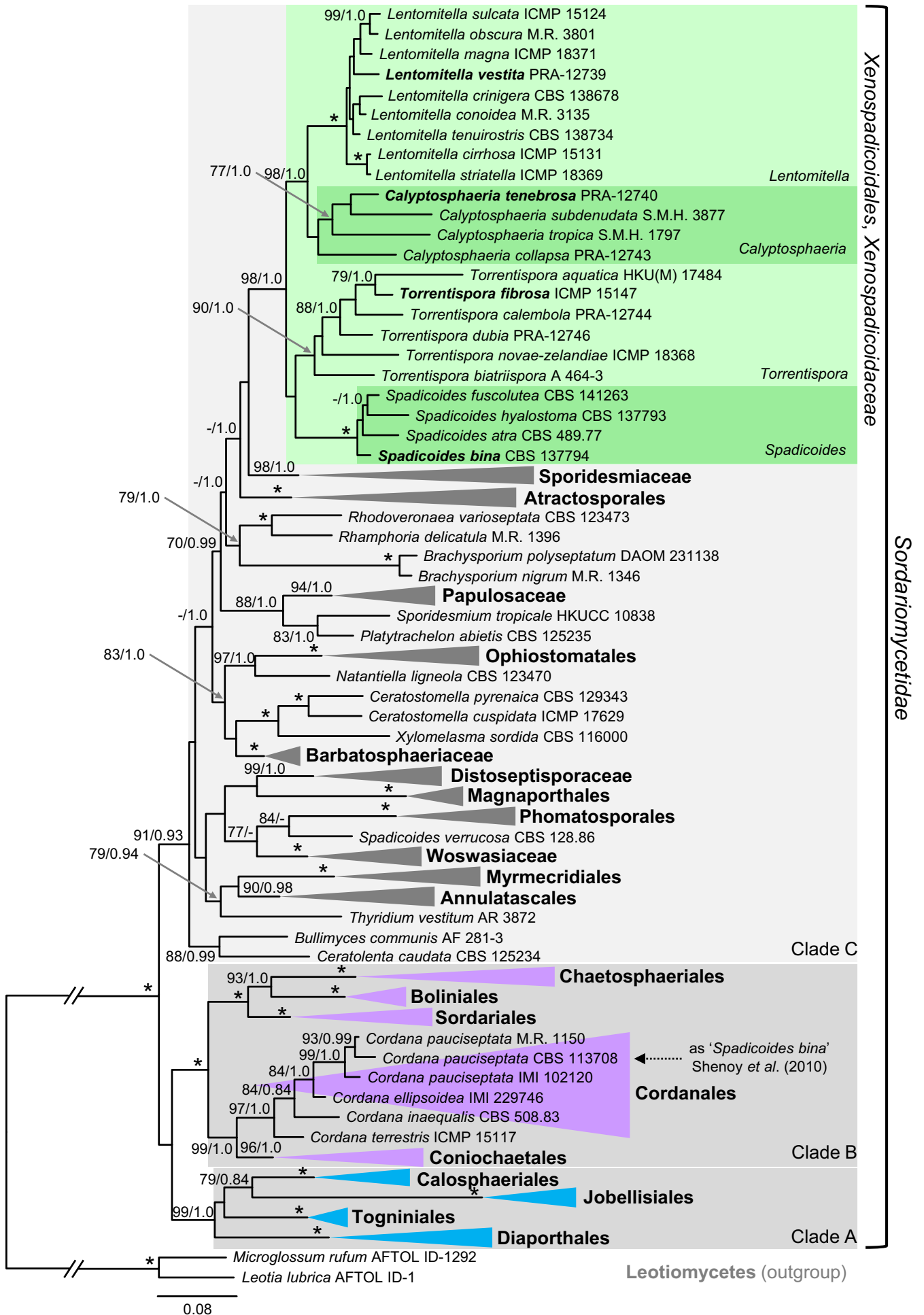
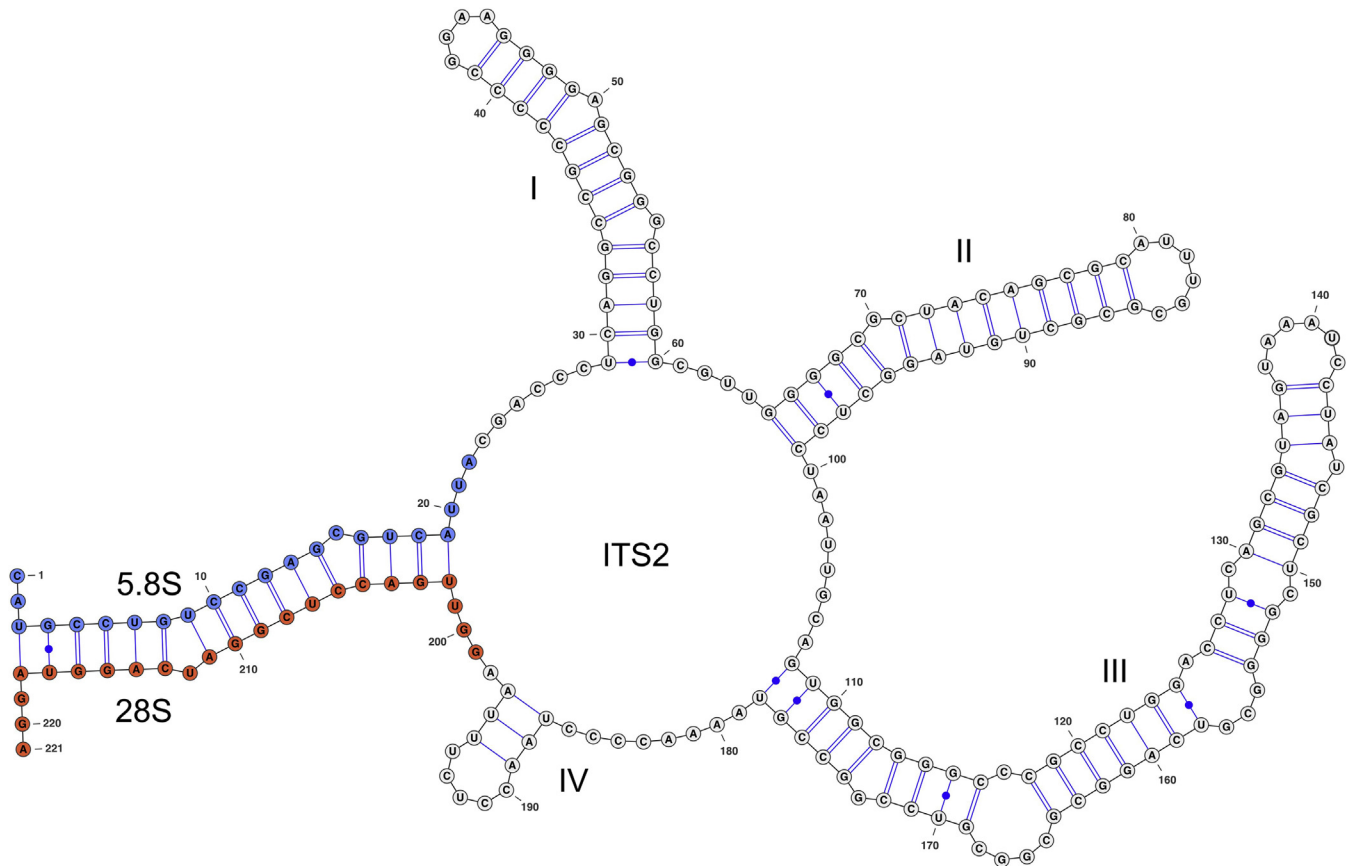


Fig. 2. Phylogenetic analysis of selected members of the *Sordariomycetidae*. Phylogram inferred from the nuclLSU-nucSSU-*rpb2* sequences with ML analysis using a GTRCAT model of evolution. Details as in Fig. 1.



ITS2: helix I

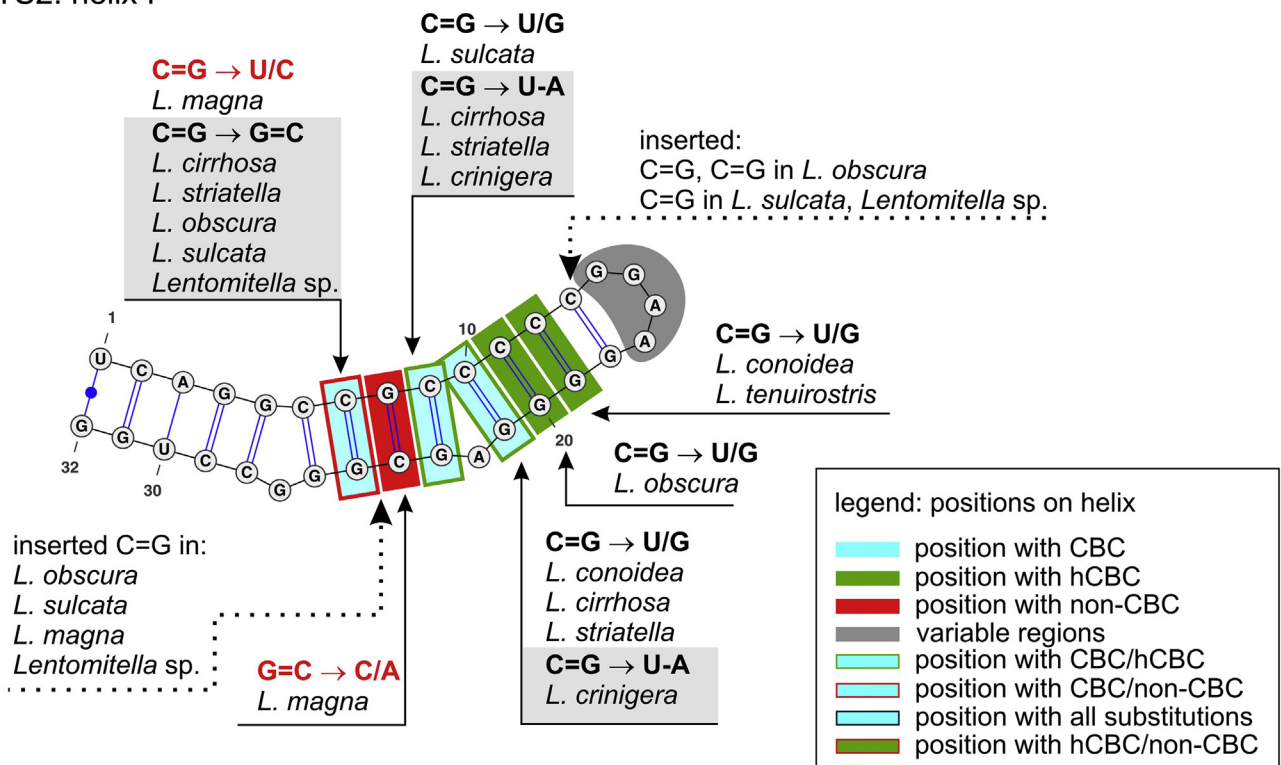
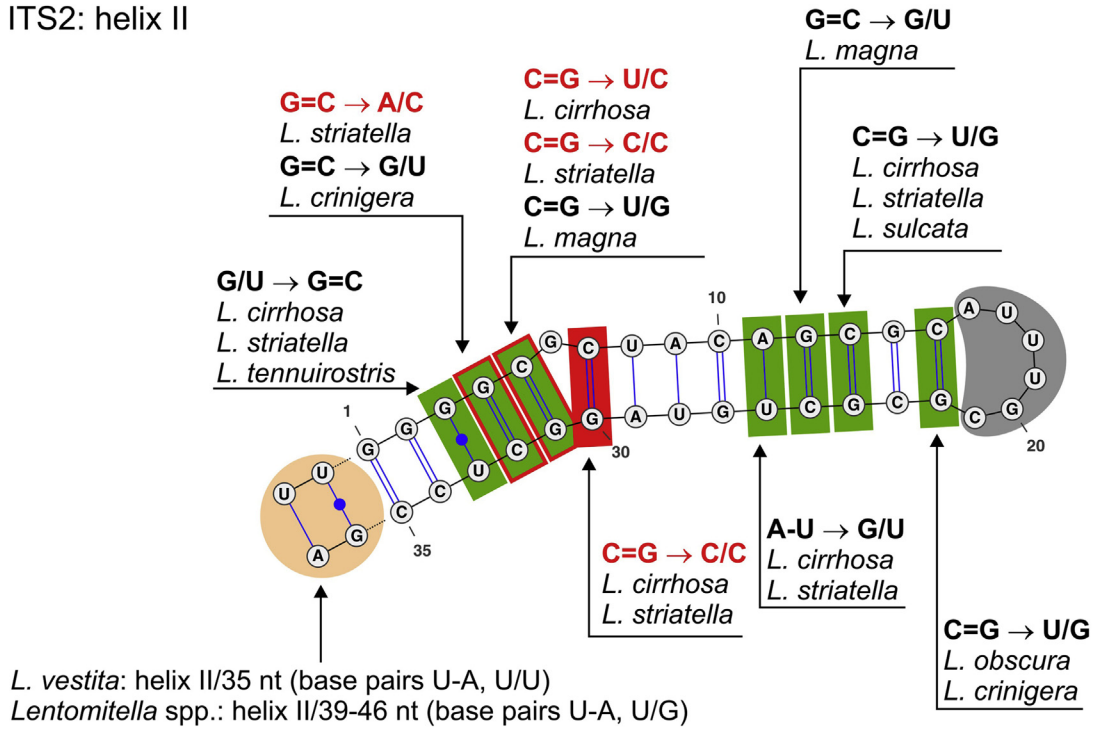


Fig. 3. ITS2 secondary structure of *Lentomitella vestita* (GenBank accession no. KY931794) and 5.8S-28S rRNA gene hybridization (proximal stem region) (above); detail of helix I (below). ITS2 helices are numbered I–IV. All substitutions recorded among members of *Lentomitella* are mapped on the 2D model. Identified substitutions are colour-coded: CBC (blue), hCBC (green) and non-CBC (red); position with all types of substitution (black). Parts of the text highlighted with grey colour refer to CBCs. Parts of hairpin loops and a helix highlighted with grey colour represent regions with a variable number of nucleotides or sequence variation.

ITS2: helix II



ITS2: helix III

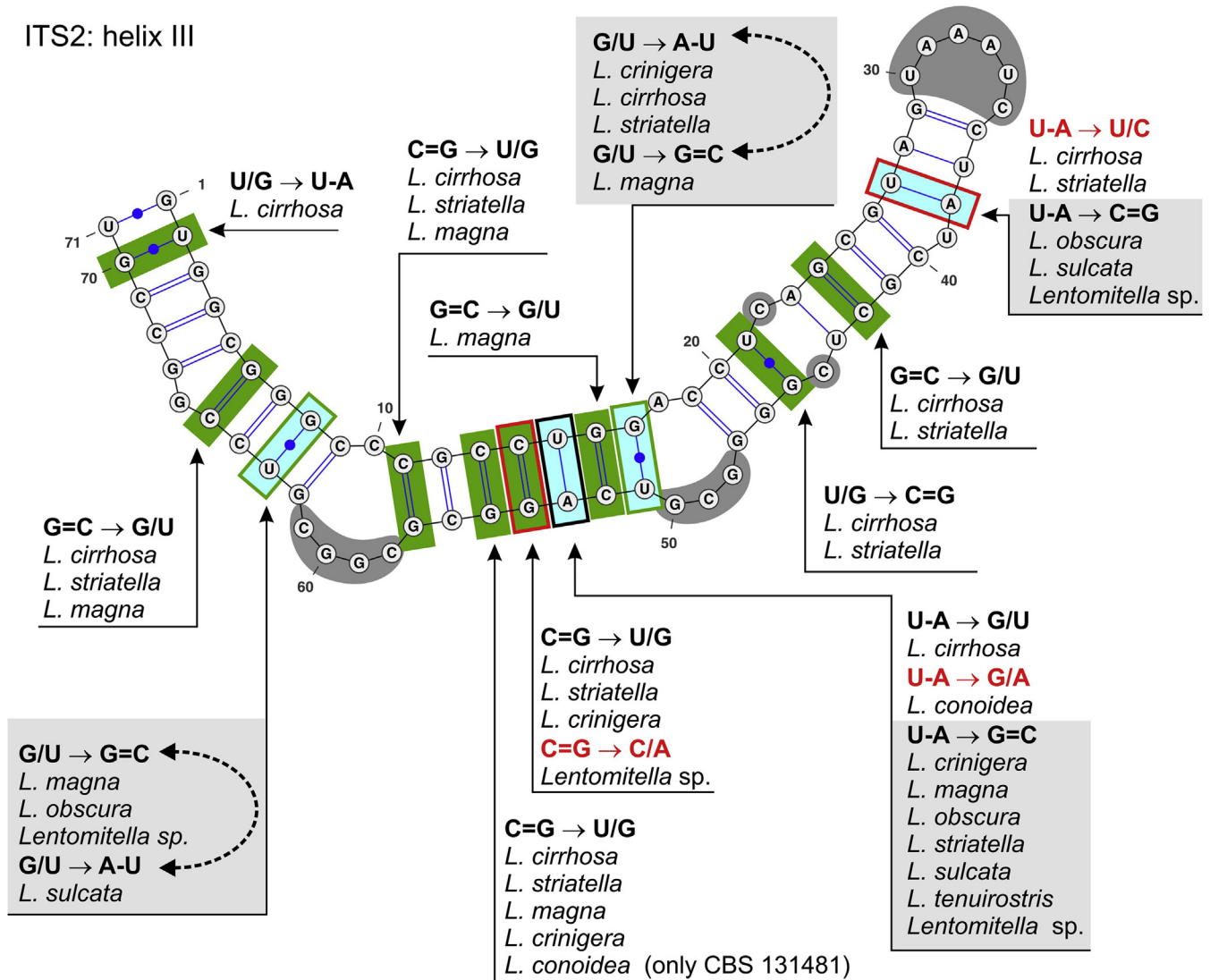


Fig. 4. ITS2 secondary structure of *Lentomitella vestita* (ITS sequence KY931794), helices II and III. Details as in Fig. 3.

two base pairs in all *Lentomitella* species than in *L. vestita*. In *L. vestita* the folding of the first two nucleotides at the 5'-end and the two last nucleotides at the 3'-end has not been predicted (leading to U-A, U/U base pairs), while in all other species of the genus the folding pattern of the first two pairs is preserved and nucleotides are conserved (base pairs U-A, U/G). The pyrimidine-pyrimidine mismatch in helix II (Mai & Coleman 1997, Schultz *et al.* 2005) was observed only in *L. cirrhosa* and *L. striatella* (base pairs U/C, C/C).

Helix III is the longest with two asymmetrical loops, bulges and a hairpin loop. It contains four CBCs on 8, 14, 16, and 24th base pairs, but also an additional 11 hCBCs and two non-CBCs. At the same position, CBC was accompanied by additional substitutions: by hCBC in four cases and in two events by non-CBC. Only the 14th base pair contained all types of substitutions involving CBC, hCBC, and non-CBC and is valuable for studying the evolution of CBC. The CBCs that characterise CBC clades and correspond to biological species were identified for *L. magna*, *L. sulcata*, *L. vestita* and one CBC delimits a clade containing *L. obscura*, *L. sulcata*, and *Lentomitella* sp. Two pairs of species that do not have CBCs between them but are separated by a hCBC in *L. cirrhosa* (G/U) and *L. striatella* (G=C), and by a non-CBC in *L. conoidea* (G/A) and *L. tenuirostris* (G=C) on the 14th base pair, suggesting an unfinished segregation of these species, are discussed below.

Taxonomy

Xenospadicoidales Hern.-Restr. *et al.*, Stud. Mycol. 86: 91. 2017; emend. Réblová & A.N. Mill.

Emended description: Lignicolous. *Ascomata* perithecial, non-stromatic. *Ostiole* periphysate. *Hamathecium* of paraphyses. *Asci* unitunicate, persistent, 8-spored, with a non-amyloid apical annulus. *Ascospores* hyaline or pale brown prior to discharge, aseptate or septate, variable in shape. *Asexual morphs* dematiaceous hyphomycetes. *Conidiophores* macronematous, mononematous. *Conidiogenous cells* tretic or holoblastic-denticulate, sympodially proliferating. *Conidia* hyaline or brown, aseptate or septate, variable in shape.

Type family: *Xenospadicoidaceae* Hern.-Restr. *et al.*

Xenospadicoidaceae Hern.-Restr. *et al.*, Stud. Mycol. 86: 91. 2017; emend. Réblová & A.N. Mill.

Synonym: *Lentomitellaceae* H. Zhang *et al.*, Fungal Div. 85: 95. 2017.

Emended description: Lignicolous. *Ascomata* perithecial, non-stromatic, with venter immersed, partially erumpent becoming superficial. Neck cylindrical or rostrate with or without sulcations. *Ostiole* periphysate. *Hamathecium* consisting of septate, tapering paraphyses. *Asci* unitunicate, persistent, cylindrical or cylindrical-clavate, 8-spored, with a non-amyloid apical annulus. *Ascospores* hyaline or pale brown prior to discharge, aseptate or septate, variable in shape, smooth-walled or ornamented. *Asexual morphs* dematiaceous hyphomycetes producing effuse colonies. *Conidiophores* macronematous, mononematous, branched or unbranched. *Conidiogenous cells* tretic or holoblastic-denticulate, sympodially proliferating. *Conidia* hyaline or brown, aseptate or septate, variable in shape.

Type genus: *Spadicoides* S. Hughes (as *Xenospadicoides* Hern.-Restr. *et al.*, Stud. Mycol. 86: 92. 2017)

Key to genera accepted in the *Xenospadicoidales*

1. Ascospores brown prior to discharge *Calyptosphaeria*
1. Ascospores hyaline prior to discharge 2
2. Ascospores thick-walled, smooth-walled, ascumatal neck without sulcations *Torrentispora*
2. Ascospores thin-walled, smooth-walled or ornamented, ascumatal neck with or without sulcations 3
3. Ascospores longitudinally striate, conidiogenesis holoblastic-denticulate *Lentomitella*
3. Ascospores smooth-walled or delicately verrucose, conidiogenesis tretic and holoblastic-denticulate *Spadicoides*

Calyptosphaeria Réblová & A.N. Mill., **gen. nov.** MycoBank MB821760

Etymology: *Kalyptó* (Gr.) meaning hide, conceal or envelop, referring to this taxon, which remained hidden within *Lentomitella* until its position could be resolved with DNA sequence data.

Sexual morph: *Ascomata* perithecial, non-stromatic, immersed, partially erumpent becoming superficial with only bases immersed, scattered or grouped, varying in position from upright to nearly horizontal; venter globose, subglobose to conical, clothed with hairs. Neck conical, cylindrical or rostrate with 3–4 deep sulcations or roughened lacking sulcations, dark brown, upright or slightly decumbent. *Ostiole* periphysate. *Ascomatal wall* fragile, two-layered. *Paraphyses* becoming partially disintegrated, septate. *Asci* unitunicate, cylindrical, short-stipitate, 8-spored; apex with a distinct, non-amyloid apical annulus. *Ascospores* ellipsoidal or ellipsoidal-fusiform, sometimes flattened on one side, hyaline becoming pale brown or dull brown prior to discharge, aseptate with a delayed formation of three transverse septa when still within the ascus, smooth-walled, without sheath or appendages. *Asexual morph*: unknown.

Type species: *Calyptosphaeria tenebrosa* Réblová & A.N. Mill.

Notes: Huhndorf *et al.* (2008) expanded the generic concept of *Lentomitella* by including two species with ellipsoidal or ellipsoidal-fusiform, smooth-walled ascospores that turn brown prior to discharge, i.e. *L. pallibrunnea* and *L. tropica*, and showed their sister relationship to *L. cirrhosa* and *L. crinigera* using partial nuLSU sequence data. Based on the combined analysis of six nuclear markers and morphology of ascospores, the new genus *Calyptosphaeria* is segregated from *Lentomitella* to accommodate *L. pallibrunnea* and *L. tropica* and two other morphologically similar taxa. The formation of septa is delayed and mature ascospores remain mostly aseptate and, in some cases, visible but indistinct cytoplasmic bands appear in areas where septa would be expected to form (Barr 1986 and this study). The ascospores are uniseriate or overlapping uniseriate within the asci, although sometimes they can be partially biseriate in the middle of the sporiferous part and asci appear slightly clavate.

Key to the species accepted in *Calyptosphaeria*

1. Ascumatal neck roughened lacking sulcations, ascospores (10–) 10.5–12(–12.5) × 4.5–5 µm *C. collapsa*
1. Ascumatal neck sulcate 2
2. Ascospore longer than 16 µm, (16–)17–20(–21) × 6–7 µm *C. tenebrosa*

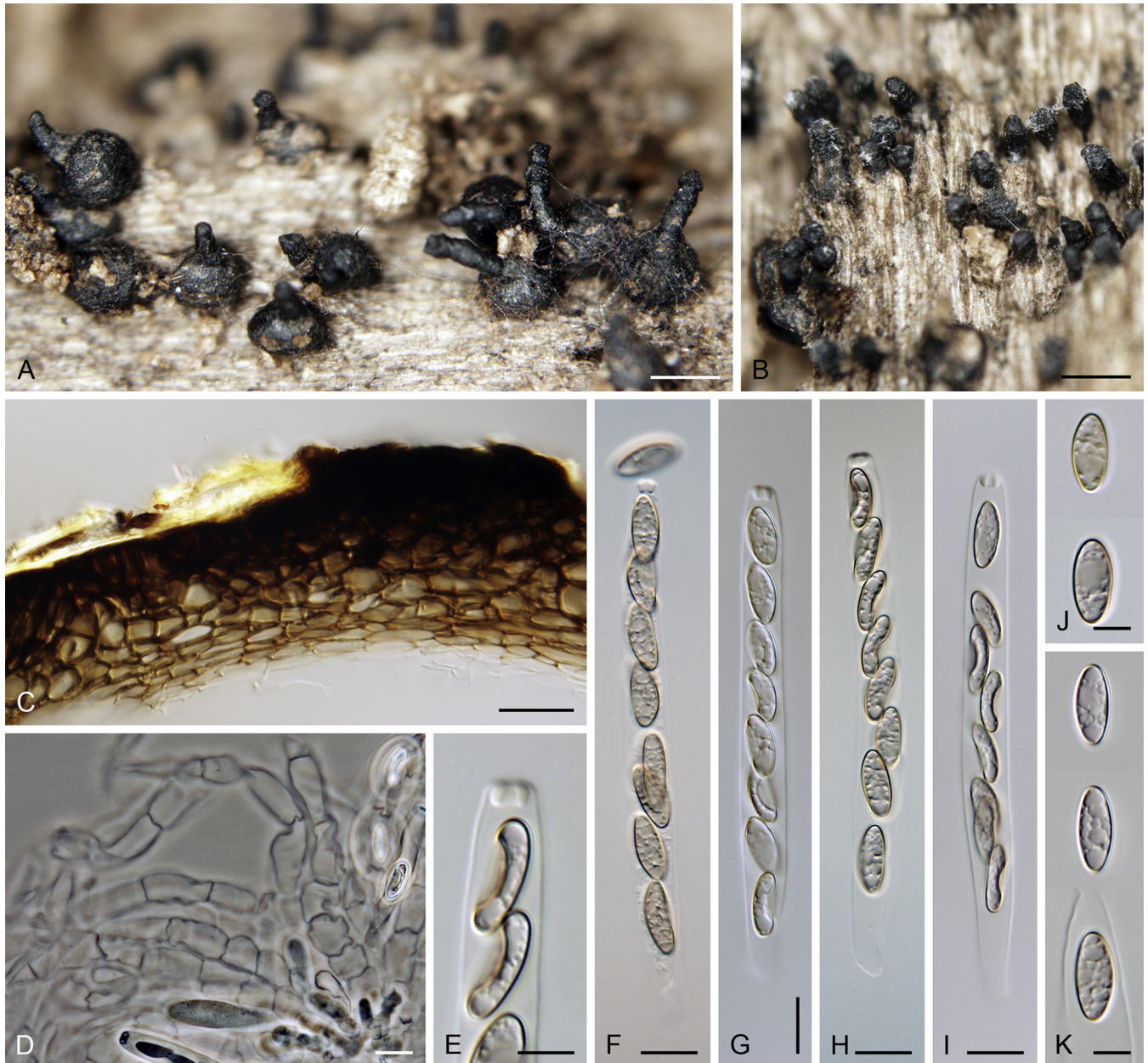


Fig. 5. *Calyptosphaeria collapsa*. A, B. Ascomata. C. Longitudinal section of the ascomal wall. D. Paraphyses. E. Ascus apex with apical annulus. F–I. Asci. J, K. Ascospores. A–K from PRA-12743. Scale bars: A, B = 500 μ m, C = 20 μ m, E, J, K = 5 μ m, D, F–I = 10 μ m.

2. Ascospores up to 16 μ m long 3
 3. Ascospores 11–14.5(–16) \times 4–5 μ m *C. subdenudata*
 3. Ascospores 14.5–16 \times 5–6 μ m *C. tropica*

Calyptosphaeria collapsa Réblová & A.N. Mill., **sp. nov.**
 MycoBank MB821761. Fig. 5.

Etymology: *Collapsus* (L.) meaning collapsed, referring to ascospores which collapse laterally upon aging.

Sexual morph: Ascomata immersed, partially erumpent becoming superficial with only bases immersed, closely grouped. Venter 350–490 μ m diam, 400–500 μ m high, subglobose, upright or sometimes lying horizontally on the host, dark brown to black, with brown, septate hairs 2–3 μ m wide sparsely covering the sides and bottom. Neck central, 120–140 μ m wide, up to 700 μ m long, cylindrical, upright, apex roughened, without sulcations. Ostiole periphysate. Ascomatal wall fragile to leathery, 44–62(–75) μ m thick, two-layered; outer

layer consisting of thick-walled, brown, polyhedral cells of *textura prismatica* to *textura epidermoidea* with opaque walls; cells tending to be darker towards the outside, more flattened and paler towards the interior. Inner layer consisting of several rows of thin-walled, hyaline, flattened cells. Paraphyses abundant, longer than the asci, becoming disintegrated with age, septate, slightly constricted at the septa, hyaline, 6.5–9.5 μ m wide, tapering to ca. 3 μ m apically. Asci 82–96(–100) \times (7–) 7.5–8.5(–9) μ m (mean \pm SD = 89.4 \pm 5.3 \times 8 \pm 0.4 μ m), 67–72(–86) μ m (mean \pm SD = 77.2 \pm 5.1 μ m) long in the sporiferous part, truncate at the apex, cylindrical, with a short stipe; with 8 overlapping uniseriate or partly biseriata ascospores; apical annulus 3.5–4 μ m wide, ca. 2.5 μ m high. Ascospores (10–)10.5–12(–12.5) \times 4.5–5 μ m (mean \pm SD = 11.3 \pm 0.6 \times 4.8 \pm 0.3 μ m), ellipsoidal to fusiform, sometimes slightly flattened on one side, often collapsing laterally upon aging, aseptate, later with up to three indistinct cytoplasmic bands, pale brown prior to discharge, smooth-walled. Asexual morph: unknown.

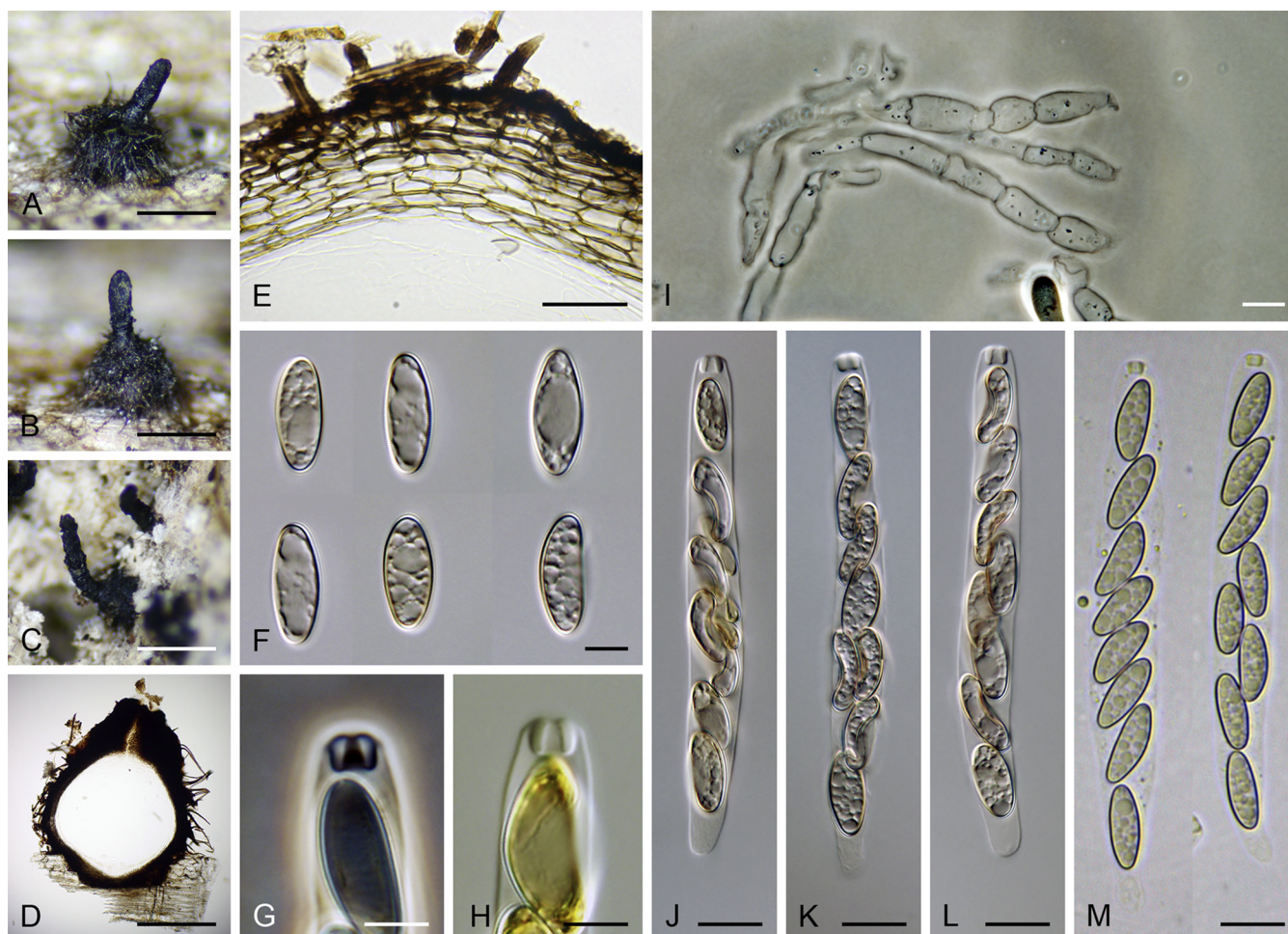


Fig. 6. *Calyptosphaeria subdenudata*. A–C. Ascomata. D, E. Longitudinal section of the ascomatal wall. F. Ascospores. G, H. Ascus apex with apical annulus. I. Paraphyses. J–M. Asci. A–M from JF 16082. Scale bars: A–C = 500 μ m, D = 250 μ m, E = 20 μ m, F–H = 5 μ m, I–M = 10 μ m.

Specimens examined: **Czech Republic**, Southern Moravia, Lednice, Nejdek old Slavic settlement, area close to the pagan burial grounds, on decaying wood of *Carpinus betulus*, 16 Nov. 2014, M. Réblová M.R. 3881 (holotype, PRA-12743); *ibid.*, M.R. 3882, M.R. 3884.

Notes: *Calyptosphaeria collapsa* differs from other species of the genus by a roughened ascomatal neck without sulcations. In the absence of an asexual morph (*Calyptosphaeria* spp. did not germinate *in vitro*) it is difficult to find any other morphological differences between them. It resembles *C. subdenudata* and *C. tropica* in the morphology of ascospores, but the ascospores are shorter in *C. collapsa*. It further differs from *C. subdenudata* in having longer asci and from *C. tropica* in having a cylindrical neck vs. conical rostrate ascomatal apex in the latter species. The collapsing ascospores were observed in water, lactic acid and Melzer's reagent.

Calyptosphaeria collapsa was found on strongly decaying wood of several fallen trunks of *Carpinus betulus* in the Czech Republic, the remains of old growth trees that were more than one hundred years old.

Calyptosphaeria subdenudata (Peck) Réblová & A.N. Mill., **comb. nov.** MycoBank MB821762. **Fig. 6.**

Basionym: *Sphaeria subdenudata* Peck, Ann. Rep. N.Y. St. Mus. nat. Hist. 32: 52. 1880 (1879).

Synonyms: *Ceratostoma subdenudatum* (Peck) Sacc., Syll. fung. 9: 481. 1891.

Ceratostomella subdenudata (Peck) M.E. Barr, Bull. N.Y. St. Mus. 459: 44. 1986.

Wegelina subdenudata (Peck) M.E. Barr, Cryptog. Bryol.-Lichénol. 19: 172. 1998.

Lentomitella pallibrunnea Huhndorf *et al.*, Mycologia 100: 948. 2008.

Xylomelasma moderata Lar.N. Vassiljeva & S.L. Stephenson, Mycosphere 5: 223. 2014.

Sexual morph: Ascomata immersed, partially erumpent with protruding necks becoming superficial with only bases immersed, scattered or in groups. Venter 390–500 μ m diam, 400–520 μ m high, subglobose, upright, more often lying horizontally on the host, dark brown to black, with reddish brown, septate hairs ca. 3.5 μ m diam sparsely covering the sides. Neck central, 100–130 μ m wide, up to 500 μ m long, cylindrical, upright, slightly roughened, apex with several deep sulcations. *Ostiole* periphysate. *Ascomatal wall* fragile, 37–40 μ m thick, two-layered; outer layer consisting of thick-walled, brown, polyhedral cells of *textura prismatica* with opaque walls; cells tending to be darker towards the outside, becoming flattened and paler towards the interior. Inner layer consisting of several rows of thin-walled, hyaline, flattened cells. *Paraphyses* sparse, becoming disintegrated with age, septate, slightly constricted at the septa, hyaline, 5–6 μ m wide. *Asci* (50–)60–85(–90) \times (7.5–)8–10 μ m (mean \pm SD = 72.5 \pm 3.2 \times 9 \pm 0.4 μ m), truncate to broadly rounded at the apex, cylindrical, with a short stipe; with 8 overlapping uniseriate or biseriate ascospores; apical annulus ca. 3 μ m wide, 2.5–3 μ m high. *Ascospores* 11–14.5(–16) \times 4–5 μ m (mean \pm SD = 13.3 \pm 1.4 \times 4.7 \pm 0.4 μ m), ellipsoidal, often slightly flattened on one side and slightly curved, aseptate or with several indistinct cytoplasmic bands, hyaline becoming light dull brown, smooth-walled. *Asexual morph:* unknown.

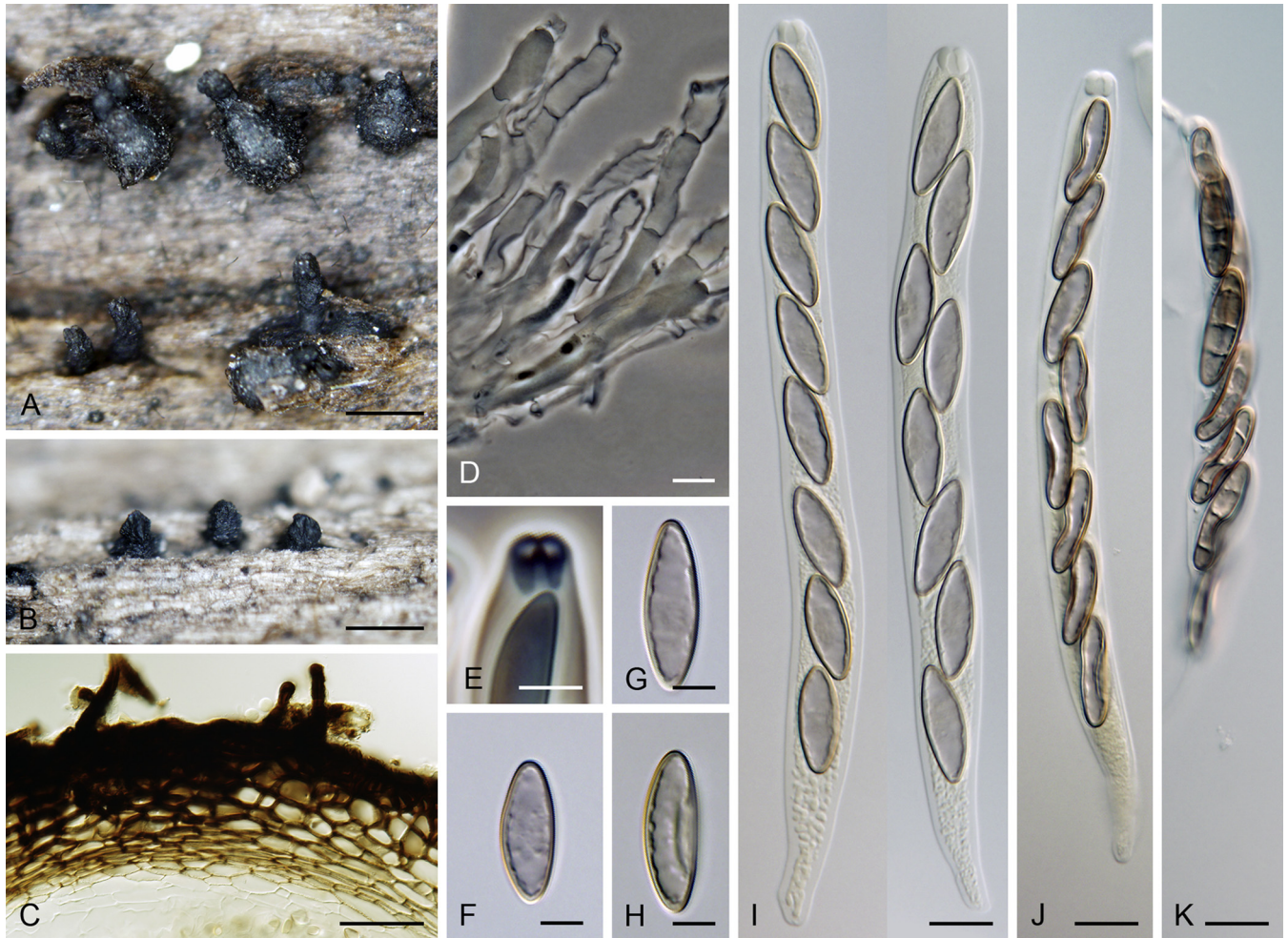


Fig. 7. *Calyptosphaeria tenebrosa*. A, B. Ascomata. C. Longitudinal section of the ascomatal wall. D. Paraphyses. E. Ascus apex with apical annulus. F–H. Ascospores. I–K. Asci. A, D, J, K from PRA-12742, C, G, F, I from PRA-12741, B, E, H from PRA-12740. Scale bars: A, B = 500 μ m, C = 20 μ m, D, I–K = 10 μ m, E–H = 5 μ m.

Specimens examined: **French West Indies**, Martinique, Sainte-Marie, La Philippe, coastal mesophilic rainforest, on decaying wood, 3 Aug. 2016, J. Fournier J.F. 16082. **USA**, New York, Delaware County, Griffins', Catskill Mts., on decaying wood, Sep. 1877, C.H. Peck (**holotype** of *Sphaeria subdenudata*, NYS); *ibid.*, Indian Lake, on decaying wood, Oct. 1878, C.H. Peck (NYS). Michigan. Berrien County, Warren Woods, south end of trail, through picnic area, up to creek, on 12 cm thick branch on the ground, 8 Nov. 1998, F.A. Fernández & A.N. Miller, S.M.H. 3877 (**holotype** of *Lentomitella pallibrunnea*, F).

Notes: *Calyptosphaeria subdenudata* is known from French West Indies (Martinique) and North America (Illinois, Massachusetts, Michigan and New York), based on recently collected material and the revision of the holotype and other herbarium material of *Lentomitella pallibrunnea* (Huhndorf et al. 2008) and *Sphaeria subdenudata* (Peck 1879, Barr 1986). *Xylomelasma moderata* (Vassiljeva & Stephenson 2014) fits well within the species concept based on the ascoma, ascus and ascospore morphology. Both latter species are placed in synonymy under *C. subdenudata*. Barr (1986) revised Peck's material of *S. subdenudata* and noted that ascospores become 1–5-pseudoseptate at maturity. Up to three cytoplasmic bands were observed in areas where septa would be expected to form during our revision of the type material of *S. subdenudata*; the paraphyses were already disintegrated. The ascospores of *L. pallibrunnea* were described as aseptate (Huhndorf et al. 2008).

Calyptosphaeria subdenudata is similar to *C. collapsa* in the ellipsoidal, brown ascospores, but it differs in having shorter asci, longer ascospores and a neck with deep sulcations.

***Calyptosphaeria tenebrosa* Réblová & A.N. Mill., sp. nov.**
Mycobank MB821763. Fig. 7.

Etymology: *Tenebrosus* (L.) meaning dark, referring to the colour of the ascospores.

Sexual morph: *Ascomata* immersed, partially erumpent with protruding necks or becoming superficial with only bases immersed, scattered or grouped sometimes in rows. Venter 310–550 μ m diam, 390–650 μ m high, subglobose to conical, straight or more often lying horizontally on the host, dark brown to black, with brown, septate hairs 4.5–5 μ m diam sparsely covering the lower part. Neck central, 120–140 μ m wide, up to 600 μ m long, cylindrical, upright, straight, often roughened, apex slightly widened with 3–4 deep sulcations. *Ostiole* periphysate. *Ascomatal wall* fragile to leathery, 55–65 μ m thick, two-layered; outer layer consisting of thick-walled, brown, polyhedral cells of *textura prismatica* to *textura angularis* with opaque walls; cells tending to be darker towards the outside, becoming flattened and paler towards the interior. Inner layer consisting of several rows of thin-walled, hyaline, flattened cells. *Paraphyses* abundant, longer than the asci, becoming disintegrated with age, septate, slightly constricted at the septa, hyaline, 5.5–9.5 μ m wide, tapering to 2.5–3.5 μ m. *Asci* (119–)122–150 \times 9–10(–11) μ m (mean \pm SD = 134.7 \pm 8.5 \times 9.5 \pm 0.3 μ m), (105–)110–130 μ m (mean \pm SD = 116.7 \pm 6.4 μ m) long in the sporiferous part, truncate at the apex, cylindrical, with a short stipe; with 8 uniseriate or partly biseriate ascospores; apical annulus 4.5–5 μ m

wide, 4–4.5 µm high. *Ascospores* (16–)17–20(–21) × 6–7 µm (mean ± SD = 18.6 ± 1.1 × 6.4 ± 0.3 µm), ellipsoidal-fusiform, tapering towards the ends, rarely inequilateral, sometimes collapsing laterally upon aging, aseptate, three transverse septa sometimes present in old ascospores, hyaline to yellowish becoming pale brown prior to discharge, smooth-walled. *Asexual morph*: unknown.

Specimens examined: **Czech Republic**, Central Bohemia, Krivoklátsko Protected landscape area, Nížbor, Vůznice Nature reserve, on decaying wood of *C. betulus*, 20 Oct. 2004, M. Réblová M.R. 2923. Northern Moravia, Podhoří 'Podhom' near Hranice, on decaying wood of *Fagus sylvatica*, Mar. 1914, F. Petrak (as *Ceratostoma operculatum*, Fl. Bohem. Morav. Exs. No. 968, PRM 655798). Southern Moravia, Lednice, Nejdek, forested area on the right side of the Nejdek crossroads, on decaying wood of *Acer campestre*, 15 Nov. 2014, M. Réblová M.R. 3871 (**holotype**, PRA-12740); *ibid.*, M.R. 3869; *ibid.*, Nejdek, old Slavic settlement near river Zámecká Dyje, on decaying wood of *Carpinus betulus*, 27 Oct. 2014, M. Réblová M.R. 3867 (PRA-12741); *ibid.*, Valtice, Rendez-vous National nature monument, on decaying wood of *Quercus cerris*, 18 Nov. 2012, M. Réblová M.R. 3704. **France**, Ariège, Lescure, Bois du Pas du Baup, 500 m. a.s.l., on decaying wood of *Alnus glutinosa*, 24 Feb. 2004, J. Fourmier J.F. 04021 (PRA-12742). **New Zealand**, Westlands, Victoria Forest Park, Rough Creek Road, 4 km S of Inangahua, on decaying wood, 22 Apr. 2005, M. Réblová M.R. 2967/NZ 810.

Notes: *Calyptosphaeria tenebrosa* can be distinguished from other species of the genus by longer asci with the largest apical annulus known in the genus and longer ellipsoidal-fusiform ascospores. It occurs on decaying wood of various hardwood trees and it is known from several localities in the Czech Republic, France and New Zealand.

Calyptosphaeria tropica (Huhndorf *et al.*) Réblová & A.N. Mill., **comb. nov.** MycoBank MB821764.

Basionym: *Lentomitella tropica* Huhndorf *et al.*, Mycologia 100: 948. 2008.

Notes: For description and illustration see Huhndorf *et al.* (2008). *Calyptosphaeria tropica* can be distinguished from other species of the genus by size of asci and ascospores, conical rostrate ascromatal apex and tropical distribution (Costa Rica and Puerto Rico).

Lentomitella Höhn., Anns mycol. 3: 552. 1906.

Sexual morph: *Ascomata* perithecial, non-stromatic, immersed or partially erumpent with protruding necks or becoming superficial, solitary or in rows or groups. Venter globose to subglobose, clothed by brown or reddish-brown hairs. Neck central, cylindrical, upright to slightly decumbent, glabrous, apex sulcate. *Ostiole* periphysate. *Ascomatal wall* fragile to leathery, two-layered. *Paraphyses* longer than the asci, becoming disintegrated with age, septate, constricted at the septa, hyaline. *Asci* cylindrical to clavate, broadly rounded or truncate at the apex, with a short stipe; with 8 uniseriate or obliquely uniseriate or overlapping, sometimes partly biseriate ascospores; with a distinct, non-amyloid apical annulus. *Ascospores* ellipsoidal, suboblong or ellipsoidal-fusiform, sometimes inequilateral, hyaline, longitudinally striate, 1–3-septate with 2–4 large drops, with a delayed formation of second and third septum. *Asexual morph*: A phaeoisaria-like asexual morph is sometimes formed *in vitro*. *Conidiophores* macronematous, mononematous, unbranched or branched apically, arising from aerial hyphae, brown near the base, subhyaline to hyaline towards the tip. *Conidiogenous cells* terminal or intercalary, hyaline, subcylindrical to slender flask-shaped, with a rachis bearing minute denticles, conidiogenesis

holoblastic-denticulate, conidial heads slimy, inconspicuous, transparent. *Conidia* globose, ellipsoidal, clavate to obovate, slightly apiculate at the base, hyaline, aseptate, smooth-walled.

Type species: *Lentomitella vestita* Höhn.

Notes: *Lentomitella* forms a strongly supported monophyletic clade in the phylogenetic analysis based on six nuclear markers. It is well-distinguished from other genera of the *Xenospadicoideales* by hyaline, septate, longitudinally striate ascospores, distinct but relatively small apical annulus (2.5–3 µm wide, 1.5–2 µm high) and ascromata with a cylindrical neck with usually 3–4 deep sulcations at the apex and venter clothed by dark interwoven hairs that can disappear upon aging. *Lentomitella* comprises 11 species; *L. cirrhosa*, *L. crinigera*, *L. unipretoriae* and *L. vestita* are accepted in the genus, two new combinations are proposed for *L. conoidea* and *L. investita*, and five species are described as new to science, i.e. *L. magna*, *L. obscura*, *L. sulcata*, *L. striatella* and *L. tenuirostris*. The phaeoisaria-like asexual morph has been experimentally proven only for *L. investita*, *L. sulcata*, and *Lentomitella* sp. The ascospores do not germinate easily. Germinating tubes appear in ca. 1–2 wk after isolation on water agar. Despite the lack of known asexual morphs, we observed that the colonies of individual species differ macroscopically at the margin. The margin consists either of densely branched hyphae, i.e. in *L. conoidea*, *L. crinigera* and *L. magna*, or unbranched or sparsely branched hyphae of the substrate mycelium in the other species.

Key to the species accepted in *Lentomitella*

1. Ascospores shorter than 11 µm 2
1. Ascospore longer than 11 µm 8
2. Ascospores 1-septate; (5.5–)6–7 × 3–3.5 µm *L. vestita*
2. Ascospores 1–3-septate, longer than 7 µm 3
3. Asci (46–)50–56(–65) × 6–7 µm, ascospores (7–)7.5–9 × 3.5–4(–4.5) µm *L. investita*
3. Asci longer than 56 µm 4
4. Ascospores usually 1–2-septate, old ascospores 3-septate 5
4. Ascospores 3-septate early in ontogeny 7
5. Ascospores 1(–3)-septate, first-formed septum in the middle, 8–10 × 4.5–5 µm *L. cirrhosa*
5. Ascospores usually 1–2-septate, first-formed septum in the middle or slightly above or below the middle 6
6. Ascospores up to 9.5 µm long; aerial mycelium on MLA woolly, woolly-floccose or almost cobwebby at the margin; margin of the colony consisting of densely branched hyphae *L. conoidea*
6. Ascospores usually slightly longer, 9–10.5 µm; aerial mycelium on MLA cottony to felty having a more compact appearance; margin of the colony consisting of unbranched or sparsely branched hyphae *L. tenuirostris*
7. Ascospores (8–)9–10.5(–11) × 4–5 µm, asci 72–81 × 6.5–7.5 µm *L. unipretoriae*
7. Ascospores longer than 10.5 µm 8
8. Ascospores (12.5–)13–15 × 5.5–6.5 µm *L. magna*
8. Ascospores shorter than 13 µm 9

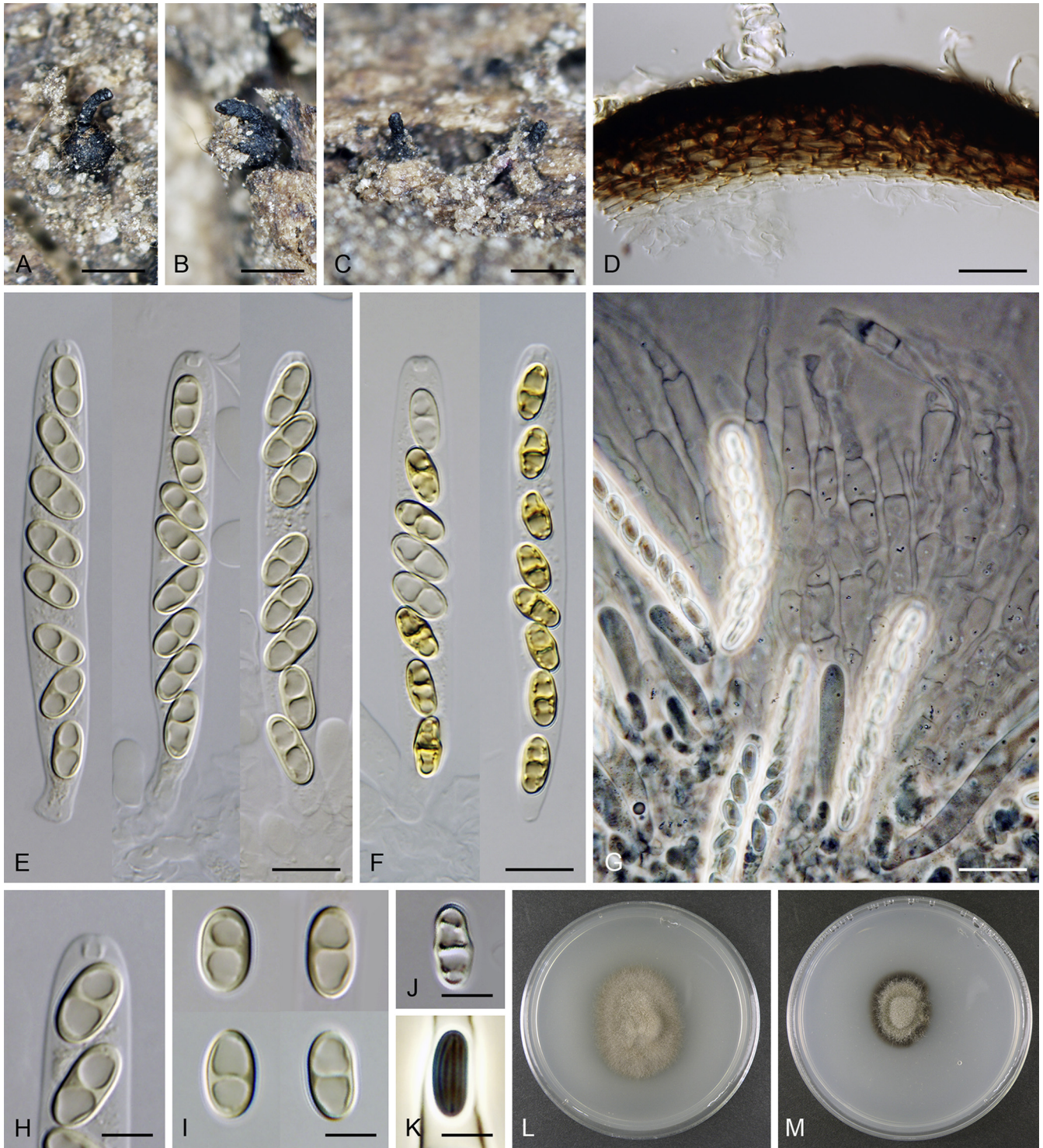


Fig. 8. *Lentomitella cirrhosa*. A–C. Ascomata. D. Longitudinal section of the ascomal wall. E, F. Asci. G. Paraphyses. H. Ascus apex with apical annulus. I–K. Ascospores. L, M. Colonies on MLA and PCA after 28 d. A–M from ICMP 15131. Scale bars: A–C = 500 µm, D, G = 20 µm, E, F = 10 µm, H–K = 5 µm.

- 9. Preferring coniferous wood; ascomata up to 600 µm diam with a neck up to 170 µm wide; ascospores (10–)10.5–13 × 4–5.5 µm, asci (66–)70–88(–90) × (7.5–)8–9.5(–10) µm *L. crinigera*
- 9. Species without substrate preferences, ascomata and necks smaller 10
- 10. Asci up to 8 µm wide, ascospores up to 5 µm wide; asci (70–)72–80(–82) × 7.5–8(–8.5) µm, ascospores (10–)11–12 × 4–5(–5.5) µm *L. obscura*
- 10. Asci wider than 8 µm, ascospores wider than 5 µm 11
- 11. Asci length/width ratio 9.4, ascospores (10.5–)11–12(–13) µm long *L. sulcata*

- 11. Asci length/width ratio 8.6, ascospores 11.5–13(–14) µm long *L. striatella*

Lentomitella cirrhosa (Pers.: Fr.) Réblová, Mycologia 98: 82. 2006. Figs 8, 9.

Basionym: *Sphaeria cirrhosa* Pers., Syn. Meth. Fung. p. 59. 1801 : Fries, Syst. Mycol. 2: 475. 1823.

Synonyms: *Cerastoma cirrhosum* (Pers.: Fr.) Fuckel, Jahrb. Nassau. Ver. Naturk. 23–24: 127. 1870.

Cerastoma cirrhosum (Pers.: Fr.) Quéél., Mém. Soc. Émul. Montbéliard, Sér. 2 5: 522. 1875.

115. *SPHAERIA CIRRHOSA*: simplex sparsa, sphaerulis immersis, ostioliis spinulosis, basi fibrillulis in ligno diuergentibus cinctis.

Rarius ad ligna exsiccata, mollia obseruatur.

Sphaerulae intra lignum latentes, pilis longis, raris obductae. *Ostiola* rudia, subfalcata, prominent; ipsa glabra, basi vero pilis s. cirris pilosis, ad sphaerulas A pertinentibus, adhuc cincta.

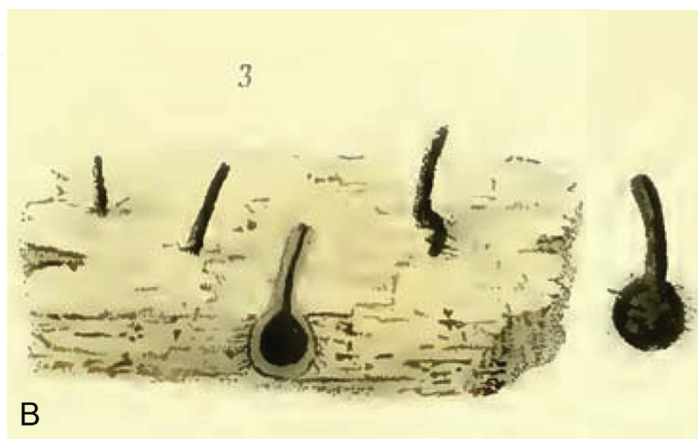


Fig. 9. *Lentomitella cirrhosa*. A. Description of *Sphaeria cirrhosa* (Persoon 1801). B. Illustration (lectotype) of *S. cirrhosa* (Persoon 1808).

Ceratostomella cirrhosa (Pers.: Fr.) Sacc., *Michelia* 1: 370. 1878.
Amphitrichum cirrhosum (Pers.: Fr.) Kuntze, *Revis. gen. pl.* 3(2): 443. 1898.

Endoxyla cirrhosa (Pers.: Fr.) Arx & E. Müll., *Beitr. Krypt-Fl. Schweiz* 11(1): 355. 1954.

Sexual morph: *Ascomata* immersed to partially erumpent becoming superficial, solitary or in small groups. Venter 300–330 µm diam, 300–340 µm high, globose to subglobose, dark brown to black, covered with sparse, dark brown, septate hairs ca. 3.5 µm wide. Neck central, 90–100 µm wide, up to 500 µm long, cylindrical, upright, straight or slightly flexuous, glabrous, tapering, apex sulcate. *Ostiole* periphysate. *Ascomatal wall* fragile to leathery, 25–40 µm thick, two-layered. Outer layer consisting of thick-walled, brown, polyhedral cells of *textura prismatica* with opaque walls; cells tending to be darker towards the outside, becoming paler towards the interior. Inner layer consisting of several rows of thin-walled, hyaline, flattened cells. *Paraphyses* abundant, longer than the asci, becoming disintegrated with age, septate, constricted at the septa, hyaline, 7–10 µm wide, tapering to ca. 2.5–3 µm. *Asci* (62–) 64–70(–73) × 6.5–7.5(–8.5) µm (mean ± SD = 66.7 ± 3.0 × 7.1 ± 0.4 µm), (55–)58–62(–66) µm (mean ± SD = 60.2 ± 2.8 µm) long in the sporiferous part, broadly rounded at the apex, cylindrical to clavate with a short stipe; with 8 uniseriate or obliquely uniseriate ascospores; apical annulus ca. 2.5 µm wide, 1.5 µm high. *Ascospores* 8–10 × 4.5–5 µm (mean ± SD = 9.4 ± 0.5 × 4.6 ± 0.3 µm), ellipsoidal, hyaline, longitudinally striate, 1–3-septate, usually 1-septate with two large drops becoming 3-septate upon aging. **Asexual morph:** unknown.

Culture characteristics: Colonies on MLA 16–19 mm diam after 14 d (19–23 mm after 21 d, 20–25 after 28 d) at 25 °C, circular, convex. Aerial mycelium abundant, cottony, margins filamentous, colony surface pale brown to cocoa brown; reverse black. Colonies on PCA 10–12 mm diam after 14 d (13–15 mm after 21 d, 14–16 mm after 28 d) at 25 °C, circular, convex. Aerial mycelium abundant, woolly, loose to cobwebby towards the margin, colony surface beige-grey with olive-brown inner ring and conspicuous dark brown marginal ring of submerged hyphae; reverse black. Vegetative hyphae branched, septate, medium to dark brown, smooth-walled. Margin of the colony consisting of unbranched or sparsely branched hyphae of substrate mycelium. Sporulation not observed.

Lectotype; designated by Réblová (2006): (Illustration) Persoon, *Icones pictae specierum rariorum Fungorum in Synopsi Methodica Descriptarum*, fasc. 4, tab. 24, fig. 3. 1808.

Specimens examined: New Zealand, South Island, Southland, Southland Distr., Fiordland National park, Kaherekoau Mts., Blue cliffs, Hump track 15 km W of Papatotara, on decaying wood, 12 Mar. 2005, M. Réblová M.R. 2952/NZ 481; *ibid.*, West Coast, Westland Distr., Hokitika, Mananui Point, Lake Mahinapua, Swimmers Beach walk, on decaying wood of *Podocarpus totara*, 5 Mar. 2003, M. Réblová M.R. 2705/NZ 206 (epitype, PDD 81434, culture ex-epitype ICMP 15131).

Notes: It is challenging to interpret *L. cirrhosa* in the absence of a type specimen in Persoon's herbarium (L). Persoon (1801) described *Sphaeria cirrhosa* just with a few words. The illustration (Persoon 1808) showing black ascomata with immersed venter clothed with sparse hairs and emerging glabrous neck represents the only original element left and is reproduced here as Fig. 9; the figure caption of tab. 24 in Persoon (1808) incorrectly refers to pictures 1, 2 but *S. cirrhosa* is depicted in picture 3. In the absence of a type specimen, this illustration (Persoon 1808) was selected as lectotype [Réblová 2006, incorrectly cited as Persoon (1800), corrected here], and in order to stabilise the species concept of *L. cirrhosa*, a collection from New Zealand on decayed wood of *Podocarpus totara* (PDD 81434) was designated as epitype (Réblová 2006).

Fuckel (1870) accepted *S. cirrhosa* in the genus *Ceratostoma* as *C. cirrhosum* and provided a description based on his own material published in *Fungi Rhen. Exs. No. 1804* [= *Lentomitella vestita*, this study]. Saccardo (1882) interpreted this species based on various collections. He transferred *S. cirrhosa* to *Ceratostomella* and described the ascomata as sparse, ca. 400 µm diam, immersed becoming partially erumpent, subglobose, clothed with hairs, with a long glabrous neck, asci cylindrical-clavate 65–75 × 7–9 µm, containing eight ellipsoidal to oblong, hyaline ascospores 9–12 × 3.5 µm, with 1–4, mostly two drops.

The species concept of *Ceratostomella cirrhosa* presented by von Arx (1952) included 12 species synonyms and was based on a revision of type and other herbarium material from Europe and North America. The synonymy was partly adopted by Réblová (2006) and *C. cirrhosa* was transferred to the reinstated *Lentomitella*. The species description of *L. cirrhosa* was based on the epitype, other herbarium material collected in Europe and on the revision of holotypes of *Sphaeria investita*, *Ceratostomella vestita* var. *vestita* and var. *varvicensis* and *Eriosphaeria conoidea*.

In the light of phylogenetic analysis of six nuclear markers and re-evaluation of morphological characters of ascospores and asci, they are not conspecific with *L. cirrhosa* and belong to three different species recognised in this study as *L. conoidea*, *L. investita* (including *C. vestita* var. *varvicensis* as its synonym) and *L. vestita*.

Although *L. cirrhosa* and *L. vestita* differ significantly in the size of asci and ascospores, and the ascospores of the latter species are regularly 1-septate vs. 1–3-septate in *L. cirrhosa*, von Arx (1952) regarded them as conspecific. He considered the holotype of *L. vestita* to be insufficiently developed and therefore ignored the smaller size of ascospores (5.5–)6–7 × 3–3.5 µm and asci 43–47(–55) × 5.5–6 µm in his description of *C. cirrhosa* [asci 50–80 µm long in the sporiferous part with stipe 20–40 µm long, ascospores 8–10 × 3.5 µm *vide* von Arx (1952)]. Another eight *Ceratostomella* species synonymised by von Arx (1952) with *L. cirrhosa*, and previously transferred to *Amphitrichum* by Kuntze (1898), were revised; they belong to the genera *Ceratostomella* (Réblová 2006), *Natantiella* (Réblová & Štěpánek 2009) and other fungi discussed below.

The ascospores of *L. cirrhosa* in the epitype (PDD 81434) are mostly 1-septate with two large drops, but old ascospores released from the asci possess three septa and four drops. The closest relative to *L. cirrhosa* is *L. striatella*, which differs by longer and wider asci and slightly longer and wider, regularly 3-septate ascospores.

Lentomitella cirrhosa is also similar to *L. investita* and *L. conoidea* in morphology of ascospores. It shares with *L. investita* mostly 1-septate ascospores with the first-formed septum positioned always in the middle and a delayed formation of two additional septa. *Lentomitella investita* differs from *L. cirrhosa* by shorter and narrower asci and slightly smaller ascospores. *Lentomitella conoidea* differs from *L. cirrhosa* by slightly longer, mostly 1–2-septate ascospores with the first septum formed in the middle or slightly above or below the middle.

Lentomitella conoidea (Feltg.) Réblová, **comb. nov.** MycoBank MB821765. Fig. 10.

Basionym: *Eriosphaeria conoidea* Feltg., Vorstud Pilzfl. Luxemb., Nachtr. 3: 282. 1903.

Sexual morph: Ascomata immersed to partially erumpent becoming superficial, solitary or in groups. Venter 350–400 µm diam, 370–450 µm high, globose to subglobose, dark brown to black, covered by dark brown to reddish brown, septate hairs 3–4 µm wide. Neck central, 100–110 µm wide, up to 800 µm long, cylindrical, upright, straight or slightly flexuous, glabrous, tapering, apex sulcate. *Ostiole* periphysate. *Ascomatal wall* leathery, 45–57 µm thick, two-layered; outer layer consisting of thick-walled, brown, polyhedral cells of *textura angularis* to *textura prismatica* with opaque walls; cells tending to be darker towards the outside, becoming flattened and paler towards the interior. Inner layer consisting of several rows of thin-walled, hyaline, flattened cells. *Paraphyses* abundant, longer than the asci, becoming disintegrated with age, septate, constricted at the septa, hyaline, 5–9 µm wide, tapering to ca. 3.5 µm. *Asci* 62–70(–75) × 6.5–7.5 µm (mean ± SD = 67.3 ± 2.9 × 7.1 ± 0.2 µm), 58–63(–66) µm (mean ± SD = 61.3 ± 2.3 µm) long in the sporiferous part, truncate at the apex, subcylindrical to clavate, with a short stipe; with 8 partially overlapping, obliquely uniseriate or partly biseriate ascospores; apical annulus ca. 2.5 µm wide, 1.5 µm high. *Ascospores* 8.5–9.5(–10.5) × 4–4.5 µm (mean ± SD = 9.0 ± 0.5 × 4.5 ± 0.2 µm), ellipsoidal to

oblong, hyaline, longitudinally striate, 1–3-septate, commonly only 1–2-septate, the first-formed septum in the middle or slightly below or above the middle, third septum developing rarely. **Asexual morph:** unknown.

Culture characteristics: Colonies on MLA 13–15 mm diam after 14 d (18–21 mm after 21 d, 24–25 mm after 28 d) at 25 °C, circular, convex. Aerial mycelium abundant, woolly to cottony becoming loose to woolly-floccose at the margin, colony surface brown-grey turning brown towards the margin; reverse black. Colonies on PCA 8–9 mm after 14 d (10–11 mm after 21 d, 10–12 after 28 d) at 25 °C, circular or slightly irregular, raised. Aerial mycelium abundant, woolly to cottony, loose or almost cobwebby towards the margin, colony surface brown-grey at the centre turning dark olive-brown towards the margin; reverse black. Vegetative hyphae branched, septate, medium to dark brown, smooth-walled. Margin of the colony consisting of densely branched hyphae of substrate mycelium. Sporulation not observed.

Specimens examined: **Belgium**, Moersdorf, on bark of *Pyrus communis*, 25 May 1902, J. Feltgen (**holotype** of *Eriosphaeria conoidea*, LUX 043455). **Czech Republic**, Southern Bohemia, Šumava Mts. National park, Stožec, Medvědice Mt., on decaying deciduous wood, 17 Sep. 2007, M. Réblová M.R. 2998 (culture CBS 141370). **Denmark**, Sjælland, Jægerspris Nordskov, distr. 44, on very rotten wood of *Quercus* sp., 4 Nov. 1963, A. Munk (C); *ibid.*, Ermelundet, on old bark of *Fraxinus excelsior*, 7 Dec. 1964, A. Munk (C); *ibid.*, Bernstorffsparken, on very rotten wood, 24 Mar. 1965, A. Munk (C); *ibid.*, Suserup Skov, on wood of *Sorbus* sp., 15 Dec. 1995, T. Læssøe TL-4062 (C 34511). **Italy**, Lazio, province Viterbo, Farnese, Selva di Lamone Nature reserve, on decaying wood of *Quercus cerris*, 19 Mar. 2010, M. Réblová M.R. 3135; *ibid.*, 3 Apr. 2011, M.R. 3607 (culture CBS 131660), M.R. 3611 (culture CBS 131481).

Notes: The examination of the holotype of *Eriosphaeria conoidea* (Feltgen 1903) revealed a fungus that fits well the description of *Lentomitella* and represents a distinct species. Therefore, it is transferred to this genus and a new combination is proposed. Höhnel (1906b) examined the holotype and concluded that *E. conoidea* is conspecific with *Ceratostomella debaryana* (Saccardo 1882) and that it shows remarkable similarity to *L. vestita* and *L. investita*. Although *C. debaryana* shares similar size of asci and ascospores with *L. conoidea*, in the protologue (Auerswald 1869) the ascospores are described and illustrated as aseptate with granulose content, and the width of ascomata (140 µm) is too small to match the size of any accepted species of *Lentomitella*. The type material of *C. debaryana* could not be located. The holotype of *E. conoidea* deviates slightly in the length of the asci from recently collected material from the Czech Republic and Denmark; the asci are 57–66 × 6.5–7.5 µm, although in the protologue of *E. conoidea* they were described as longer, 62–72 × 6–8 µm by Feltgen (1903). Similar length of asci of *E. conoidea* (ca. 70 µm) was reported also by Höhnel (1906b).

Lentomitella conoidea is represented by four strains in our phylogeny. The ascospores are mostly 1–2-septate, the first septum is formed in the middle or slightly above or below the middle. Ascospores with three septa were observed only in the collections from Denmark. The length of the neck and presence of hairs covering the venter vary among collections.

Lentomitella conoidea is most similar to *L. tenuirostris* in morphology of asci and ascospores, but it differs by slightly shorter ascospores, slightly longer asci and larger ascomata. In culture, the aerial mycelium of *L. conoidea* is woolly to cottony, loose to woolly-floccose or almost cobwebby at the margin, while in *L. tenuirostris* the aerial mycelium is cottony to felty resulting in more compact aerial hyphae; the colony surface is paler, because substrate mycelium and the brown hue in the agar do

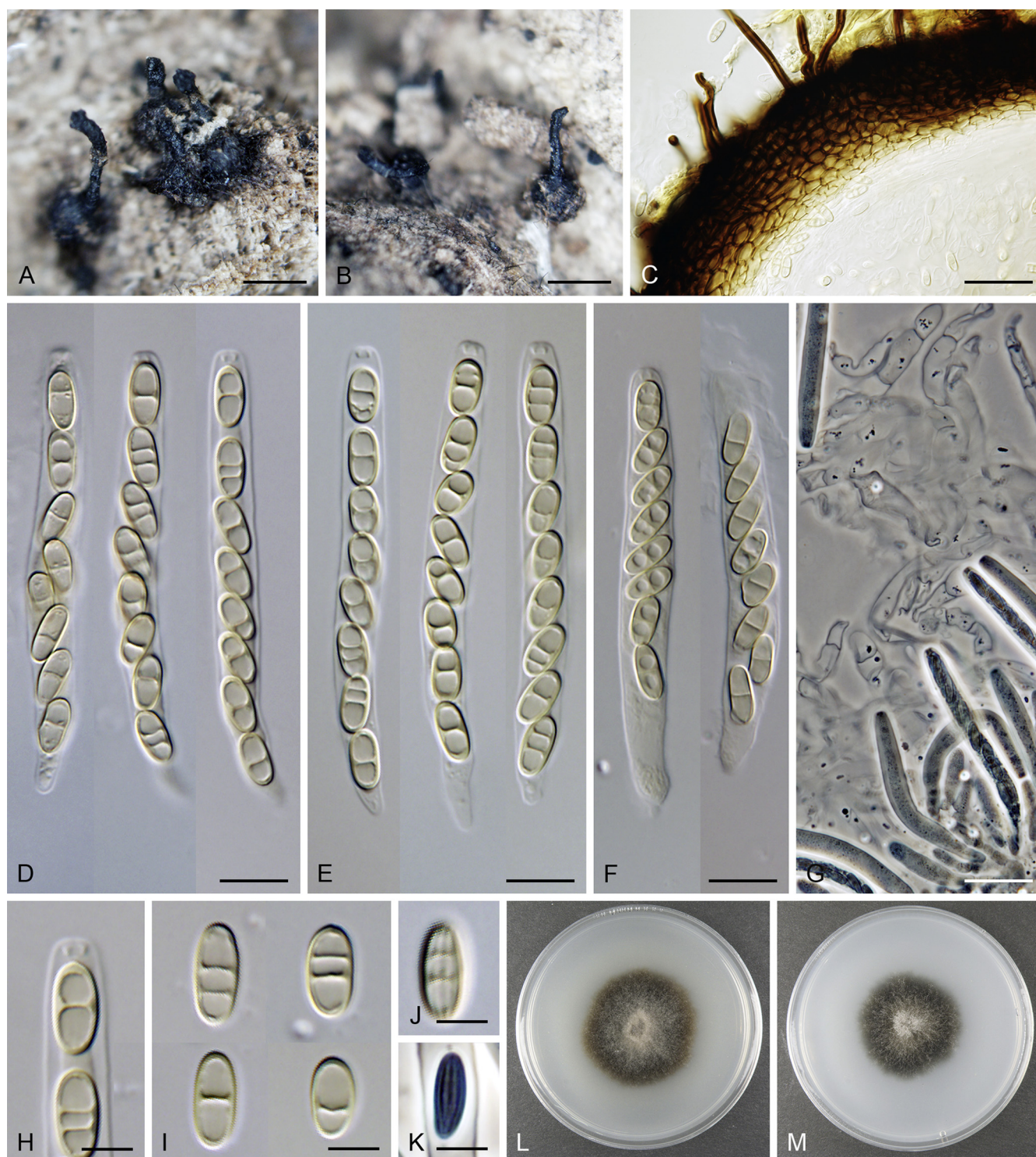


Fig. 10. *Lentomitella conoidea*. **A, B.** Ascomata. **C.** Longitudinal section of the ascomal wall. **D–F.** Asci. **G.** Paraphyses. **H.** Ascal apex with apical annulus. **I–K.** Ascospores. **L, M.** Colonies on MLA and PCA after 28 d. **A, B, J, K** from CBS 141370, **C, E** from M.R. 3135, **F** from LUX 043455, **D, G, H, I, L, M** from CBS 131660. Scale bars: **A, B** = 500 μ m, **C, G** = 20 μ m, **D–F** = 10 μ m, **H–K** = 5 μ m.

not show through loose aerial hyphae as is the case of *L. conoidea*. Moreover, the margin of the colony of *L. conoidea* consists of densely branched hyphae of substrate mycelium, while the margin of *L. tenuirostris* is formed of unbranched or sparsely branched hyphae. Most specimens of *L. conoidea* were collected on various hardwoods in deciduous forests in lowlands, while specimens of *L. tenuirostris* were collected in the mountain regions of the Czech Republic and France. For further comparison see [Discussion](#) and also comments of *L. tenuirostris*.

Lentomitella conoidea can be also compared to *L. investita*, but the latter differs by shorter asci and ascospores that possess the first-formed septum always in the middle and two additional septa that form symmetrically.

Lentomitella crinigera (Cooke) Réblová, Mycologia 98: 83. 2006. **Fig. 11.**

Basionym: *Sphaeria crinigera* Cooke, Grevillea 1: 156. 1873.

Synonyms: *Ceratosphaeria crinigera* (Cooke) Sacc. Syll. fung. 2: 227. 1883.

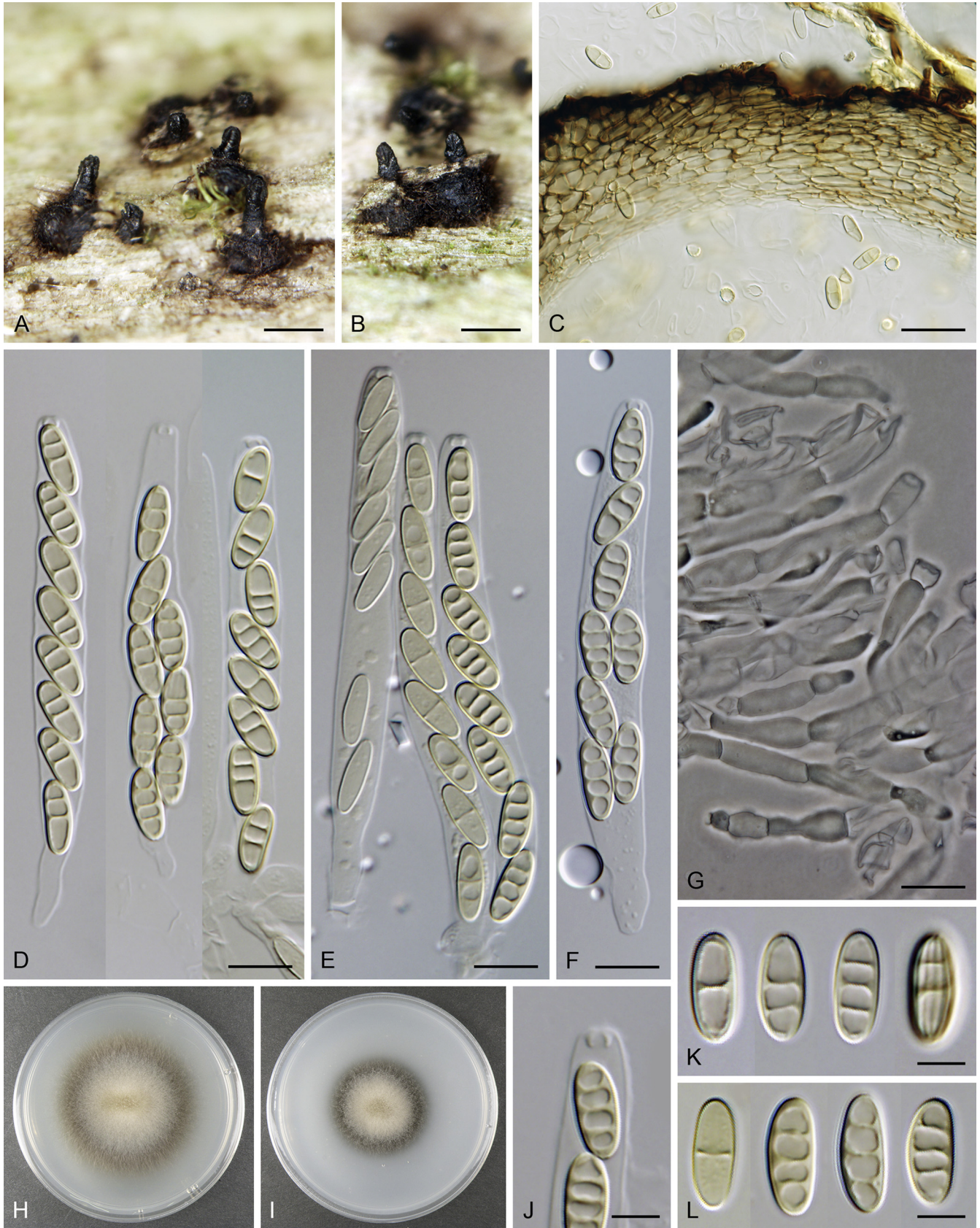


Fig. 11. *Lentomitella crinigera*. **A, B.** Ascomata. **C.** Longitudinal section of the ascomal wall. **D–F.** Asci. **G.** Paraphyses. **H, I.** Colonies on MLA and PCA after 28 d. **J.** Ascus apex with apical annulus. **K, L.** Ascospores. A–D, G–I, K from CBS 138678, E, J, L from M.R. 1671, F from M.R. 1526. Scale bars: A, B = 500 μ m, C, G = 20 μ m, D–F = 10 μ m, J–L = 5 μ m.

Ceratostomella crinigera (Cooke) Cooke, Grevillea 17: 49. 1889.
Ceratostomella triseptata Petr., Anns mycol. 23: 135. 1925.

Sexual morph: *Ascomata* immersed with protruding necks or partially erumpent becoming superficial with base immersed, solitary, in rows or small groups. Venter 450–600 µm diam, 510–650 µm high, globose to subglobose, dark brown, with dark brown, septate hairs 3.5–5 µm wide. Neck central, 120–170 µm wide, up to 1 mm long, cylindrical, upright, straight or slightly flexuous, glabrous, tapering; apex sulcate. *Ostiole* periphysate. *Ascomatal wall* fragile to leathery, 35–55(–65) µm thick, two-layered; outer layer consisting of thick-walled, brown, polyhedral cells of *textura angularis* to *textura prismatica* with opaque walls; cells tending to be darker towards the outside, becoming flattened and paler towards the interior. Inner layer consisting of several rows of thin-walled, hyaline, flattened cells. *Paraphyses* abundant, longer than the asci, becoming disintegrated with age, septate, constricted at the septa, hyaline, 6.5–10.5 µm wide, tapering to 3.5–4.5 µm. *Asci* (66–)70–88(–90) × (7.5–) 8–9.5(–10) µm (mean ± SD = 78.7 ± 4.4 × 8.5 ± 0.6 µm), (62–) 68–76 µm (mean ± SD = 69.1 ± 4.4 µm) long in the sporiferous part, truncate at the apex, cylindrical to clavate, with a short stipe; with 8 obliquely uniseriate or biseriate ascospores; apical annulus ca. 2.5–3 µm wide, 1.5–2 µm high. *Ascospores* (10–) 10.5–13 × 4–5.5 µm (mean ± SD = 11.5 ± 0.3 × 4.8 ± 0.3 µm), ellipsoidal-fusiform, slightly inequilateral, hyaline, longitudinally striate, 1–3-septate. **Asexual morph:** unknown.

Culture characteristics: Colonies on MLA 10–13 mm diam after 14 d (13–15 mm after 21 d, 15–17 after 28 d) at 25 °C, circular, convex. Aerial mycelium abundant, woolly to cottony, margin filamentous, colony surface pale brown to beige with a dark brown marginal ring; reverse black. Colonies on PCA 4–5 mm diam after 14 d (5–7 mm after 21 d, 6–8 mm after 28 d) at 25 °C, circular, convex. Aerial mycelium abundant, cottony, loose towards the margins, margin filamentous, colony surface beige to pale brown, with a brown ring of submerged hyphae at the margin; reverse black. Vegetative hyphae branched, septate, medium to dark brown, smooth-walled. Margin of the colony consisting of densely branched hyphae of substrate mycelium. Sporulation not observed.

Specimens examined: **Czech Republic**, Northern Moravia, Podhoří 'Podhorn' near Hranice, on decaying coniferous wood, Nov. 1913, F. Petrak (**holotype** of *Ceratostomella triseptata*, W 18093). Southern Bohemia, Novohradské hory Mts., Dobrá voda, Hojná voda National nature monument, on decaying wood, 4 Oct. 2012, M. Réblová M.R. 3742 (culture CBS 138678). Southern Bohemia, Šumava Mts. National park, Železná Ruda, glacial cirque of the Certovo jezero Lake National nature reserve, on decaying wood of *Abies alba*, 28 Aug. 1997, M. Réblová, M.R. 997, M.R. 1034; *ibid.*, on decaying wood of *Picea abies* 12 Aug. 1999, M.R. 1544, M.R. 1585; 21 Aug. 2000, M.R. 1672; *ibid.*, glacial cirque of the Černé jezero Lake National nature reserve, on decaying wood of *Abies alba*, 13 Aug. 1999, M.R. 1526, M.R. 1546; *ibid.*, Boubínský prales National nature reserve, on decaying wood of *Picea abies*, 17 Aug. 1999, M.R. 1611; *ibid.*, Prášíly, Ždanidla Mt., 24 Aug. 2000, on decaying wood of *Picea abies*, M.R. 1671; *ibid.*, Modrava, Ptačí nádrž, on decaying wood of *Picea abies*, 14 Aug. 1999, M.R. 1457; *ibid.*, Modrava, Modravské slatě, Pytlácký roh, on decaying wood of *Picea abies*, 14 Aug. 1999, M.R. 1652. **Sweden**, Fries' Scleromyceti Sueciae No. 346, on decaying wood (UPS). **UK**, England, Norfolk, King's Lynn, on decaying pine wood, C.B. Plowright (**holotype** of *Sphaeria crinigera*, K 84422).

Notes: *Lentomitella crinigera* is characterised by 1–3-septate, ellipsoidal-fusiform ascospores, with all three septa developed early in the ontogeny. Compared to other *Lentomitella* spp. the ascomata of *L. crinigera* are larger, exceeding 500 µm diam, and the neck is wider, 120–170 µm. It is probably the only member of

the genus which expresses a clear preference for coniferous wood. The examination of the holotype of *Ceratostomella triseptata* revealed that this name is a synonym of *L. crinigera*.

Lentomitella crinigera is most similar to *L. obscura*, *L. sulcata* and *L. striatella* in morphology and size of ascospores and asci. Based on phylogenetic evidence, none of these three species is closely related to *L. crinigera* and their distinction is supported at the RNA structural level. However, in the absence of DNA sequence data, morphological distinction of these species is challenging. Both *L. striatella* and *L. sulcata* are known only from New Zealand and were collected on decaying wood of *Nothofagus* sp.; the length of their asci is in the upper range typical of *L. crinigera*. On the other hand, the asci of *L. obscura* are shorter than those of *L. sulcata* and *L. striatella* and their length is in the lower range of *L. crinigera*. *Lentomitella obscura* can be distinguished from *L. crinigera* in having slightly shorter ascospores and by occurrence on deciduous wood; all three strains of *L. obscura* originate from various deciduous hardwoods from three localities in Ariège, southern France. Therefore, the host determination is important to aid the identification of these morphologically similar species.

The substrate of the specimen of *L. crinigera* sequenced in this study (M.R. 3742, culture CBS 138678) has not been determined. The wood is very rotten and was collected in a locality with stands of *Fagus sylvatica*, *Picea abies* and old fallen trunks of *Abies alba*. Our attempts to isolate DNA from herbarium material or cultivate *L. crinigera* from identified coniferous substrates were not successful.

***Lentomitella investita* (Schw.) Réblová, comb. nov.** MycoBank MB821766. Fig. 12.

Basionym: *Sphaeria investita* Schw., Trans. Amer. Phil. Soc. 2, Vol. 4: 216. 1834.

Synonyms: *Ceratostoma investitum* (Schw.) Ellis & Everh., North Amer. Pyrenom. p. 193. 1892.

Ceratostomella investita (Schw.) Starbäck, Bih. Kongl. Svenska Vet.-Akad. Handl. 19(2): 26. 1894.

Amphitrichum investitum (Schw.) Kuntze, Revis. Gen. Pl. 3(2): 443. 1898.

Ceratostomella vestita Sacc. var. *varvicensis* Grove, J. Bot. 23: 131. 1885.

Ceratostomella maderensis Petr., Bot. Jahrb., Beibl. 142: 98. 1929.

Sexual morph: *Ascomata* immersed to partially erumpent with protruding necks becoming superficial with only base immersed, solitary or in groups. Venter 300–350(–400) µm diam, 320–360 µm high, globose to subglobose, dark brown to black, with sparse, brown to reddish-brown, septate hairs 3.5–4 µm wide at the lower part. Neck central, 90–110 µm wide, up to 800 µm long, cylindrical, upright, straight or slightly flexuous, glabrous, tapering, apex sulcate. *Ostiole* periphysate. *Ascomatal wall* fragile to leathery, 37–56 µm thick, two-layered; outer layer consisting of thick-walled, brown, polyhedral cells of *textura angularis* to *textura prismatica* with opaque walls; cells tending to be darker towards the outside, becoming flattened and paler towards the interior. Inner layer consisting of several rows of thin-walled, hyaline, flattened cells. *Paraphyses* becoming disintegrated with age, septate, constricted at the septa, hyaline, 4.5–10 µm wide, tapering to ca. 3.5 µm. *Asci* (46–) 50–56(–65) × 6–7 µm (mean ± SD = 54.3 ± 2.3 × 6.7 ± 0.3 µm), 45–52 µm (mean ± SD = 49.3 ± 2.3 µm) long in the sporiferous part, truncate at the apex, cylindrical to clavate, with a short stipe;

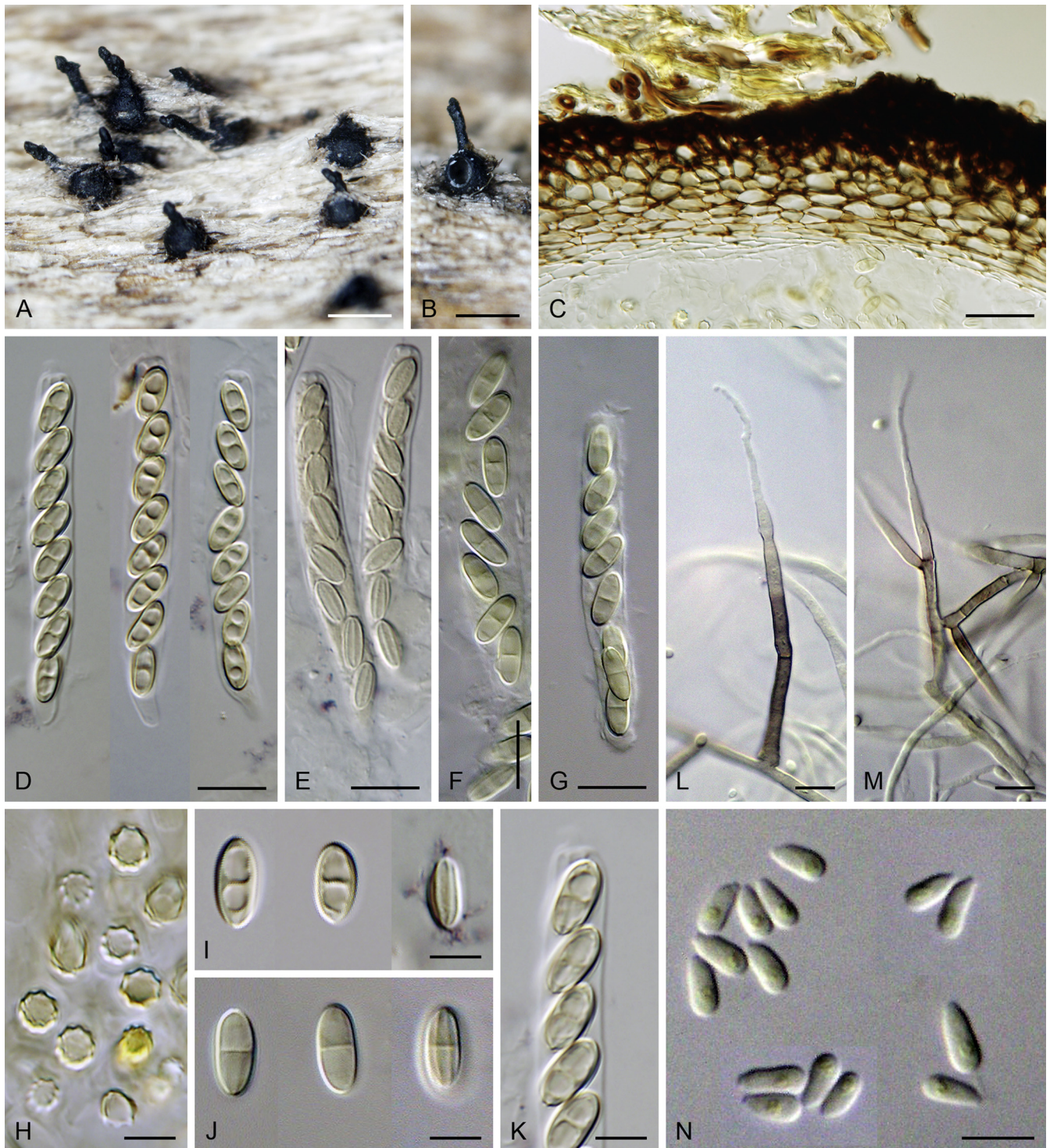


Fig. 12. *Lentomitella investita*. A, B. Ascomata. C. Longitudinal section of the ascomal wall. D–G. Asci. H–J. Ascospores. K. Ascus apex with apical annulus. L, M. Conidiophores. N. Conidia. A–E, H, I, K–N from PDD 110876, F, G, J from PH 01016198. Scale bars: A, B = 500 μ m, C = 20 μ m, D–G = 10 μ m, H–N = 5 μ m.

with 8 obliquely uniseriate, partly overlapping ascospores; apical annulus ca. 2.5–3 μ m wide, 1.5 μ m high. *Ascospores* (7–) 7.5–9 \times 3.5–4(–4.5) μ m (mean \pm SD = 8.1 \pm 0.3 \times 3.7 \pm 0.3 μ m), ellipsoidal or ellipsoidal-fusiform, slightly inequilateral, hyaline, longitudinally striate, 1(–3)-septate, first-formed septum in the middle, with two large drops. *Asexual morph*: A phaeoisaria-like asexual morph was formed *in vitro*. Sporulation sparse, widespread throughout the colony. *Conidiophores* macronematous, mononematous, arising terminally or laterally from aerial hyphae, unbranched or branched apically, brown near the base, subhyaline to hyaline towards the tip, 64–80 \times 2–2.5 μ m. *Conidiogenous cells* terminal or intercalary, pale brown to subhyaline at the bottom, hyaline in the conidiogenous part,

subcylindrical or slender flask-shaped, tapering toward the apex, with a rachis 16–20 \times 1.5–2 μ m at the tip; conidiogenesis holoblastic-denticulate, conidial heads slimy, inconspicuous, transparent. *Conidia* clavate to obovate, slightly apiculate at the base, broadly rounded at the apical end, 4.5–7 \times 2 (mean \pm SE = 5.2 \pm 0.9 \times 2) μ m, hyaline, aseptate, smooth.

Specimens examined: **Germany**, Nassau, on decaying wood, in autumn 1894, L. Fuckel (as *Ceratostomella rhenana*, Herb. Barbey-Boissier 603, G). **Great Britain**, Sutton, Driffold Lane, on decaying wood, 25 Oct. 1884, W.B. Grove (**holotype** of *Ceratostomella vestita* var. *varvicensis*, K 124145). **Madeira**, Ribeiro frio, on decaying wood of *Laurus novocanariensis*, 3 Jun. 1926, A. Ade (**holotype** of *Ceratostomella maderensis*, W 03981). **New Zealand**, South Island, Southland, Southland Distr., Fiordland National park, Lake Monowai 40 km S of Manapouri, Borland Nature Walk 300 m NW of Borland Lodge, on decaying wood

of *Nothofagus* sp., 9 Mar. 2005, M. Réblová M.R. 2951/NZ 443 (PDD 110876); *ibid.*, West Coast, Buller Distr., Victoria Forest Park, Big River Inanganua track 14 km SE of Reefton, on decaying wood of *Nothofagus* sp., 6 Mar. 2003, M. Réblová M.R. 2721/NZ 222, M.R. 2726/NZ 227; *ibid.*, Westland Distr., Arthur's Pass National Park, Kelly Shelter 5 km W of Otira, Cockayne Nature Walk, on decaying wood of *Nothofagus* sp., 16 Mar. 2003, M. Réblová M.R. 2829/NZ 339. USA, Pennsylvania, Northampton County, Bethlehem, on decaying wood, L.D. Schweinitz, S.F. 1621.476 (holotype of *Sphaeria investita*, PH 01016198).

Notes: *Lentomitella investita* is characterised by ellipsoidal, mostly 1-septate ascospores with the septum positioned in the middle, with two additional septa developed symmetrically but rarely upon aging only in the collections from New Zealand. The longitudinally striate walls of the ascospores are conspicuous and individual ridges are often seen protruding at the poles. The holotypes of *Ceratostomella vestita* var. *varvicensis* (Grove 1885) and *Ceratostomella maderensis* (Petraik 1929) were examined. Based on the morphology of ascomata, asci and ascospores they are considered conspecific with *L. investita*. The holotype of *C. maderensis* deviates slightly in the length of the asci from the holotype of *L. investita* and other recently collected material; they are 52–63(–68) × 6–7.5 µm. Our specimens from New Zealand fit well the description of *L. investita*, although the ascospores in PDD 110876 are more tapering towards the ends. This collection was isolated into axenic culture, which is, unfortunately, no longer available. The fungus formed in vitro a phaeoisaria-like asexual morph, which is consistent with asexual morphs observed in *L. sulcata* and *Lentomitella* sp. The DNA extraction from herbarium material was not successful.

Lentomitella investita, *L. vestita* and *L. cirrhosa* were formerly treated as conspecific (von Arx 1952, Réblová 2006). Based on molecular evidence the two latter are accepted as separate species in our study. Although no DNA sequence data of *L. investita* are available, given the size of asci and ascospores, the species is intermediate between *L. vestita* and *L. cirrhosa* and therefore regarded as distinct. *Lentomitella cirrhosa* differs from *L. investita* by longer and wider ascospores and longer asci. On the other hand, *L. vestita* is well-distinguished from *L. investita* by shorter, regularly 1-septate ascospores and shorter asci.

Lentomitella investita resembles *L. conoidea* in the size of ascospores, but the latter differs by longer asci and mostly 1–2-septate ascospores with the first-formed septum in the middle or slightly above or below the middle.

***Lentomitella magna* Réblová, sp. nov.** MycoBank MB821767. Fig. 13.

Etymology: *Magnus* (L.) meaning big, large, referring to the large ascospores, which are the largest of the known *Lentomitella* species.

Sexual morph: *Ascomata* immersed to partially erumpent becoming superficial with only base immersed, solitary. Venter 300–390 µm diam, 310–380 µm high, globose to subglobose, dark brown to black, with dark brown, septate hairs 3–3.5 µm wide growing at the exposed sides. Neck central, 90–110 µm wide, up to 2000 µm long, cylindrical, upright or decumbent, flexuous, glabrous, tapering, sometimes laterally flattened, apex sulcate. *Ostiole* periphysate. *Ascomatal wall* fragile to leathery, 50–56 µm thick, two-layered; outer layer consisting of thick-walled, brown, polyhedral cells of *textura angularis* to *textura prismatica* with opaque walls; cells tending to be darker towards the outside, becoming flattened and paler towards the interior. Inner layer consisting of several rows of thin-walled, hyaline, flattened cells. *Paraphyses* abundant, longer than the asci,

becoming disintegrated with age, septate, constricted at the septa, hyaline, 5.5–7.5 µm wide, tapering to ca. 3 µm. *Asci* (89–) 93–102(–105) × (9.5–)10–12 µm (mean ± SD = 97.5 ± 4.7 × 10.7 ± 1.4 µm), (75–)88–95 µm (mean ± SD = 88.1 ± 6.0 µm) long in the sporiferous part, truncate at the apex, cylindrical to clavate, with a short stipe; with 8 obliquely uniseriate or partly biseriate ascospores; apical annulus 3.5–4 µm wide, 2 µm high. *Ascospores* (12.5–)13–15 × 5.5–6.5 µm (mean ± SD = 13.7 ± 0.9 × 6 ± 0.4 µm), ellipsoidal to ellipsoidal-fusiform, inequilateral, hyaline, with longitudinal ridges that are often discontinuous, 3-septate with four large drops. *Asexual morph:* unknown.

Culture characteristics: Colonies on MLA 10–12 mm diam after 14 d (13–14 mm after 21 d, 15–16 after 28 d) at 25 °C, circular to slightly irregular, mostly flat, raised at the centre. Aerial mycelium sparse, cottony at the centre surrounded by a wide zone of loose to almost cobwebby mycelium, margin filamentous, colony surface beige in the centre with olive-brown ring of submerged hyphae at the margin; reverse black. Colonies on PCA 3–4 mm diam after 14 d (4–6 mm after 21 d, 5–7 mm after 28 d) at 25 °C, circular to slightly irregular, flat, raised at the centre. Aerial mycelium sparse, cottony to woolly, cobwebby towards the margin, margin filamentous, colony surface pale brown with dark olive-brown ring of submerged hyphae at the margin; reverse black. Vegetative hyphae branched, septate, medium to dark brown, smooth-walled. Margin of the colony consisting of densely branched hyphae of substrate mycelium. Sporulation not observed.

Specimen examined: New Zealand, South Island, West Coast, Westland Distr., Westland Tai Poutini National park, Lake Matheson, 5 km SW from Fox Glacier, on decaying wood, 13 Apr. 2005, M. Réblová M.R. 2961/NZ 781 (holotype, PDD 110877, culture ex-type ICMP 18371).

Notes: *Lentomitella magna* is characterised by 3-septate, ellipsoidal-fusiform, inequilateral ascospores and asci, which are the largest of all *Lentomitella* species accepted in this study. It is known only from a single collection from New Zealand. The ascomata are mostly superficial with decumbent or upright necks and horizontally lying venter covered with dark brown hairs. The position of ascomata and necks on the substrate was influenced by their growth under decaying, partly peeled off bark. The longitudinal ridges in the ascospore wall are partly discontinuous giving the ascospore wall a reticulate appearance.

***Lentomitella obscura* Réblová, sp. nov.** MycoBank MB821768. Fig. 14.

Etymology: *Obscure* (L.) meaning indistinct, obscure, referring to the morphology of ascospores.

Sexual morph: *Ascomata* immersed with protruding necks to partially erumpent or becoming superficial, solitary or densely aggregated. Venter 380–500 µm diam, 370–510 µm high, globose to subglobose, dark brown to black, with brown to reddish-brown, septate hairs 3.5–4 µm wide. Neck central, 120–150 µm wide, up to 1500 µm long, cylindrical, upright or partly decumbent, straight or slightly flexuous, glabrous, tapering, apex sulcate. *Ostiole* periphysate. *Ascomatal wall* fragile to leathery, 35–50 µm thick, two-layered; outer layer consisting of thick-walled, brown, polyhedral cells of *textura angularis* to *textura prismatica* with opaque walls; cells tending to be darker towards the outside, becoming flattened and paler towards the interior. Inner layer consisting of several rows of thin-walled,

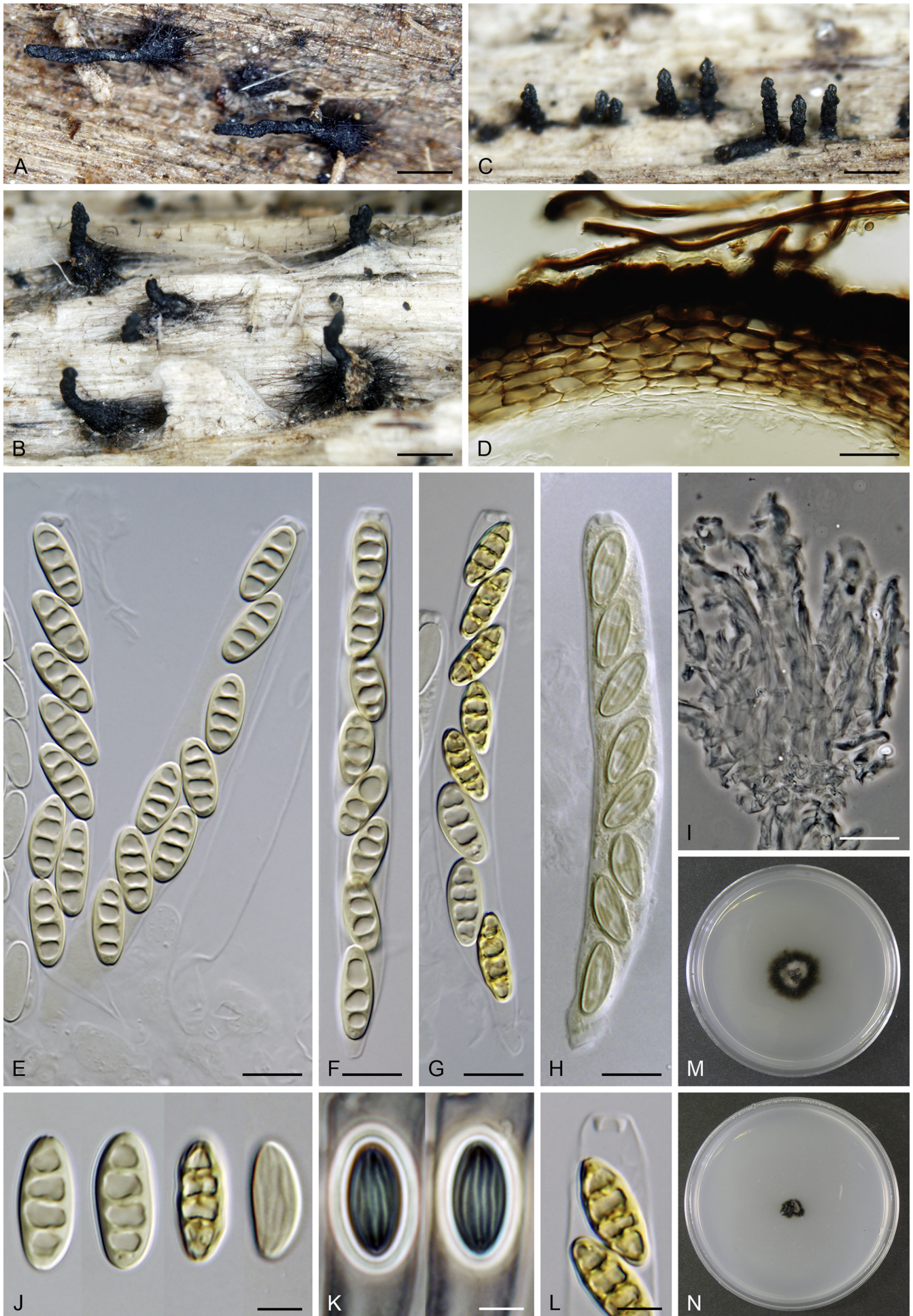


Fig. 13. *Lentomitella magna*. A–C. Ascomata. D. Longitudinal section of the ascomal wall. E–H. Asci. I. Paraphyses. J, K. Ascospores. L. Ascus apex with apical annulus. M, N. Colonies on MLA and PCA after 28 d. A–N from ICMP 18371. Scale bars: A–C = 500 μ m, D, I = 20 μ m, E–H = 10 μ m, J–L = 5 μ m.



Fig. 14. *Lentornitella obscura*. **A–C.** Ascomata. **D.** Longitudinal section of the ascomal wall. **E, F.** Asci. **G.** Paraphyses. **H.** Ascus apex with apical annulus. **I–K.** Ascospores. **L, M.** Colonies on MLA and PCA after 28 d. **A–C, F, G, I** from CBS 138735, **D, E, H, J–M** from CBS 138736. Scale bars: **A–C** = 500 μm , **D, G** = 20 μm , **E, F** = 10 μm , **H–K** = 5 μm .

hyaline, flattened cells. *Paraphyses* abundant, longer than the asci, becoming disintegrated with age, septate, constricted at the septa, hyaline, 5–8 µm wide, tapering to ca. 3 µm. *Asci* (70–) 72–80(–82) × 7.5–8(–8.5) µm (mean ± SD = 76.2 ± 3.2 × 8.1 ± 0.2 µm), 65–76 µm (mean ± SD = 71.8 ± 3.4 µm) long in the sporiferous part, truncate at the apex, cylindrical to clavate, with a short stipe; with 8 obliquely uniseriate or partly biseriate ascospores; apical annulus ca. 3 µm wide, 1.5–2 µm high. *Ascospores* (10–) 11–12 × 4–5(–5.5) µm (mean ± SD = 11.7 ± 0.6 × 5 ± 0.4 µm), ellipsoidal-fusiform, hyaline, longitudinally striate, 1–3-septate. *Asexual morph*: unknown.

Culture characteristics: Colonies on MLA 19–23 mm diam after 14 d (30–32 mm after 21 d, 37–42 after 28 d) at 25 °C, circular, convex. Aerial mycelium abundant, woolly, loose towards the margins, margin filamentous, colony surface pale brown-beige with a brown ring of submerged hyphae at the margin; reverse black. Colonies on PCA 7–10 mm diam after 14–28 d in CBS 138736; 10–13 mm after 14 d in CBS 138735 and CBS 137799 (20–21 mm after 21 d, 27–28 mm after 28 d) at 25 °C; circular to irregular, convex. Aerial mycelium abundant, cottony to woolly, loose towards the margins, margin filamentous, colony surface beige-grey with olive-brown ring of submerged hyphae at the margin; reverse black. Vegetative hyphae branched, septate, medium to dark brown, smooth-walled. Margin of the colony consisting of unbranched or sparsely branched hyphae of substrate mycelium. Sporulation not observed.

Specimens examined: France, Ariège, Rimont, Las Muros, banks of the Peyrau brook 440 m a.s.l., on decaying wood of *Pinus* sp., 30 Sep. 2013, M. Réblová M.R. 3707 (PRA-12736, culture CBS 138735); *ibid.*, banks of La Maille brook, 550 m a.s.l., on decaying wood, 2 Oct. 2013, M. Réblová M.R. 3784 (**holotype**, PRA-12737, culture ex-type CBS 138736); *ibid.*, along D18 1.5 km S of the village, banks of Le Baup brook, on decaying wood of *Quercus* sp., 3 Oct. 2013, M. Réblová M.R. 3801 (culture CBS 137799).

Notes: The specimens of *L. obscura* were collected in three different localities in the Ariège region in France. The ascomatal necks vary greatly in length within one collection. They are elongated up to 1500 µm in more humid areas, especially in cracks of wood, and much shorter (ca. 600 µm) when growing on the surface of the wood, where they are more exposed to air and sun. The hairs, which abundantly cover the venter, disappear with age leaving the ascomata almost glabrous, but remnants of hairs can be seen as a tomentum tightly attached to the base of ascomata and wood.

Although all three strains of *L. obscura* form a strongly supported monophyletic clade and their DNA sequences are identical, the morphological delimitation of this species was hindered by different stages of their growth and maturation resulting in a variable morphology of the ascospores. Two specimens, i.e. M.R. 3707 (culture CBS 138735) and M.R. 3801 (culture CBS 137799), showed mostly ellipsoidal, 1–2-septate ascospores with the third septum developing rarely and mostly in the shrinking ascospores. Moreover, their ascospores measuring 9–10(–11) × 4–4.5(–5) µm and asci 65–72(–75) × 6.5–7.5 µm were shorter than those of the third strain, which is designated as holotype (PRA-12737, ex-type strain CBS 138736). The holotype of *L. obscura* exhibits a perfectly mature stage with ellipsoidal-fusiform ascospores that are regularly 3-septate. *In vitro*, the colonies of all three strains have identical appearance on MLA and PCA media except that the ex-type strain grows slower on PCA (7–10 mm vs. 27–28 mm after 28 d). Given these circumstances, it is extremely difficult to identify the strains with shorter ascospores based on sexual

characters only; in such case at least ITS sequences should be produced for further comparison.

In the phylogenetic tree (Fig. 1), *L. obscura* is placed with *Lentomitella* sp., *L. magna* and *L. sulcata* in a highly supported subclade; all these species having ellipsoidal-fusiform, 3-septate ascospores. The latter three species all originate from New Zealand. *Lentomitella obscura* is similar to *L. sulcata* in morphology and size of ascospores, but the latter differs in longer asci and it is delimited at the RNA structural level by a unique CBC (Fig. 4), see Discussion.

***Lentomitella striatella* Réblová, sp. nov.** MycoBank MB821769. Fig. 15.

Etymology: Diminutive of *Striatus* (L.) meaning striped, referring to a fine linear marking in the longitudinally striate ascospores.

Sexual morph: *Ascomata* immersed to partially erumpent with protruding necks, solitary or in groups. Venter 330–400 µm diam, 310–410 µm high, globose to subglobose, dark brown to black, with sparse, dark brown, septate hairs ca. 3.5 µm wide. Neck central, 90–110 µm wide, 600–1500 µm long, cylindrical, upright, straight, glabrous, tapering, apex sulcate. *Ostiole* periphysate. *Ascomatal wall* fragile to leathery, 40–44 µm thick, two-layered; outer layer consisting of thick-walled, brown, polyhedral cells of *textura prismatica* with opaque walls; cells tending to be darker towards the outside, becoming flattened and paler towards the interior. Inner layer consisting of several rows of thin-walled, hyaline, flattened cells. *Paraphyses* abundant, longer than the asci, becoming disintegrated with age, septate, constricted at the septa, hyaline, 6.5–9.5 µm wide, tapering to ca. 4 µm. *Asci* (75–) 82–88 × 9–10.5 µm (mean ± SD = 85 ± 3.9 × 9.8 ± 0.6 µm), 68–78(–81) µm (mean ± SD = 75.8 ± 4.4 µm) long in the sporiferous part, truncate at the apex, cylindrical to clavate, with a short stipe; with 8 obliquely uniseriate or partly biseriate ascospores; apical annulus 3–3.5 µm wide, 1.5–2 µm high. *Ascospores* 11.5–13(–14) × 5–5.5 µm (mean ± SD = 12 ± 0.7 × 5.2 ± 0.3 µm), ellipsoidal, slightly inequilateral, hyaline, longitudinally striate, 3-septate. *Asexual morph*: unknown.

Culture characteristics: Colonies on MLA 12–16 mm diam after 14 d (15–19 mm after 21 d, 18–21 after 28 d) at 25 °C, circular, raised. Aerial mycelium abundant, cottony, loose towards the margin, colony surface brown to dark olive-brown turning brown towards the margin; reverse black. Colonies on PCA 11–12 mm diam after 14 d (13–16 mm after 21 d, 14–18 mm after 28 d) at 25 °C, circular, raised. Aerial mycelium abundant, cottony to woolly, loose towards the margin, colony surface brown-grey with olive-brown ring of submerged hyphae at the margin; reverse black. Vegetative hyphae branched, septate, medium to dark brown, smooth-walled. Margin of the colony consisting of unbranched or sparsely branched hyphae of substrate mycelium. Sporulation not observed.

Specimens examined: New Zealand, South Island, West Coast, Buller Distr., Victoria Forest Park, Duffy's Creek Track, 30 km SE from Reefton, on decaying wood of *Nothofagus* sp., 7 Apr. 2005, M. Réblová M.R. 2959/NZ 751 (**holotype**, PDD 110878, culture ex-type ICMP 18369); *ibid.*, Palmers Hut 18 km SW of Springs Junction on unpaved road, Lake Christabel track, on decaying wood of *Nothofagus* sp., 1 Mar. 2003, M. Réblová M.R. 2694/NZ 195; *ibid.*, Westland Distr., Arthur's Pass National park, Arthur's Pass village, on decaying wood of *Nothofagus solandri*, 17 Mar. 2003, M. Réblová M.R. 2870/NZ 387.

Notes: *Lentomitella striatella* appears as sister to *L. cirrhosa* and together they form a strongly supported monophyletic subclade at the base of the *Lentomitella* clade. It differs from *L. cirrhosa* in

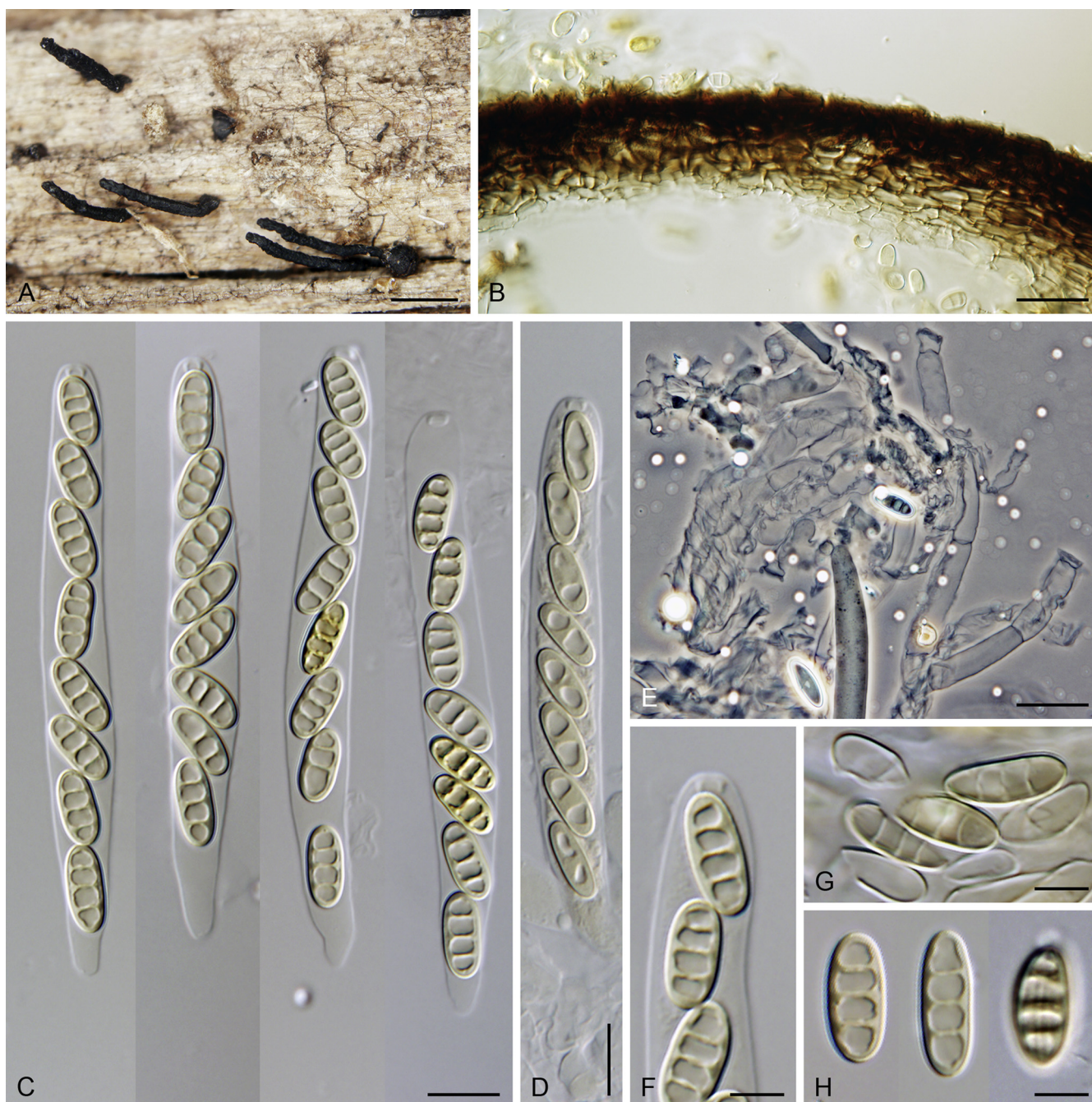


Fig. 15. *Lentomitella striatella*. A. Ascomata. B. Longitudinal section of the ascomal wall. C, D. Asci. E. Paraphyses. F. Ascus apex with apical annulus. G, H. Ascospores. A from M.R. 2694, B–H from ICMP 18369. Scale bars: A = 500 μ m, B, E = 20 μ m, C, D = 10 μ m, F–H = 5 μ m.

having longer and wider asci and longer, 3-septate ascospores. The septa are formed early in ontogeny still within the asci, while ascospores of *L. cirrhosa* are mostly 1-septate with two additional septa observed occasionally in released and shrinking ascospores.

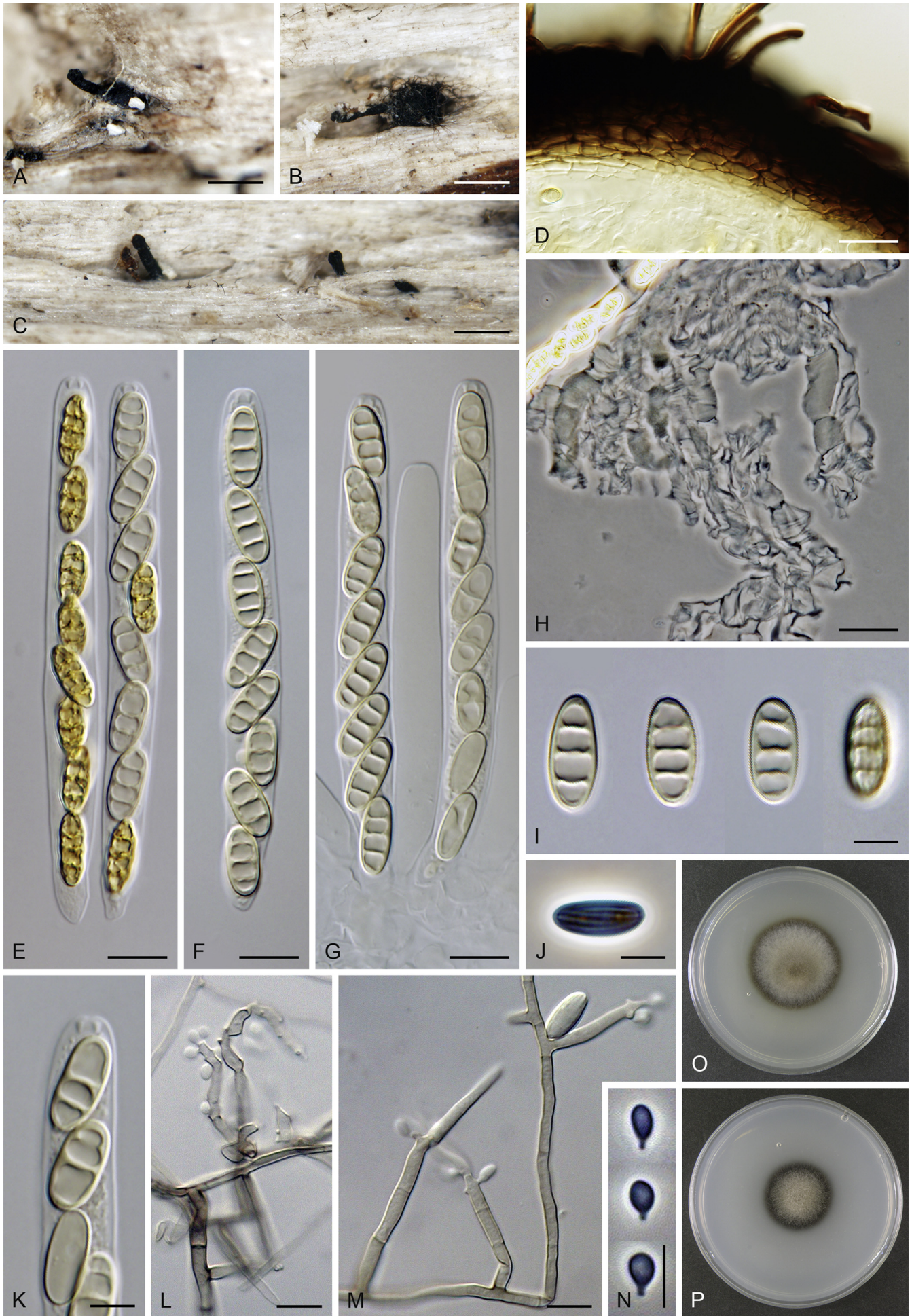
In morphology of ascospores, *L. striatella* resembles *L. crinigera*, *L. magna*, *L. obscura* and *L. sulcata*. *Lentomitella crinigera* and *L. sulcata* differ from *L. striatella* by shorter ascospores and slightly longer asci, and *L. magna* is well-distinguished from *L. striatella* by longer ascospores and asci, while *L. obscura* possesses much shorter asci. The ascospore wall of *L. striatella* is longitudinally striate, but the ridges are shallow and appear less conspicuous compared to other species.

***Lentomitella sulcata* Réblová, sp. nov.** MycoBank MB821770.

Fig. 16.

Etymology: *Sulcatus* (L.) meaning furrowed or grooved, referring to the apex of the ascomatal neck, which has several deep sulcations.

Sexual morph: *Ascomata* immersed to partially erumpent with protruding necks, solitary. Venter 300–400 μ m diam, 310–400 μ m high, globose to subglobose, dark brown to black, with sparse dark brown to reddish-brown, septate hairs 3–4 μ m wide covering the lower part. Neck central, 100–120 μ m wide, up to 700 μ m long, cylindrical, upright, straight or slightly flexuous, glabrous, apex sulcate. *Ostiole* periphysate. *Ascomatal wall* fragile to leathery, 30–45 μ m thick, two-layered; outer layer consisting of thick-walled, brown, polyhedral cells of *textura angularis* to *textura prismatica* with opaque walls; cells tending to be darker towards the outside, becoming flattened and paler towards the interior. Inner layer consisting of several rows of thin-



walled, hyaline, flattened cells. *Paraphyses* longer than the asci, becoming disintegrated with age, septate, constricted at the septa, hyaline, 8–12.5 µm wide. *Asci* 79–90(–93) × 8.5–9.5(–10) µm (mean ± SD = 86.4 ± 4.0 × 9.2 ± 0.4 µm), 72–84(–86) µm (mean ± SD = 80.3 ± 4.1 µm) long in the sporiferous part, broadly rounded to truncate at the apex, cylindrical to clavate, with a short stipe; with 8 obliquely uniseriate ascospores; apical annulus ca. 3 µm wide, 2 µm high. *Ascospores* (10.5–)11–12(–13) × 5–5.5 µm (mean ± SD = 11.7 ± 0.5 × 5.3 ± 0.3 µm), ellipsoidal to ellipsoidal-fusiform, slightly inequilateral, hyaline, longitudinally striate, 1–3-septate with four large drops, when vital. *Asexual morph*: *Conidiophores in vitro* macronematous, mononematous, arising terminally or laterally from aerial hyphae, unbranched or rarely branched apically, pale brown near the base, subhyaline to hyaline towards the tip, 24–45 × 2–2.5 µm. *Conidiogenous cells* terminal or intercalary, hyaline, cylindrical, tapering toward the apex, with a rachis 9–20(–25) × 2–2.5 µm at the tip bearing 2–10 hyaline denticles 0.5–1 × 0.5–1 µm; conidiogenesis holoblastic-denticulate, conidial heads slimy, inconspicuous, transparent. *Conidia* ellipsoidal to globose, apiculate at the base, 4–6 × 2–2.5 µm (mean ± SE = 5.2 ± 0.2 × 2.2 ± 0.3 µm), hyaline, aseptate, smooth.

Culture characteristics: Colonies on MLA 19–22 mm diam after 14 d (23–25 mm after 21 d, 25–26 after 28 d) at 25 °C, circular, convex. Aerial mycelium abundant, cottony to woolly, margin filamentous, colony surface beige-brown with olive-brown marginal ring of submerged hyphae; reverse black. Colonies on PCA 12–15 mm diam after 14 d (15–17 mm after 21 d, 18–19 mm after 28 d) at 25 °C, circular, convex. Aerial mycelium abundant, woolly, loose towards the margin, margin filamentous, colony surface beige-grey with dark olive-brown marginal ring of submerged hyphae; reverse black. Vegetative hyphae branched, septate, medium to dark brown, smooth-walled. Margin of the colony consisting of unbranched or sparsely branched hyphae of substrate mycelium. Sporulation copious, widespread throughout the colony.

Specimen examined: **New Zealand**, South Island, West Coast, Buller Distr., Victoria Forest park, Reefton, Lake Stream track, 30 km SE of Reefton, on decaying wood of *Nothofagus* sp., 27 Feb. 2003, M. Réblová M.R. 2659/NZ 145 (**holotype**, PDD 81435, culture ex-type ICMP 15124 = CBS 113655).

Notes: Although the specimen PDD 81435 was formerly treated under *L. crinigera* (Réblová 2006), it is introduced as a new species, *L. sulcata*, in this study. Their distinction as two different species, though morphologically difficult, is corroborated by molecular and RNA structural data.

Lentomitella sulcata is nested together with *L. magna*, *L. obscura* and *Lentomitella* sp. in a monophyletic clade. It is characterised by 3-septate, longitudinally striate ascospores and it forms simple, rarely branched conidiophores with globose to ellipsoidal, apiculate conidia *in vitro*. The asexual morph is most similar to *Lentomitella* sp. and also comparable to that produced by *L. investita*.

***Lentomitella tenuirostris* Réblová, sp. nov.** MycoBank MB821771. Fig. 17.

Etymology: *Tenuis* (L.) meaning thin, *rostrum* (L.) meaning beak, referring to ascomata with a slender projecting neck.

Sexual morph: *Ascomata* immersed to partially erumpent with protruding necks, becoming superficial, solitary, sometimes in rows or small groups. Venter 300–410 µm diam, 300–420 µm high, globose to subglobose, black, upright sometimes positioned horizontally towards the substrate, with sparse, dark brown, septate hairs 3–4 µm wide growing from the bottom and lower part, disappearing with age, venter later appears almost glabrous. Neck central, 90–110 µm wide, up to 900 µm long, cylindrical, upright, straight or slightly flexuous, tapering, apex sulcate. *Ostiole* periphysate. *Ascomatal wall* fragile to leathery, 32–42 µm thick, two-layered; outer layer consisting of thick-walled, brown, polyhedral cells of *textura prismatica* with opaque walls; cells tending to be darker towards the outside, becoming flattened and paler towards the interior. Inner layer consisting of several rows of thin-walled, hyaline, flattened cells. *Paraphyses* abundant, longer than the asci, becoming disintegrated with age, septate, constricted at the septa, hyaline, 5–9 µm wide, tapering to ca. 3.5 µm. *Asci* (58–)60–66(–69) × 7–7.5(–8) µm (mean ± SD = 62.9 ± 3.0 × 7.4 ± 0.5 µm), 52–62 µm (mean ± SD = 57.7 ± 3.2 µm) long in the sporiferous part, truncate at the apex, cylindrical, with a short stipe; with 8 uniseriate partially overlapping or obliquely uniseriate ascospores; apical annulus ca. 2.5 µm wide, 1.5 µm high. *Ascospores* (8.5–)9–10.5 × 4–4.5 µm (mean ± SD = 9.8 ± 0.6 × 4.3 ± 0.3 µm), ellipsoidal to suboblong, slightly inequilateral, sometimes slightly curved, hyaline, longitudinally striate, 1–3-septate, mostly 1–2-septate, the first-formed septum in the middle or slightly above or below the middle, formation of the third septum delayed, visible in old ascospores. *Asexual morph*: unknown.

Culture characteristics: Colonies on MLA 10–13 mm diam after 14 d (12–14 mm after 21 d, 19–20 mm after 28 d) at 25 °C, circular, convex to pulvinate. Aerial mycelium abundant, cottony to felty, loose to floccose towards the margin, margin filamentous, colony surface beige to brown-grey with outer olivaceous ring and darker olive-brown ring of submerged hyphae at the margin; reverse black. Colonies on PCA 7–10 mm diam after 14 d (9–10 mm after 21 d, 10–12 after 28 d) at 25 °C, circular, convex. Aerial mycelium abundant, cottony to felty, floccose towards the margin, margin filamentous, colony surface beige-grey with dark olive-brown ring consisting of submerged hyphae at the margin; reverse black. Margin of the colony consisting of unbranched or sparsely branched hyphae of substrate mycelium. Sporulation not observed.

Specimens examined: **Czech Republic**, Southern Bohemia, Novohradské hory Mts., Pohoří na Šumavě, Myslivna Mt., on decaying wood of *Sorbus aucuparia*, 6 Oct. 2012, M. Réblová M.R. 3771 (**holotype**, PRA-12738, culture ex-type CBS 138734); *ibid.*, Dobrá voda, Hojná voda National nature monument, on decaying wood of *Fagus sylvatica*, 4 Oct. 2012, M.R. 3735; *ibid.*, 28 Sep. 2014, M.R. 3859. Šumava Mts. National park, Železná Ruda, glacial cirque of the Černé jezero lake National nature reserve, on decaying wood of *Picea abies*, 22 Oct. 1998, M.R. 858; *ibid.*, Boubínský prales National nature reserve, on decaying wood of *Fagus sylvatica*, 14 Aug. 1999, M.R. 1533; *ibid.*, Mt. Spáleníště near Stožec, on decaying wood of *Fraxinus excelsior*, 16 Aug. 1999, M.R. 1545; *ibid.*, Povydí National nature reserve, Čeňkova Pila, on decaying wood of *Ulmus glabra*, 27 Aug. 2000, M.R. 1677. **France**, Ariège, Rimont, Las Muros, banks of the Peyrau

Fig. 16. *Lentomitella sulcata*. A–C. Ascomata. D. Longitudinal section of the ascomal wall. E–G. Asci. H. Paraphyses. I, J. Ascospores. K. Ascal apex with apical annulus. L, M. Conidiophores. N. Conidia. O, P. Colonies on MLA and PCA after 28 d. A–P from ICMP 15124. Scale bars: A–C = 500 µm, D, H = 20 µm, E–G = 10 µm, I–N = 5 µm.

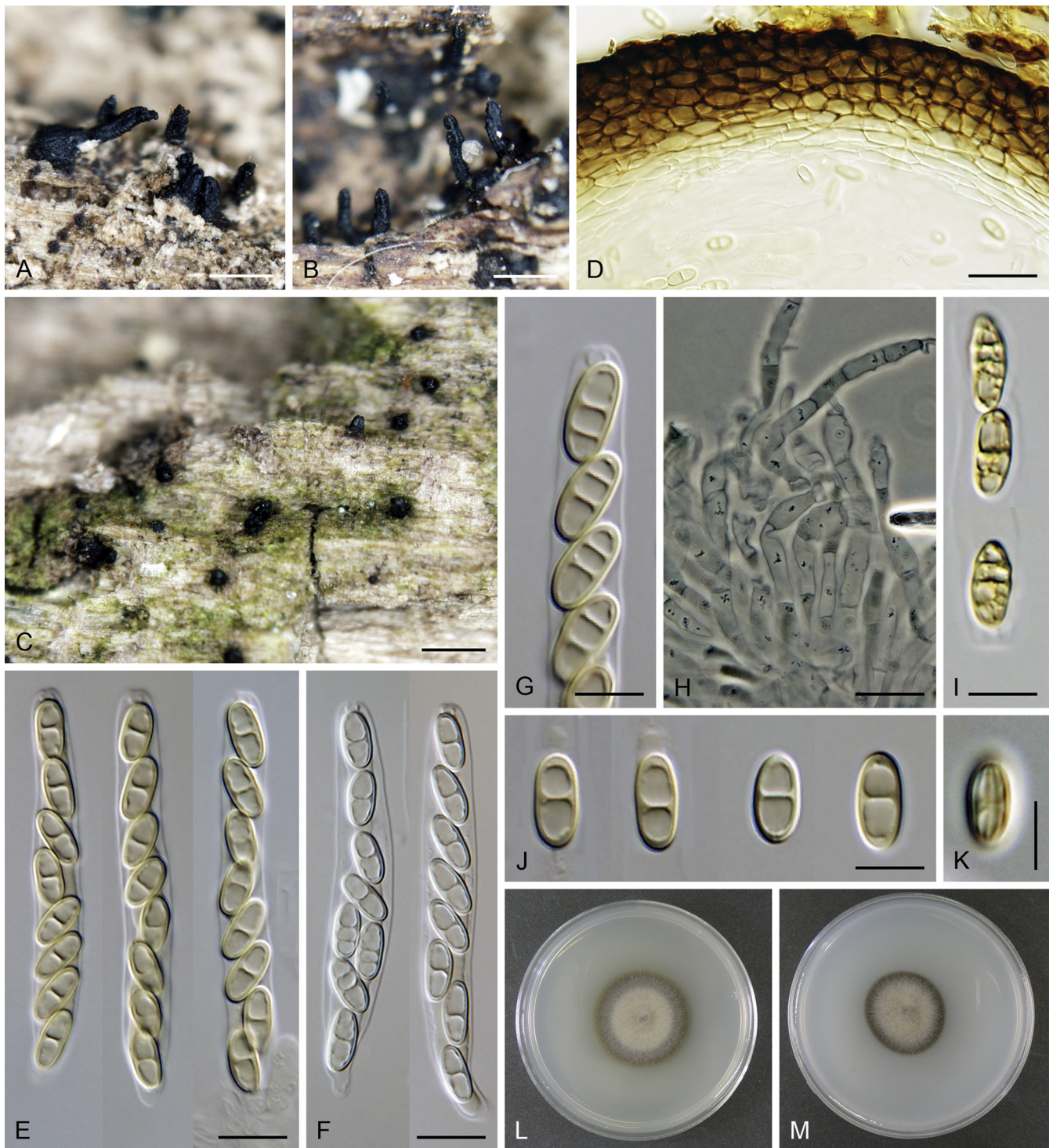


Fig. 17. *Lentomitella tenuirostris*. **A–C.** Ascomata. **D.** Longitudinal section of the ascomal wall. **E, F.** Asci. **G.** Ascus apex with apical annulus. **H.** Paraphyses. **I–K.** Ascospores. **L, M.** Colonies on MLA and PCA after 28 d. **A, B, E, G** from CBS 141371, **C, D, H, J–M** from CBS 138734, **F, I** from M.R. 3712. Scale bars: **A–C** = 500 μ m, **D, H** = 20 μ m, **E, F** = 10 μ m, **G, I–K** = 5 μ m.

brook 440 m a.s.l., on decaying wood, 30 Sep. 2013, M. Réblová M.R. 3715 (culture CBS 141371), M.R. 3712, M.R. 3714.

Notes: *Lentomitella tenuirostris* and *L. conoidea* form a pair of closely related and morphologically highly similar species. There are only a few subtle differences in ascus and ascospore characters and the colony appearance *in vitro*, which make their correct identification challenging in the absence of molecular data. *Lentomitella tenuirostris* differs from *L. conoidea* by slightly shorter asci, slightly longer ascospores and generally smaller ascomata clothed by sparse dark brown to black hairs, but the venter soon becomes glabrous. The development of the third septum in ascospores of *L. tenuirostris* was observed in

shrinking ascospores still within the asci only in specimen M.R. 3712 collected in the same locality and on the same day as specimen M.R. 3715, whose culture CBS 141371 was sequenced in our study. Only two strains of *L. tenuirostris* were isolated in axenic culture. Several other specimens from France and the Czech Republic fit well the description of this species.

Lentomitella tenuirostris can be distinguished from the morphologically similar *L. investita* by shorter asci and shorter, mostly 1-septate ascospores of the latter. *Lentomitella unipretoriae* (Marincowitz et al. 2008) has similar ascospore size, but it differs from *L. tenuirostris* by regularly 3-septate ascospores and longer asci.

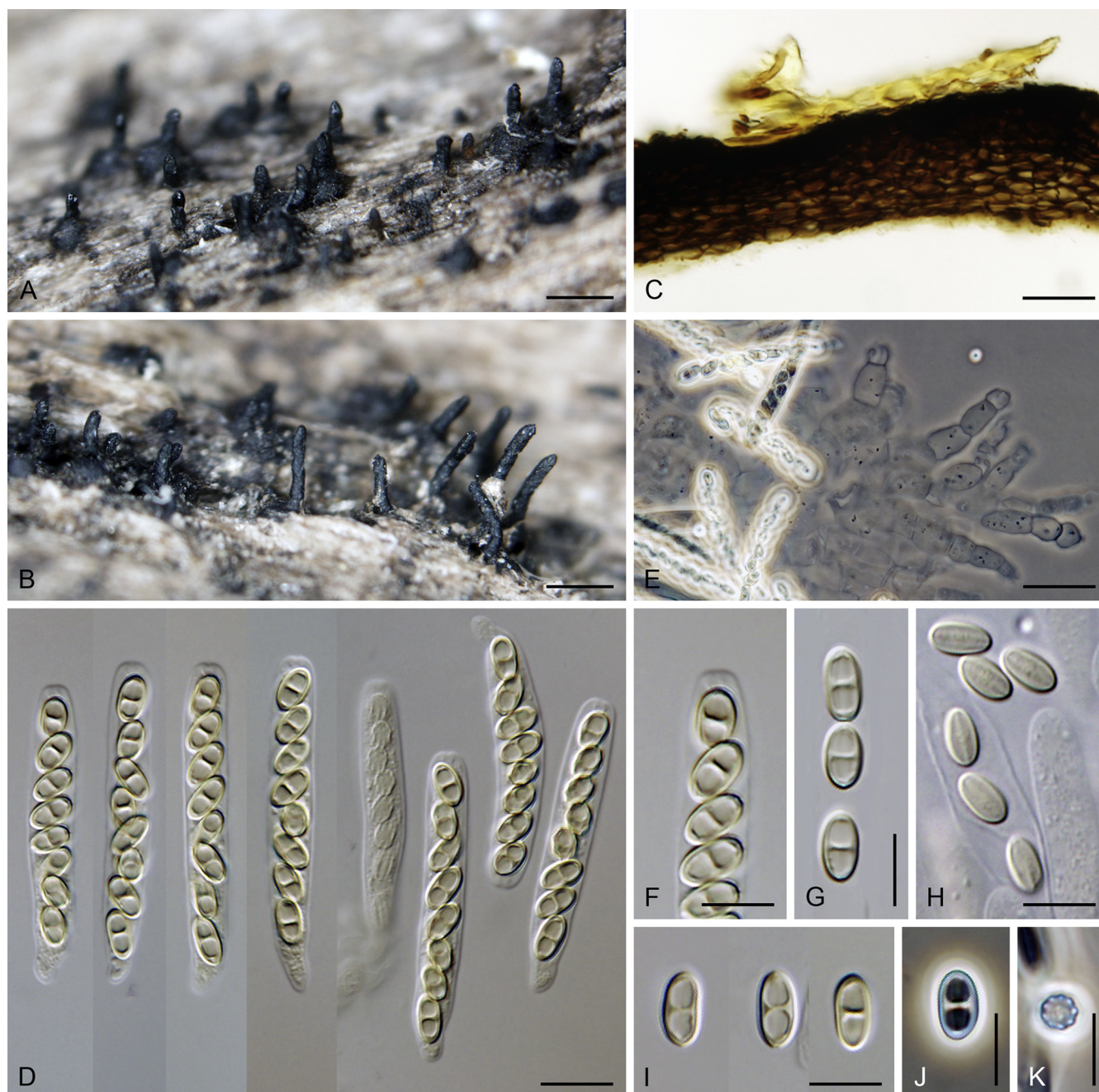


Fig. 18. *Lentomitella vestita*. A, B. Ascomata. C. Longitudinal section of the ascomal wall. D. Ascus. E. Paraphyses. F. Ascus apex with apical annulus. G–K. Ascospores. A–K from PRA-12739. Scale bars: A, B = 500 μ m, C, E = 20 μ m, D = 10 μ m, F–K = 5 μ m.

Lentomitella unipretoriae M.J. Wingf. *et al.*, CBS Biodiversity Ser. 7: 60. 2008.

Notes: For description and illustration see [Marincowitz *et al.* \(2008\)](#). The authors emphasized the evanescent nature of paraphyses as a unique character of this species, however, this is a character common to all members of *Lentomitella*. *Lentomitella unipretoriae* originates from South Africa where it was collected on a senescent flower head of *Protea lepidocarpodendron*. It is most similar to *L. crinigera*, *L. magna*, *L. striatella* and *L. sulcata* in 3-septate, ellipsoidal ascospores, but differs from them by smaller ascospores whose length does not exceed 11 μ m, (8–) 9–10.5(–11) \times 4–5 μ m *vide* [Marincowitz *et al.* \(2008\)](#). No DNA sequence data nor a living culture of this species are available.

Lentomitella vestita (Sacc.) Höhn., *Anns mycol.* 3: 548. 1906.
Fig. 18.

Basionym: *Cerastostomella vestita* Sacc., *Michelia* 1: 370. 1878.
Synonyms: *Cerastomis vestita* (Sacc.) Clem., *Gen. Fungi* p. 259. 1931.

Endoxyla vestita (Sacc.) Munk, *Bot. Tidskr.* 61: 64. 1965.

Sexual morph: Ascomata immersed to partially erumpent with protruding necks or becoming superficial, solitary or in small groups. Venter 300–380 μ m diam, 310–400 μ m high, globose to subglobose, dark brown to black, with dark brown, septate hairs 4–4.5 μ m wide covering the lower part. Neck central, 90–110 μ m wide, up to 600 μ m long, cylindrical, upright, straight, glabrous, apex sulcate. Ostiole periphysate. Ascomatal wall fragile to leathery, 33–40 μ m thick, two-layered; outer layer consisting of thick-walled, brown, polyhedral cells of *textura angularis* to *textura prismatica* with opaque walls; cells tending to be darker towards the outside, becoming flattened and paler towards the interior. Inner layer consisting of several rows of thin-walled,

hyaline, flattened cells. *Paraphyses* abundant, longer than the asci, becoming disintegrated with age, septate, constricted at the septa, hyaline, 6–10 µm wide, tapering to 3.5–4 µm. *Asci* (40–) 42–51(–55) × (5.5–)6–7 µm (mean ± SD = 47 ± 3.9 × 6.5 ± 0.3 µm), 36–45(–48) µm (mean ± SD = 41.2 ± 3.1 µm) long in the sporiferous part, truncate at the apex, cylindrical to clavate, with a short stipe; with 8 obliquely uniseriate ascospores; apical annulus 2–2.5 µm wide, 1.5 µm high. *Ascospores* (5.5–) 6–7 × 3–3.5 µm (mean ± SD = 6.7 ± 0.4 × 3.3 ± 0.2 µm), ellipsoidal, broadly rounded at both ends but sometimes slightly tapering, hyaline, longitudinally striate, 1-septate. *Asexual morph*: unknown.

Specimens examined: **Czech Republic**, Central Bohemia, Lysá nad Labem, Bysický, Hrbáčkovy tůně National nature reserve, on decaying wood of *Quercus* sp., 11 Nov. 2012, M. Réblová M.R. 3677 (PRA-12739). **Denmark**, Fyn, Snarup Mose SW of Kværndrup, on inner side of bark of *Betula* sp., 1 Apr. 1999, J. Vesterholt JV99-015 (C 45296); *ibid.*, Sjælland, Charlottenlund skov, on decaying wood, 10 Nov. 1964, A. Munk (C); *ibid.*, Dyrehaven, on decaying wood, 26 Nov. 1964, A. Munk (C); *ibid.*, on decaying wood of *Fagus sylvatica*, 2 Dec. 1963, A. Munk (C). **Germany**, Oestrich forest, on decaying wood, autumn, L. Fuckel (Fungi Rhen. Exs. No. 1804, G); *ibid.*, on decaying wood of *Fagus sylvatica*, L. Fuckel (as *Ceratostomella rostrata*, Herbarium Barbey-Boissier, G). **Italy**, on decaying wood, Sep. 1878. P.A. Saccardo (**holotype** of *Ceratostomella vestita*, PAD).

Notes: *Lentomitella vestita* is well-distinguished from other *Lentomitella* species by the shortest ascospores and asci in the genus and the 1-septate ascospores that do not develop additional septa. The neck in the holotype does not appear sulcate, i.e. the tip of the neck is without longitudinal ridges and instead it appears only slightly roughened. However, the material is old and the ridges could have disappeared upon aging and some of the tips were broken. All other collections of *L. vestita* that were examined in this study have ascomata with necks distinctly sulcate at the tip, which is a character common to all *Lentomitella* species.

Lentomitella vestita resembles *L. investita* in 1-celled ellipsoidal ascospores, but the latter differs in having longer asci and longer and wider ascospores that occasionally develop two additional septa upon aging.

Despite our numerous attempts we did not obtain *L. vestita* in culture. Therefore, the DNA was extracted from herbarium material of our collection PRA-12739 that matches the holotype. Some ascospores in this collection seem to taper slightly at the poles, which is caused to a certain extent by protrusion of the fine longitudinal ridges, a character we also observed in *L. investita*.

***Lentomitella* sp. Fig. 19.**

Sexual morph: *Ascomata* immersed to partially erumpent with protruding necks, solitary. Venter 390–480 µm diam, 370–500 µm high, globose to subglobose, dark brown to black, with sparse brown, septate hairs 3.5–4 µm wide. Neck central, 110–130 µm wide, up to 700 µm long, cylindrical, upright, straight or slightly flexuous, glabrous, tapering, apex sulcate. *Ostiole* periphysate. *Ascomatal wall* fragile to leathery, 35–43 µm thick, two-layered; outer layer consisting of thick-walled, brown, polyhedral cells of *textura angularis* to *textura prismatica* with opaque walls; cells tending to be darker towards the outside, becoming flattened and paler towards the interior. Inner layer consisting of several rows of thin-walled, hyaline, flattened cells. *Paraphyses* abundant, becoming disintegrated with age, septate, constricted at the septa, hyaline, 4.5–8 µm wide. *Asci* (61–)63–70(–75) × (7.5)8–9.5 µm (mean ± SD = 67.1 ± 4.5 × 8.7 ± 0.7 µm), (55–)60–63 µm (mean ± SD =

61.1 ± 4.7 µm) long in the sporiferous part, truncate at the apex, cylindrical to clavate, with a short stipe; with 8 obliquely uniseriate or partly biseriolate ascospores; apical annulus ca. 3 µm wide, 1.5–2 µm high. *Ascospores* 9.5–11 × 4.5–5 µm (mean ± SD = 10.5 ± 0.5 × 4.8 ± 0.3 µm), ellipsoidal-fusiform, inequilateral, hyaline, longitudinally striate, 1–3-septate. *Asexual morph*: Sporulation *in vitro* sparse, widespread throughout the colony. *Conidiophores* macronematous, mononematous, unbranched or rarely branched apically, arising terminally or laterally from aerial hyphae, pale brown, subhyaline towards the tip, 40–45 × 2–2.5 µm. *Conidiogenous cells* terminal or intercalary, pale brown or subhyaline, cylindrical, slightly tapering toward the apex, with a rachis 15–25 × 2(–2.5) µm, at the tip bearing numerous hyaline denticles 0.5–1 µm wide, 0.5–1 µm long, conidiogenesis holoblastic-denticulate, conidial heads slimy, inconspicuous, transparent. *Conidia* ellipsoidal to globose, apiculate at the base, 2–3(–4) × 2–3 (mean ± SE = 3.1 ± 0.9 × 2.6 ± 0.4) µm, hyaline, aseptate, smooth.

Specimen examined: **New Zealand**, South Island, Southland Distr., Catlins Coastal Rain Forest park, Haldane, Kiwi Walk along the Waipohatu stream, at the end of Waipohatu Road, 11 km W of Waikawa, 14 Mar. 2005, on decaying wood, M.R. 2953/NZ 500.

Notes: This collection from New Zealand is grouped in a monophyletic clade consisting of this and the three species *L. magna*, *L. obscura* and *L. sulcata*; all are characterised by 3-septate, ellipsoidal-fusiform, slightly inequilateral ascospores. It is most similar to *L. sulcata*, which also originates from New Zealand, in morphology of ascospores and conidia but differs in shorter ascospores and asci. For comparison of this clade at the RNA structural level see [Discussion](#). The specimen M.R. 2953 was scarce and contained only a few ascomata; because no material is left after isolation and examination, and the culture is no longer available, this specimen is labelled *Lentomitella* sp. for the time being and its morphological description, illustration and DNA sequences are published in this study.

Spadicoides S. Hughes, *Canad. J. Bot.* 36: 805. 1958; emend. Réblová & A.N. Mill.

Synonyms: *Xenospadicoides* Hern.-Restr. *et al.*, *Stud. Mycol.* 86: 92. 2017.

Pseudodiplococcium Hern.-Restr. *et al.*, *Stud. Mycol.* 86: 92. 2017.

Sexual morph: *Ascomata* perithecial, non-stromatic, immersed to partially erumpent with protruding necks, solitary, in short rows or grouped. Venter globose or subglobose, often pinched laterally upon drying, dark brown to black, clothed with septate dark hairs; surface sometimes covered by a bright waxy layer staining the surrounding substrate. Neck central, upright, sometimes slightly decumbent, glabrous, the projecting part dark brown, light fulvous to subhyaline, cylindrical, apex smooth or with several sulcations. *Ostiole* periphysate. *Ascomatal wall* fragile to leathery, two-layered. *Paraphyses* becoming disintegrated apically, anastomosing, septate. *Asci* cylindrical to clavate, with a short stipe, 8-spored, apex with a distinct, non-amyloid apical annulus. *Ascospores* ellipsoidal to ovoid, often inequilateral, aseptate or with a middle septum usually developed upon aging, hyaline, smooth-walled or delicately verrucose. *Asexual morph*: *Colonies* dark, effuse, stroma absent. *Conidiophores* macronematous, mononematous, unbranched, occasionally with branches, erect or ascending, straight or flexuous, septate, brown, paler towards the apex. The upper three-quarters or less

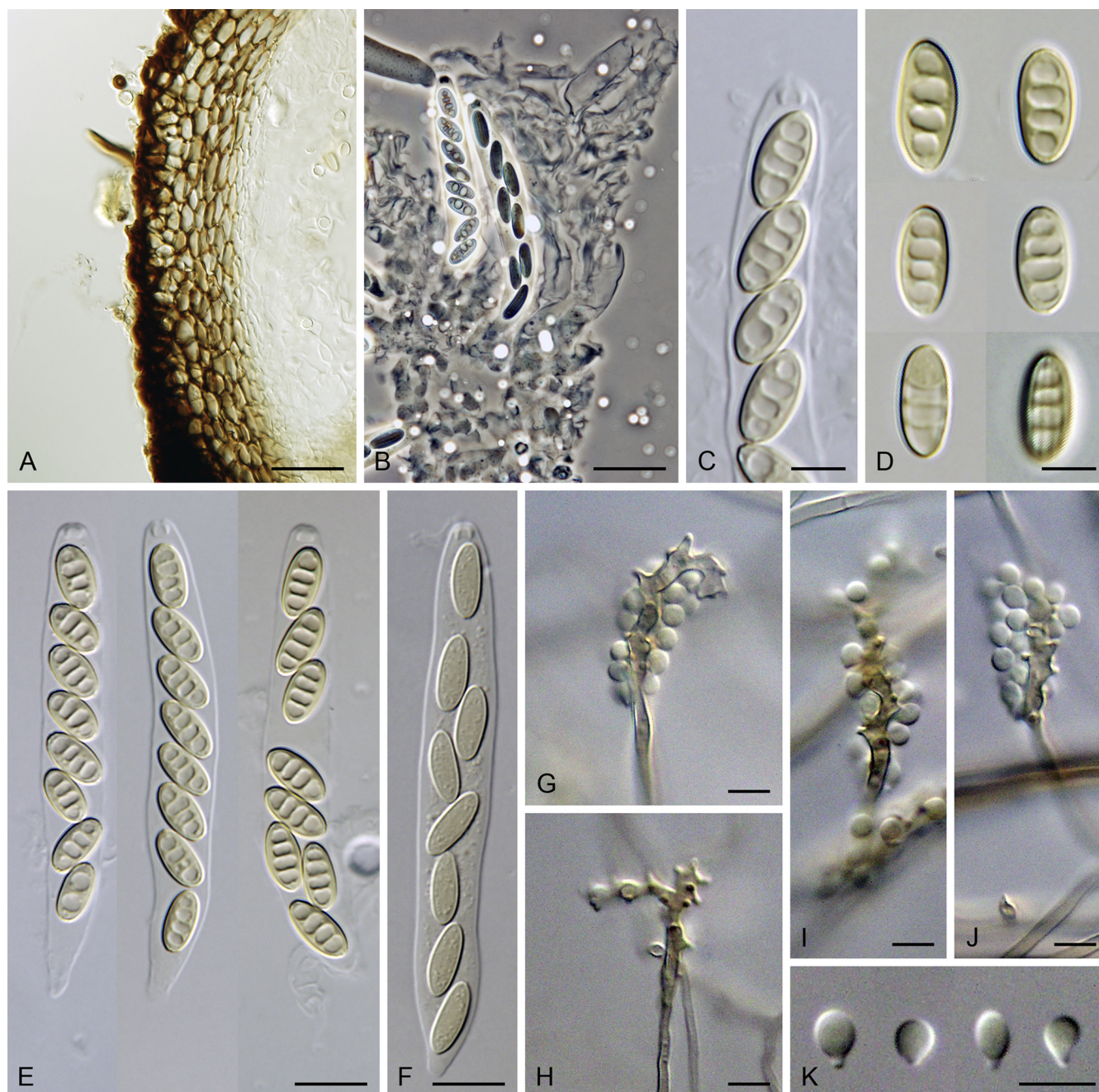


Fig. 19. *Lentomitella* sp. **A.** Longitudinal section of the ascomal wall. **B.** Paraphyses. **C.** Ascus apex with apical annulus. **D.** Ascospores. **E, F.** Asci. **G–J.** Conidiophores. **K.** Conidia. A–K from M.R. 2953. Scale bars: A, B = 20 μ m, C, D, G–K = 5 μ m, E, F = 10 μ m.

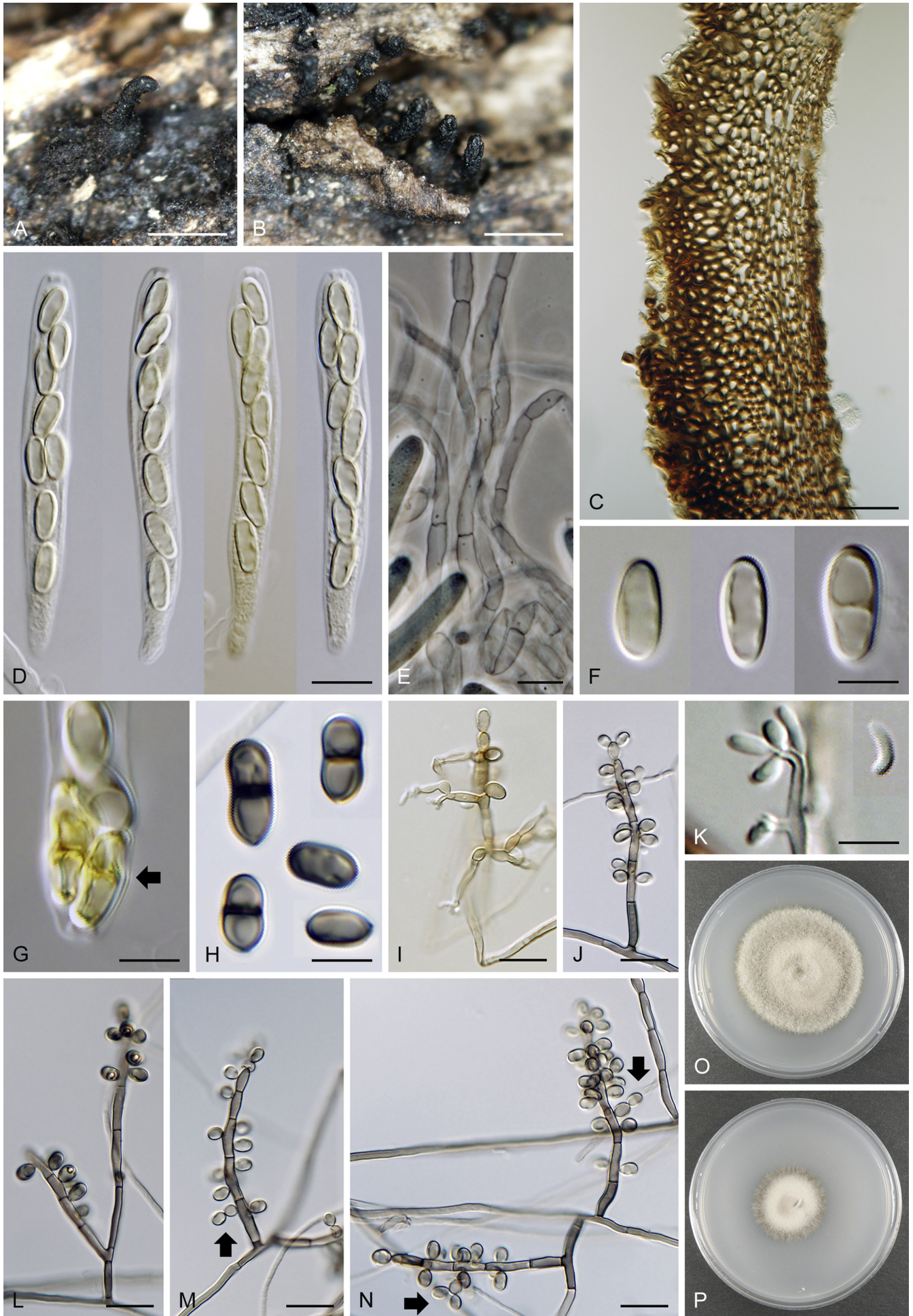
of the conidiophores are usually conidiogenous. *Conidiogenous cells* terminal or intercalary in the upper part of the conidiophore, cylindrical, with numerous small pores in the wall, conidia formed singly or in chains at the apex and laterally, conidiogenesis tretic. The number of pores per conidiogenous cell usually 5–15 causing the conidia to entirely envelope the conidiophore in a dry mass. *Conidia* oblong, ellipsoidal or obovoid, aseptate or several-septate, brown, borne singly or occasionally in chains at the apex and laterally in the position of pores and secede readily. *Synasexual morph*: A selenosporella-like is sometimes formed *in vitro* and *in vivo*. *Conidiophores* macronematous or semi-macronematous, mononematous, branched or unbranched, often reduced to conidiogenous cells. *Conidiogenous cells* discrete, terminal or intercalary, subcylindrical to flask-shaped, polyblastic, sympodially proliferating with a short terminal

rachis, often arising from vegetative hyphae or directly from conidia, sometimes reduced to a few denticles. *Conidia* clavate, oblong or narrow fusiform, hyaline, aseptate, smooth-walled.

Type species: *Spadicoides bina* (Corda) S. Hughes

Notes: Based on a revision of the holotypes of the two *Cerastostomella* species, their novel DNA sequence data and cultures, and nuLSU sequence of the ex-type strain of *Pseudodiplococcium ibericum* (Hernández-Restrepo *et al.* 2017), three new combinations are proposed in *Spadicoides*, namely *S. fuscolutea* with *Lentomitella tomentosa* and *S. grovei* as synonyms, *S. hyalostoma* and *S. iberica*.

The sexual-aseexual relationship of *Spadicoides* was experimentally proven in our study for *S. bina*, *S. fuscolutea* and *S. hyalostoma*. *Spadicoides atra* and *S. iberica* remain asexual.



A selenosporella-like synasexual morph has been encountered for *S. bina* and *S. fuscolutea* *in vitro* (see [Discussion](#)). Given these results, the description of *Spadicoides* is expanded to include sexual and asexual characters.

The *Spadicoides* sexual morphs, especially *S. bina* and *S. fuscolutea*, are strongly reminiscent of *Lentomitella* in morphology of ascomata with a sulcate neck and venter clothed by dark interwoven hairs and cylindrical short-stipitate asci with a distinct apical annulus. However, *Lentomitella* differs from *Spadicoides* by 1–3-septate, longitudinally striate vs. aseptate or rarely 1-septate, smooth-walled or verrucose ascospores.

The main mode of conidiogenesis of *Spadicoides* is tretic, rarely accompanied by a holoblastic-denticulate conidiogenesis of a selenosporella-like synasexual morph. A key to holomorphic *Spadicoides* is provided below. Keys to asexual morphs of *Spadicoides* were published in [Ellis \(1963\)](#), [Wang \(1976\)](#), [Holubová-Jechová \(1982\)](#), [Goh & Hyde \(1996\)](#) and [Ma et al. \(2016\)](#).

Key to sexually reproducing *Spadicoides* species

1. Ascospores delicately verrucolose *S. hyalostoma*
1. Ascospores smooth-walled 2
2. Ascospores (7.5–)8–9.5 × 3.5–4.5 µm *S. bina*
2. Ascospores (13–)14–16(–17) × (5–)5.5–6(–7) µm *S. fuscolutea*

Spadicoides bina (Corda) S. Hughes [as 'binum'], *Canad. J. Bot.* 36: 806. 1958. [Fig. 20](#).

Basionym: *Helminthosporium binum* Corda [as 'Helmisporium'], in Zobel, *Icon. Fung.* 6: 9. 1854.

For full synonymy see [Hughes \(1958\)](#).

Sexual morph: *Ascomata* non-stromatic, immersed to partially erumpent with protruding necks, solitary, in rows or small groups. Venter 420–510 µm diam, 390–500 µm high, globose to subglobose, slightly pinched laterally upon drying, upright or lying horizontally, dark brown to black, with dark brown, septate hairs 3–3.5 µm wide covering the lower part. Neck central, 100–120 µm wide, up to 800 µm long, rostrate, glabrous, upright, apex sulcate becoming deeply roughened with age. *Ostiole* periphysate. *Ascomatal wall* fragile to leathery, 45–55(–63) µm, two-layered; outer layer consisting of brown, polyhedral cells of *textura prismatica* to *textura angularis* with opaque walls; cells tending to be darker towards the outside, and becoming flattened and paler towards the interior. Inner layer consisting of several rows of thin-walled, hyaline, flattened cells. *Paraphyses* abundant, longer than the asci, becoming slightly disintegrated at the apex, septate, constricted at the septa, hyaline, 4–5 µm wide, tapering to ca. 2.5 µm. *Asci* 60–67(–73) × (7.5–)8–9 µm (mean ± SD = 65.1 ± 1.5 × 8.4 ± 0.4 µm), 52–58 µm (mean ± SD = 54.8 ± 2.6 µm) long in the sporiferous part, truncate at the apex, cylindrical to clavate, with a short stipe, ascospores overlapping uniseriate or partly biseriata; with 8 uniseriate to partially biseriata ascospores; apical annulus ca. 2.5 µm wide, 1.5 µm high. *Ascospores* (7.5–)8–9.5 × 3.5–4.5 µm (mean ± SD = 8.8 ± 0.5 × 3.9 ± 0.4 µm), ellipsoidal to ovoid, aseptate, rarely with a cytoplasmic band in

the middle or a middle septum developed in old and shrinking ascospores, hyaline, with one or two large drops, smooth-walled. *Asexual morph*: Remnants of conidiophores and conidia identical to those developed *in vitro* were observed in the intimate juxtaposition to ascomata; *conidia* aseptate 6.5–7 × 3.5 µm, 1-septate 7.5–8 × 3.5 µm. *Conidiophores in vitro* macro-nematous, 30–75 µm long, 2.5–3 µm wide, unbranched or with short branches, erect, straight or flexuous, septate, brown, paler towards the apex, smooth-walled. *Conidiogenous cells* integrated, terminal or intercalary in the upper part of the conidiophore, 2.5–3 µm wide, cylindrical, polytretic with numerous small pores in the wall. *Conidia* mostly aseptate, 5–6 × 3–3.5 µm (mean ± SD = 5 ± 0.5 × 3.4 ± 0.3 µm), pale to brown, ellipsoidal, rounded at the apical end, with a slightly apiculate basal scar, thick-walled, formed singly through pores or in short chains, at maturity becoming 1-septate, 7–9.5 × 3.5–4 µm (mean ± SD = 7.9 ± 1.1 × 3.8 ± 0.2 µm), pale brown to dark brown, ellipsoidal to oblong, with the middle septum obscured by a black band, slightly constricted at the septum, smooth-walled. *Synasexual morph*: A selenosporella-like was formed on MLA and PCA in 28 d at 25 °C. *Conidiophores* semimacronematous, branched or unbranched, pale brown to subhyaline, often reduced to conidiogenous cells. *Conidiogenous cells* discrete or integrated, terminal, intercalary, often arising directly from dark brown, aseptate conidia, hyaline, subcylindrical or narrowly flask-shaped, 6.5–11.5 µm long, ca. 2 µm wide, tapering to 1–1.2 µm, apically slightly swollen or elongated, polyblastic, sympodially proliferating with a short terminal rachis. *Conidia* 3.5–4.5 × 1–1.5 µm (mean ± SD = 3.8 ± 0.3 × 1.3 ± 0.2 µm), clavate, oblong, slightly curved, hyaline, aseptate, smooth-walled.

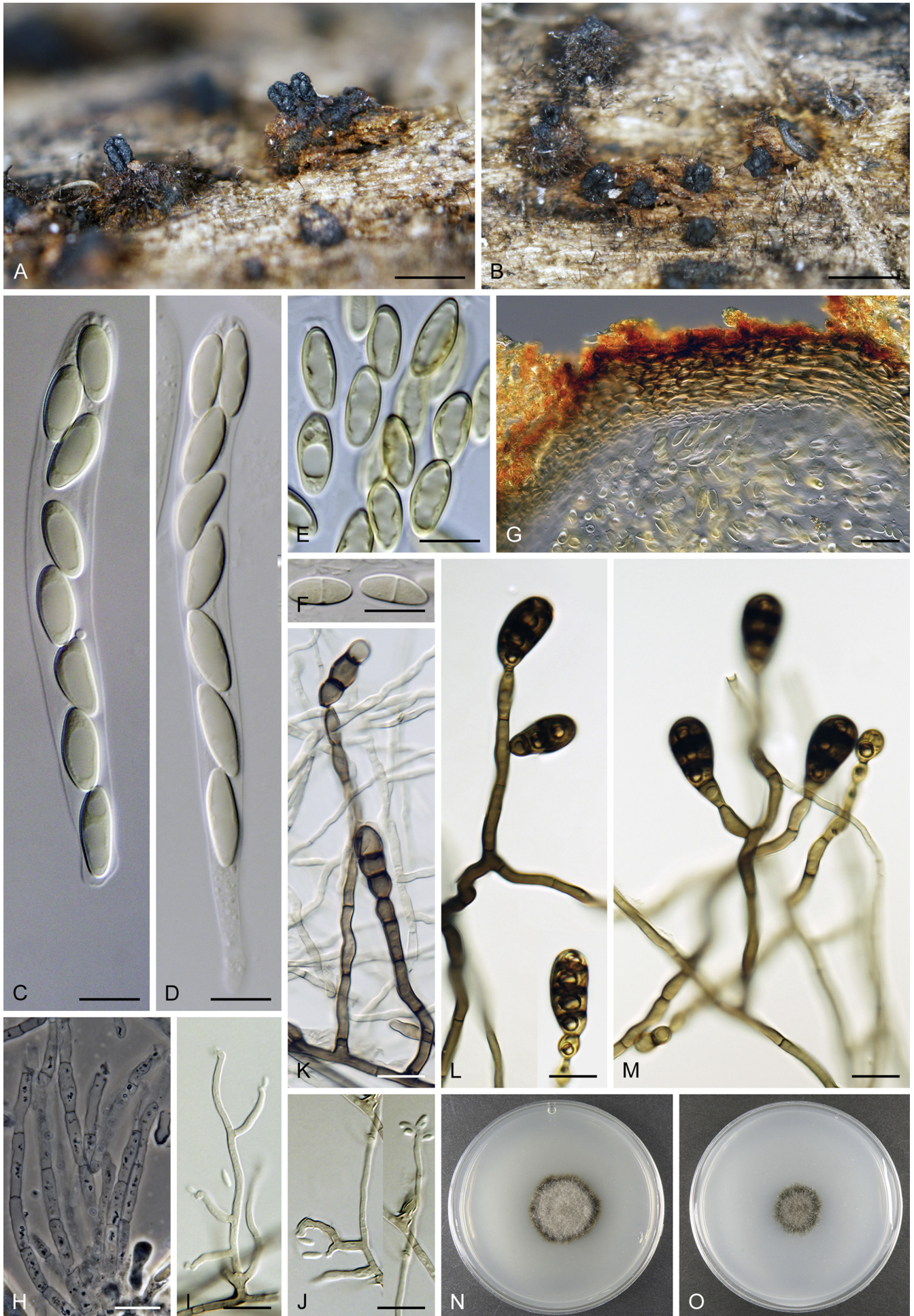
Culture characteristics: Colonies on MLA 14–15 mm diam after 14 d (20–23 mm after 21 d, 34–35 mm after 28 d) at 25 °C, circular, raised. Aerial mycelium abundant, cottony to woolly, margins filamentous, colony surface beige-brown with a thin brown margin of submerged hyphae, the margin disappears as colony ages and is overgrown by aerial hyphae; reverse dark brown. Colonies on PCA 15–16 mm diam after 14 d (19–20 mm after 21 d, 22–23 mm after 28 d) at 25 °C, circular, flat. Aerial mycelium abundant, cottony to felty, margins filamentous, colony surface beige with a brown margin of submerged hyphae, margin disappears as colony ages and is overgrown by aerial hyphae; reverse dark brown. Vegetative hyphae branched, septate, pale brown, 1.5–2.5 µm wide, smooth-walled. Sporulation in 21 d at the margin of the colony.

Specimen examined: **Czech Republic**, Southern Moravia, Valtice, Rendez-vous National nature monument, on decaying wood of *Quercus cerris*, 17 Nov. 2012, M. Réblová M.R. 3686 (PRA-13420, culture CBS 137794).

Notes: *Spadicoides bina* is most similar to *S. fuscolutea* in morphology of ascomata, asci and ascospores, but the latter differs in presence of orange-red pigment on the outer ascomatal wall layer, larger ascospores, asci and obovate or clavate, 3-septate conidia.

The conidia of *S. bina* are 0–1-septate, occasionally a second septum can develop ([Ellis 1963](#)). [Hughes \(1973a\)](#) examined the type, "cotype" (syntype) and other authentic material and

Fig. 20. *Spadicoides bina*. **A, B.** Ascomata. **C.** Longitudinal section of the ascomatal wall. **D.** Asci. **E.** Paraphyses. **F.** Ascospores. **G.** Shrinking ascospores with a middle septum (see arrow). **H.** Conidia. **I, K.** Selenosporella-like synasexual morph. **J, L–N.** Conidiophores with conidia (arrows indicate conidia in short chains). **O, P.** Colonies on MLA and PCA after 28 d. **A–G** from PRA-13420, **H–P** from CBS 137794. Scale bars: **A, B** = 500 µm. **C** = 20 µm, **D, E, I, J, L–N** = 10 µm, **F, G, H, K** = 5 µm.



concluded that the number of septa in conidia can vary in different collections. Ellis (1963) illustrated 1-septate conidia of *S. bina* as usually oblong to oval, non-constricted or slightly constricted with a conspicuous reddish-brown band obscuring the middle septum. Hughes (1973a) noted that 1-septate conidia are “generally waisted” at the middle septum. The 1-septate conidia observed *in vivo* and those formed *in vitro* in the strain CBS 137794 were always slightly constricted at the middle septum. The formation of the septum was delayed, conidia were mostly aseptate. *Spadicoides bina* resembles *S. canadensis* (Hughes 1973b) in 1-septate, brown, oblong to ellipsoidal conidia, but the latter species differs by somewhat wider conidia (5.2–6.3 µm *vide* Hughes 1973b) and a septum formed slightly below the middle of the conidium. *Spadicoides bina* occurs on decaying wood and bark of various deciduous and coniferous trees (Ellis 1963, Hughes 1973a, Holubová-Jechová 1982).

Spadicoides fuscolutea (Rehm) Réblová, **comb. nov.** MycoBank MB821772. Fig. 21.

Basionym: *Cerastostomella fuscolutea* Rehm, *Annls mycol.* 6: 320. 1908.

Synonyms: *Lentomitella tomentosa* Réblová & J. Fourn., *Mycologia* 98: 86. 2006.

Spadicoides grovei M.B. Ellis, *Mycol. Pap.* 93: 12. 1963.

Diplococcium grovei (M.B. Ellis) R.C. Sinclair *et al.*, *Trans. Br. mycol. Soc.* 85: 736. 1986.

Sexual morph: *Ascomata* non-stromatic, immersed with protruding necks or becoming superficial, solitary, in short rows or groups. Venter 350–500 µm diam, 400–550 µm high, globose to subglobose, pinched laterally upon drying, dark brown to black, with septate, pale brown to reddish-brown hairs ca. 3–5 µm wide; surface of the venter covered by an orange to orange-red waxy layer up to 13 µm thick sometimes disappearing with age; granules of the same pigment also attached to the surface of hairs and also staining the surrounding substrate. Neck central, 100–150(–180) µm wide, 500–700 µm long, cylindrical, upright, tapering, apex with 3–5 deep sulcations. *Ostiole* periphysate. *Ascomatal wall* fragile to leathery, 45–55 µm, two-layered; outer layer consisting of brown, thick-walled, polyhedral cells of *textura prismatica* to *textura angularis* with opaque walls. Inner layer consisting of several rows of thin-walled, hyaline, flattened cells. *Paraphyses* becoming disintegrated apically, anastomosing, septate, constricted at the septa, hyaline, 4.5–6 µm wide, tapering to 2.5–3 µm. *Asci* (75–)80–102(–110) × 9.5–11 µm (mean ± SD = 89.1 ± 4.5 × 10.6 ± 1.1 µm), (65–)70–85(–90) µm (mean ± SD = 73.9 ± 4.2 µm) long in the sporiferous part, broadly rounded or truncate at the apex, cylindrical to clavate, with a short stipe; with 8 obliquely uniseriate or biseriate ascospores in the upper sporiferous part; apical annulus 3–3.5 µm wide, 2–2.5 µm high. *Ascospores* (13–)14–16(–17) × (5–)5.5–6(–7) µm (mean ± SD = 14.5 ± 0.4 × 5.8 ± 0.3 µm), ellipsoidal to ovoid, sometimes inequilateral, aseptate, rarely with a middle septum, hyaline, smooth-walled. **Asexual morph:** *Conidiophores in vitro* macronematous, 45–100 µm long, 3–4 µm wide, unbranched, rarely with short branches, erect, straight or flexuous, septate, dark brown, smooth-walled. *Conidiogenous cells* integrated, intercalary, terminal, positioned in the upper two-

thirds of the conidiophore, ca. 3.5(–4) µm wide, cylindrical, with 1–3 pores in the wall visible after the secession of conidia. *Conidia* 16.5–20(–21) × (7.5–)8–10(–11) µm (mean ± SD = 18.8 ± 1.3 × 8.8 ± 1.0 µm), formed singly through the pores, obovate or clavate, rounded at the apical end, conico-truncate at the base, brown to dark brown, 3-septate, often only with two septa developed; septa thick and dark brown due to the band of colour on the wall. **Synasexual morph:** A selenosporella-like was formed on MLA in 8 wk at 25 °C. *Conidiophores* macronematous or semimacronematous, branched, often reduced to conidiogenous cells, pale brown to hyaline, 10–55 µm long, 1.5–2 µm wide. *Conidiogenous cells* integrated, terminal or intercalary, subhyaline to hyaline, subcylindrical, 10–15 µm long, ca. 2.5 µm wide near the base, tapering to 1.5 µm, polyblastic, sympodially proliferating with a short terminal rachis. *Conidia* 4–5.5 × 1.5(–2) µm (mean ± SD = 4.6 ± 0.5 × 1.4 ± 0.2 µm), clavate or oblong, slightly curved, hyaline, aseptate, smooth-walled.

Culture characteristics: Colonies on MLA 8–10 mm diam after 14 d (16–17 mm after 21 d, 18–20 mm after 28 d) at 25 °C, circular, convex. Aerial mycelium abundant, woolly, margins filamentous, colony surface beige grey, brown olivaceous towards the margin; reverse black to dark brown. Colonies on PCA 4–5 mm diam after 14 d (6–7 mm after 21 d, 13–14 mm after 28 d) at 25 °C, circular, convex. Aerial mycelium abundant, woolly, margins filamentous, colony surface brown-grey, brown-olivaceous towards the margin; reverse black. Sporulation in 21 d at the margins of the colony.

Specimens examined: **Czech Republic**, Southern Bohemia, Novohradské hory Mts., Pohoří na Šumavě, Myslivna Mt., on decaying wood of *Fagus sylvatica*, 6 Oct. 2012, M. Réblová M.R. 3776 (culture CBS 141263); *ibid.*, Horní Stropnice, Hojná Voda National nature monument, on decaying wood of *Fagus sylvatica*, 4 Oct. 2012, M. Réblová M.R. 3744 (culture CBS 141262); *ibid.*, 13 Oct. 2013, M.R. 3813 (associated with *Spadicoides hyalostoma*). **Denmark**, Sjælland, Dyrehaven, on decaying wood of a stump, 3 Oct. 1964, A. Munk (C); *ibid.*, 20 Mar. 1965, A. Munk (C). Silkeborg, Spring area near Almindsø, on decaying wood of *Alnus glutinosa*, 4 Sep. 1953, A. Munk (C). **France**, Finistère, Plohars, Forêt de Carnoët, Pont Douar, 40 m a.s.l., on decaying wood of *Fagus sylvatica*, 26 Oct. 2002, J. Fournier J.F. 02196, associated with the asexual morph (**holotype** of *Lentomitella tomentosa*, PRM 902274). **Germany**, Swabia, Allgäu, Hochgrat Mt., on decaying wood of *Fagus sylvatica*, 1881, M. Britzelmayer [**holotype** of *Cerastostomella fuscolutea*, F11132 (S)].

Notes: *Spadicoides fuscolutea* is distinguished from other members of the genus by *ascomata*, which are covered by a thin layer of orange-red pigment that also stains the surrounding wood and 3-septate, brown to dark brown, obovate or clavate conidia, which are truncate at the base and arise singly or in short chains from polytretic conidiogenous cells. The bright pigment dissolves in KOH.

The asexual morph was originally described by Ellis (1963) as *Spadicoides grovei* from decaying wood of *Fagus sylvatica* and other trees, while the sexual morph was introduced as *Cerastostomella fuscolutea* (Rehm 1908) and *Lentomitella tomentosa* (Réblová 2006), both from wood of *F. sylvatica*. The link between the two morphs was experimentally proven by ascospore isolation of two specimens M.R. 3744 (culture CBS 141262) and M.R. 3776 (culture CBS 141263) collected on beech wood in the Czech Republic. Both collections fit well into the species concept

Fig. 21. *Spadicoides fuscolutea*. **A, B.** *Ascomata*. **C, D.** *Asci*. **E, F.** *Ascospores*. **G.** Longitudinal section of the *ascomatal wall*. **H.** *Paraphyses*. **I, J.** Selenosporella-like synasexual morph. **K–M.** *Conidiophores* with conidia. **N, O.** Colonies on MLA and PCA after 28 d. A–C, G from PRM 902274, D–F, H, I, J, N, O from CBS 141263, K–M from CBS 141262. Scale bars: A, B = 500 µm, C–F, H–M = 10 µm, G = 20 µm.

of *C. fuscolutea*. Identical conidia and remnants of conidiophores were also observed in the holotype of *L. tomentosa* (PRM 902274) and in M.R. 3776 around ascomata on the wood or trapped among the ascomatal hairs. Based on the evidence from a taxonomic revision of the holotypes of *C. fuscolutea* and *L. tomentosa* and cultivation data, *C. fuscolutea* is transferred to *Spadicoides* and *S. grovei* and *L. tomentosa* are accepted as its synonyms.

The development of the orange-red layer covering the venter varies. For example, in the holotype of *L. tomentosa* (Réblová 2006), this layer is conspicuous, while in specimens M.R. 3774 and M.R. 3776 the orange layer almost disappeared probably as a result of aging, but the orange pigment staining the surrounding wood is still visible. In the holotype of *Ceratostomella fuscolutea* (F11132, S), the orange-pigmented wood surrounding the ascomata is also prominent.

The asexual morph resembles *S. xylogena* in 3-septate, brown conidia, but the latter taxon differs by longer, oval to broadly ellipsoidal conidia with narrower black bands at the septa (Ellis 1963, Hughes 1973c). Based on DNA sequence data, *S. xylogena* is related to the *Pleosporales* (Shenoy et al. 2010). *Spadicoides constricta*, *S. klotzschii*, and *S. obovata* resemble *S. fuscolutea* in clavate, obovate or sometimes also ellipsoidal conidia; *S. constricta* differs from *S. fuscolutea* by longer conidia constricted at the septa (Wang & Sutton 1982), while *S. klotzschii* and *S. obovata* differ by conidia that are 2-septate, shorter and narrower (Hughes 1973d, e, Holubová-Jechová 1982).

Spadicoides hyalostoma (Munk) Réblová, **comb. nov.** MycoBank MB821773. Fig. 22.

Basionym: *Endoxyla hyalostoma* Munk, Bot. Tidsskr. 61: 62. 1965.

Synonym: *Ceratostomella hyalostoma* (Munk) Unter., Mycologia 85: 307. 1993.

Sexual morph: Ascomata non-stromatic, immersed to partially erumpent with protruding necks, solitary or grouped. Venter 270–350 µm diam, 280–380 µm high, subglobose, often laterally pinched upon drying, dark brown, glabrous with brown, septate hyphae at the base. Neck central, 90–130 µm wide, 130–170 µm at the widest part, slightly narrower at the base, 250–800 µm long, cylindrical, upright, straight or slightly flexuous, the projecting part subhyaline to light fulvous with darker zones. *Ostiole* periphysate. *Ascomatal wall* leathery, 35–42 µm, two-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. Cells in the neck of *textura porrecta* with thick-walled clavate cells on the surface. *Paraphyses* abundant, persistent, becoming disintegrated at the apex, septate, constricted at the septa, hyaline, 3.5–5 µm wide, tapering to ca. 2.5 µm. *Asci* (36–) 40–45(–48) × (5–)5.5–7(–8) µm (mean ± SD = 43.5 ± 2.9 × 6.1 ± 0.4 µm), truncate at the apex, cylindrical to clavate, non-stipitate or with a short narrowly rounded stipe; with 8 obliquely uniseriate or partially biseriate ascospores in the lower sporiferous part; apical annulus ca. 2 µm wide, 1.5–2 µm high. *Ascospores* (5.5–)6–7 × 3–3.5 µm (mean ± SD = 6.1 ± 0.4 × 3.1 ± 0.2 µm), ellipsoidal to ovoid, 0–1-septate, with one or two large drops, hyaline, delicately verruculose. **Asexual morph:** *Conidiophores in vitro* macro-nematous, 30–130 µm long, 2.5–3 µm wide, unbranched or with short branches, upright, septate, brown, subhyaline or pale

brown when young, dark brown at maturity, smooth-walled. *Conidiogenous cells* integrated, terminal, intercalary, positioned in the upper two thirds of the conidiophore, ca. 2.5 µm wide, cylindrical, polytretic with numerous pores dispersed per cell. *Conidia* 4.5–6 × 3.5–4(–4.5) µm (mean ± SD = 5.4 ± 0.5 × 3.7 ± 0.4 µm), formed singly through the pores, subglobose to ellipsoidal, sometimes inequilateral, tapering towards base and truncate, aseptate, hyaline becoming dark brown.

Culture characteristics: Colonies on MLA 16–17 mm diam after 14 d (29–30 mm after 21 d, 40–41 mm after 28 d) at 25 °C, circular, raised. Aerial mycelium abundant, cottony to woolly, margins filamentous, colony surface beige with a brown margin of submerged hyphae; reverse dark brown. Colonies on PCA 15–18 mm diam after 14 d (24–26 mm after 21 d, 27–28 mm after 28 d) at 25 °C, circular, raised. Aerial mycelium abundant, cottony to woolly, margins filamentous, colony surface beige-grey, with a brown-olivaceous margin of submerged mycelium; reverse dark brown. Vegetative hyphae branched, septate, smooth-walled, 2–3.5 µm wide, hyaline; hyphae on which the conidiophores arise brown. Periodically arranged clusters of cells bearing short branches are present on submerged hyphae at the colony margin. Sporulation observed after 2 mo at the margins of the colony.

Specimens examined: **Czech Republic**, Central Bohemia, Krivoklátsko Protected Landscape Area, Karlova Ves, Vysoký Tok Nature Reserve, on decaying wood of *Quercus* sp., 29 Sep. 2012, M.R. 3662 (culture CBS 137793). Southern Bohemia, Novohradské hory Mts., Horní Stropnice, Hojná Voda National nature monument, on decaying wood of *Fagus sylvatica*, 13 Oct. 2013, M. Réblová M.R. 3813, associated with *S. fuscolutea* (culture CBS 138688). Northern Moravia, Podhoří 'Podhorn' near Hranice, on decaying wood, 7 Aug. 1923, F. Petrak (as *Ceratostomella subpilosa*, Fl. Bohem. Morav. Exs. No. 1809, PRM 481212). Southern Moravia, Lednice, Nejdek old Slavic settlement, on decaying wood of *Fraxinus excelsior*, 27 Oct. 2014, M. Réblová M.R. 3866 (culture CBS 139771); *ibid.*, Břeclav, obora Soutok near Lanžhot, on decaying wood, 23 Oct. 2004, M. Réblová M.R. 2597. **Denmark**, Sjælland, Ermelunden forest near Copenhagen, on decaying wood, 15 Dec. 1963, A. Munk (**holotype** of *Endoxyla hyalostoma*, collection no. 14, C); *ibid.*, Høje Sandbjerg, decaying wood, 18 Dec. 1964, A. Munk (C); *ibid.*, Dyrehaven, on decaying wood, 3 Nov. 1964, A. Munk (C); *ibid.*, Lellinge, decaying wood, 23 May 1964, A. Munk (C); *ibid.*, Bernstorffsparken, on decaying wood, 23 Mar. 1965, A. Munk (C); *ibid.*, Boserup, on decaying wood of *Ulmus* sp., soc. *Capronia pilosella*, 1 Apr. 1963, A. Munk (C); *ibid.*, Rude Skov, on decaying wood of *Alnus* sp., 4 Feb. 1964, A. Munk (C); *ibid.*, on decaying wood of *Fagus sylvatica*, 17 Nov. 1963, A. Munk (C); *ibid.*, forest W of Frederikssund, on decaying wood, soc. *Ruzenia spermoides*, A. Munk (C). **Italy**, Lazio, province Viterbo, Caprarola, Mt. Venere, on decaying wood of *Fagus sylvatica*, 2 Apr. 2011, M. Réblová M.R. 3610 (culture CBS 131268).

Notes: *Spadicoides hyalostoma* can be distinguished from other species of the genus by subhyaline to light fulvous necks with darker zones and verruculose, aseptate ascospores. A selenosporella-like synasexual morph has not been observed *in vitro* or on the natural substrate in any examined collection.

The asexual morph of *S. hyalostoma* strongly resembles *S. atra* in the morphology of conidia. Although the size of conidia of both species overlap, i.e. conidia of *S. atra* 4–6.5 × 3–4 µm *vide* Ellis (1963), 3.7–6.3 × 2.5–4.6 µm *vide* Hughes (1973f) and 4–6.5 (7.5) × 2.5–3.5 (4.5) µm *vide* Holubová-Jechová (1982), the latter species is distinguished by conidia rounded at both ends. *Spadicoides atra* is represented in our phylogeny by the strain CBS 489.77 (Czech Republic, Lány, Lánská obora game park, on decaying wood of *Quercus petraea*, 12 Jun. 1976, V. Holubová-Jechová) and it is shown basal to other *Spadicoides* species. *Spadicoides hyalostoma* is also highly similar to *S. subsphaerica*, but the latter species differs in having shorter, subglobose,



Fig. 22. *Spadicoides hyalostoma*. A–D. Ascomata. E. Asci. F. Paraphyses. G. Ascospores. H. Conidia. I–K. Conidiophores. L, M. Colonies on MLA and PCA after 28 d. A–D from CBS 137793, E, G from CBS 139771, H–M from CBS 138688. Scale bars: A–D = 250 μ m, E, F, I–K = 10 μ m, G, H = 5 μ m.

globose or broadly ellipsoidal conidia rounded at both ends (Li 2010). It can be also compared with several other *Spadicoides* species with aseptate, brown conidia, i.e. *S. arengae*, *S. cuneata*, *S. macrocontinua*, and *S. sphaerosperma*. These taxa differ from *S. hyalostoma* by larger, differently shaped conidia.

Spadicoides iberica (Hern.-Restr. et al.) Réblová & A.N. Mill., **comb. nov.** MycoBank MB823341

Basionym: *Pseudodiplococcium ibericum* Hern.-Restr. et al., Stud. Mycol. 86: 92. 2017.

Notes: For description and illustration see Hernández-Restrepo et al. (2012, 2017). This species produces branched conidiophores and (0–)1-septate conidia in long often branched chains.

Torrentispora K.D. Hyde et al., Mycol. Res. 104: 1399. 2000; emend. Shearer & F.R. Barbosa, Mycologia 105: 338. 2013.

Synonyms: *Pseudoannulatasacus* Z.L. Luo et al., Phytotaxa 239: 179. 2015.

Fusoidispora Vijaykr. et al., Sydowia 57: 272. 2005.

Sexual morph: Ascomata perithecial, non-stromatic, immersed, partially erumpent becoming superficial with only bases immersed, scattered or grouped, varying in position from upright to nearly horizontal. Venter globose, subglobose to conical, glabrous or sparsely clothed with hairs. Neck rostrate or cylindrical, without sulcations at the apex, dark brown, glabrous or hairy, upright or lying horizontally on the host. *Ostiole* periphysate. *Ascomatal wall* fragile, two-layered, with layers of cylindrical cells in surface view. *Paraphyses* becoming partially disintegrated, tapering, septate. *Asci* unitunicate, cylindrical, stipitate, 8-spored, apex with a non-amyloid, massive, refractive apical annulus. *Ascospores* ellipsoidal, ellipsoidal-fusiform or fusiform, or rarely cymbiform to cylindrical, often flattened on one side, sometimes slightly curved, hyaline, aseptate or with several transverse septa at maturity, thick-walled, smooth-walled or with a fibrillar sheath. *Asexual morph:* unknown.

Type species: *Torrentispora fibrosa* K.D. Hyde et al.

Notes: *Torrentispora* comprises eight species from freshwater and terrestrial environments. It is characterised by immersed to partially erumpent or almost superficial, mostly glabrous ascomata with a rostrate or cylindrical neck, disintegrating paraphyses, hyaline, ellipsoidal to fusiform to elongate-fusiform ascospores and a distinct apical annulus. Barbosa et al. (2013) emended the generic description by including taxa with glabrous or hairy ascomata, asci with simple or bipartite apical rings and ascospores with or without a gelatinous sheath that become septate at maturity. Four previously described species are accepted, i.e. *T. crassiparietis*, *T. fibrosa*, *T. fusiformis* and *T. pilosa* (Hyde et al. 2000, Fryar & Hyde 2004, Barbosa et al. 2013). Based on novel DNA sequences and morphology, *T. calembola* and *T. novae-zelandiae* are described as new to science and three new combinations in *Torrentispora* are proposed below for *Ceratostomella dubia*, *Fusoidispora aquatica* and *Pseudoannulatasacus biatriisporus*. The genera *Fusoidispora* and *Pseudoannulatasacus* are synonymised with *Torrentispora*.

Torrentispora can be distinguished from other members of the *Xenospadicoidales* in having ascomatal necks that are never sulcate, a massive apical annulus and hyaline, thick-walled

ascospores (except in *T. aquatica*, see Discussion). The delayed development of septa in ascospores observed in *T. biatriispora*, *T. crassiparietis* and *T. pilosa* (Barbosa et al. 2013) is also typical of the closely related *Calyptosphaeria*, *Lentomitella* and *Spadicoides*. A relatively large range in the ascospore length of *Torrentispora* spp. causes frequent overlapping in the size of ascospores of individual species. The proportion between the length of the sporiferous part and stipe of the ascus may vary slightly regarding the position and spacing of ascospores.

The asexual morph of *Torrentispora* is unknown. Two species, *T. fibrosa* and *T. novae-zelandiae* were obtained in axenic culture, but only sterile dematiaceous mycelium is formed.

Key to species of *Torrentispora*

1. Ascospores longer than 40 µm 2
1. Ascospores shorter than 40 µm 3
2. Ascospores elongate-fusiform with slightly swollen ends enclosed in a thin, irregular mucilaginous sheath, 40–58 × 8–10 µm *T. biatriispora*
2. Ascospores cymbiform to fusiform or cylindrical, with globose mucilaginous pads at both ends, 42–50 × 4–6 µm *T. aquatica*
3. Ascospores longer than 20 µm 4
3. Ascospore length range from below 20 µm 8
4. Ascospores 20–30 µm long 5
4. Ascospores longer than 30 µm 7
5. Ascomatal neck glabrous 6
5. Ascomatal neck covered by short hairs, ascospores 21–30 × 7–8 µm *T. pilosa*
6. Neck rostrate, ascospores (19–)20–25(–27.5) × (6.5–)7–8 µm *T. dubia*
6. Neck cylindrical, ascospores 22–25(–27) × 6.5–8(–8.5) µm *T. calembola*
7. Ascospores 32–48 × 8–14 µm, wall 2–3 µm thick at sides, 3–4 µm at the ends *T. crassiparietis*
7. Ascospores 24–32.5 × 6–9 µm, thinner-walled *T. fusiformis*
8. Ascospores 13.5–19.5 × 5–7 µm *T. fibrosa*
8. Ascospores (17.5–)18–25(–26) × (6–)7–8.5 µm *T. novae-zelandiae*

Torrentispora aquatica (Vijaykr. et al.) Réblová & A.N. Mill., **comb. nov.** MycoBank MB821774.

Basionym: *Fusoidispora aquatica* Vijaykr. et al., Sydowia 57: 272. 2005.

Notes: For description and illustration see Vijaykrishna et al. (2005). Based on the partial nuLSU sequence data of the holotype of *Fusoidispora aquatica*, this species grouped in *Torrentispora* and a new combination is proposed. *Torrentispora aquatica* was originally collected on wood submerged in fresh water in Hong Kong, China. The main feature distinguishing *T. aquatica* from other members of this genus are thin-walled, elongate-fusiform to cymbiform, septate ascospores with globose mucilaginous pads at

both ends. The pads disappear soon after ascospores are released from the asci (Vijaykrishna *et al.* 2005).

Torrentispora biatriispora (K.D. Hyde) Réblová & A.N. Mill., **comb. nov.** MycoBank MB821775.

Basionym: *Annulatascus biatriisporus* K.D. Hyde, Nova Hedw. 61: 120 (1995)

Synonym: *Pseudoannulatascus biatriisporus* (K.D. Hyde) Z.L. Luo *et al.*, Phytotaxa 239: 179. 2015.

Notes: For description and illustration see Hyde (1995) and Barbosa *et al.* (2013). Based on DNA sequence data of a freshwater specimen of *P. biatriisporus* from Costa Rica, this species was nested in the *Torrentispora* clade and a new combination is proposed. *Torrentispora biatriispora* is distinguished from other species of the genus by long fusiform ascospores surrounded by thin irregular mucilage mostly at the poles and weakly swollen ends. It was reported from submerged wood from the tropics in the southern and northern hemispheres including Australia (Hyde 1995), China (Tsui *et al.* 2002), Costa Rica (Barbosa *et al.* 2013) and the Seychelles (Hyde & Goh 1998).

Torrentispora calembola Réblová & A.N. Mill., **sp. nov.** MycoBank MB821776. Fig. 23A–I.

Etymology: *Cal-* from *kalós* (Gr.) meaning beautiful, *émbolon* (Gr.) meaning the beak of a ship, referring to the long necks that give the fungus a decorative look.

Sexual morph: *Ascomata* immersed to partially erumpent with protruding necks becoming superficial, solitary or grouped, venter 300–420 µm diam, 310–450 µm high, subglobose to conical, upright, dark brown to black, with brown, septate hairs 2–3 µm wide, sparsely covering the sides. Neck central, 100–140 µm wide, up to 700 µm long, cylindrical, upright, flexuous, tapering, apex roughened without sulcations. *Ostiole* periphysate. *Ascomatal wall* fragile to leathery, 38–58 µm thick, two-layered; outer layer consisting of thick-walled, brown, polyhedral cells of *textura prismatica* to *textura angularis* with opaque walls; cells tending to be darker towards the outside, becoming flattened and paler towards the interior. Inner layer consisting of several rows of thin-walled, hyaline, flattened cells. *Paraphyses* abundant, longer than the asci, becoming disintegrated with age, septate, slightly constricted at the septa, hyaline, 5–6.5 µm wide, tapering to 2.5–3 µm. *Asci* (195–)207–236 × (9–)10–11.5 µm (mean ± SD = 216.4 ± 10.2 × 10.7 ± 0.7 µm), 162–191(–196) µm (mean ± SD = 171.6 ± 11.1 µm) long in the sporiferous part, truncate at the apex, cylindrical, stipitate; with 8 uniseriate ascospores; apical annulus 5–5.5 µm wide, 4–5 µm high. *Ascospores* 22–25(–27) × 6.5–8(–8.5) µm (mean ± SD = 23.2 ± 1.3 × 7.1 ± 0.5 µm), ellipsoidal to fusiform, flattened on one side, hyaline, aseptate, smooth- and thick-walled (0.8–0.9 µm), usually with a large drop when fresh. *Asexual morph:* unknown.

Specimens examined: **Czech Republic**, Southern Bohemia, Šumava Mts. National park, Železná Ruda, glacial cirque of the Čertovo jezero lake, on decaying wood of *Fagus sylvatica*, 23 Oct. 1996, M. Réblová M.R. 903. Southern Moravia, Břeclav distr., Valtice, U tří Grácií, on decaying wood of *Quercus* sp., 15 Nov. 2012, M. Réblová M.R. 3679; *ibid.*, Valtice, Rendez-vous National nature monument, on decaying wood of *Quercus cerris*, 28 Nov. 2013, M. Réblová M.R. 3843. **France**, Ariège, Montségur, shores of the Le Lesset stream along D9 road, 880–890 m a.s.l., on decaying wood, 1 Oct. 2013, M. Réblová M.R. 3726 (**holotype**, PRA-12744); *ibid.*, Rimont, La Maille brook, ca. 550 m a.s.l., on submerged wood of *Fraxinus excelsior* staining deep green, 13 Mar. 2014, incubated in moist chamber until 28 Apr. 2014, J. Fournier J.F. 14027 (PRA-12745).

Notes: The five specimens of *T. calembola* from terrestrial and freshwater habitats in the Czech Republic and France fit well within the concept of the genus and are introduced as a new species supported by molecular DNA data. *Torrentispora calembola* closely resembles *T. fusiformis* and *T. pilosa* in morphology and size of ascospores, but it can be distinguished from *T. pilosa* in that the latter possesses shorter and narrower asci and hairy ascomatal necks. The main features distinguishing *T. fusiformis* from *T. calembola* are smaller ascomata and longer ascospores exceeding 30 µm. *Torrentispora fusiformis* is known only from a freshwater habitat in Brunei. Because the ascospores of *T. calembola* did not germinate *in vitro*, the DNA was extracted directly from the holotype.

Torrentispora crassiparietis Fryar & K.D. Hyde, Cryptog. Mycol. 25: 255. 2004.

Notes: For description and illustration see Fryar & Hyde (2004) and Barbosa *et al.* (2013). This species is known from submerged wood in freshwater habitats from Brazil, Brunei and Costa Rica. *Torrentispora crassiparietis* can be distinguished from other members of the genus by having ascospores with considerably thicker walls, 2–3 µm thick at sides, 3–4 µm at the ends *vide* Barbosa *et al.* (2013). These authors also enlarged its description based on material from Brazil and Costa Rica including hairy ascomata and larger asci and ascospores that stain blue in aqueous nigrosine and become 2–3-septate at maturity.

Torrentispora dubia (Sacc.) Réblová & A.N. Mill., **comb. nov.** MycoBank MB821777. Fig. 23J–S.

Basionym: *Melanomma dubium* Sacc., Fungi Veneti novi vel critici. Series III. Michelia 1: 449. Fungi Italici Autographice Delineati. Fasc. 5–8. fig. 299. 1878.

Synonyms: *Zignoëlla dubia* (Sacc.) Sacc., Michelia 1: 346. 1878. *Ceratostomella dubia* (Sacc.) Sacc., Syll. fung. 1: 410. 1882.

Amphitrichum dubium (Sacc.) Kuntze, Revis. gen. pl. 3(2): 443. 1898.

Sexual morph: *Ascomata* partially erumpent becoming superficial with only base immersed, solitary or grouped. Venter 300–370(–420) µm diam, 300–350(–450) µm high, subglobose to conical, upright or lying slightly horizontally on the host, dark brown to black, glabrous or with brown, septate hairs 2–3 µm diam, sparsely covering the bottom and exposed sides. Neck central, 90–110 µm wide, up to 500 µm long, conical to rostrate, upright, apex without sulcations. *Ostiole* periphysate. *Ascomatal wall* fragile to leathery, 37–43 µm thick, two-layered; outer layer consisting of thick-walled, brown, polyhedral cells of *textura prismatica* to *textura angularis* with opaque walls; cells tending to be darker towards the outside, becoming flattened and paler towards the interior. Inner layer consisting of several rows of thin-walled, hyaline, flattened cells. *Paraphyses* sparse, longer than the asci, becoming disintegrated with age, septate, slightly constricted at the septa, hyaline, 8–7 µm wide, tapering to 3–3.5 µm. *Asci* 180–240 × (9–)9.5–10.5 µm (mean ± SD = 209.2 ± 5.9 × 9.8 ± 0.5 µm), 150–182(–192) µm (mean ± SD = 175.3 ± 6.0 µm) long in the sporiferous part, truncate at the apex, cylindrical, stipitate; with 8 uniseriate ascospores; apical annulus 4.5–5.5 µm wide, 3.5–4.5 µm high. *Ascospores* (19–)20–25(–27.5) × (6.5–)7–8 µm (mean ± SD = 22.9 ± 1.3 × 7.6 ± 0.5 µm), ellipsoidal to fusiform, flattened on one side, hyaline, aseptate, smooth- and thick-walled (0.6 µm), filled with one large or numerous small drops. *Asexual morph:* unknown.



Specimens examined: **Czech Republic**, Southern Bohemia, Šumava Mts. National park, Prášíly, Mt. Zdanidla, on decaying wood of *Fagus sylvatica*, 24 Aug. 2000, M. Réblová M.R. 1681; *ibid.*, Stožec, Oslí vrch Mt., on decaying wood of *Sorbus aucuparia*, 16 Oct. 2010, M. Réblová M.R. 2985 (PRA-12744). **Germany**, Eberbach, on decaying wood of *Fagus sylvatica*, Herb. Barbey-Boissier No. 620 (G). **Italy**, Treviso, Cansiglio, on decaying wood of *Fagus sylvatica*, Oct. 1874, P.A. Saccardo (**holotype** of *Melanomma dubium*, PAD).

Notes: A revision of the type material of *Melanomma dubium* (Saccardo 1878b), although in poor condition and containing only a few perithecia on a piece of wood of *Fagus sylvatica*, revealed a fungus that matches well the description of *Torrentispora*. A specimen from Barbey-Boissier herbarium No. 620 (G) and both collections from the Czech Republic correspond most closely to *M. dubia*. The transfer of *M. dubia* to *Torrentispora* is supported by novel DNA sequences of the Bohemian specimen PRA-12744. All examined collections occur on strongly decayed wood of deciduous trees with a preference for *F. sylvatica*.

Torrentispora dubia is easily distinguished by ascomata with a conical rostrate neck vs. cylindrical neck in other members of *Torrentispora*. It is most similar to *T. calembola* in morphology of the ascospores, but it differs in shorter and narrower asci and anatomy of the neck. Both species are known from terrestrial habitats.

Torrentispora fibrosa K.D. Hyde *et al.*, Mycol. Res. 104: 1399. 2000. Fig. 24.

Sexual morph: Ascumata immersed to partially erumpent with protruding necks, solitary or grouped. Venter 300–340 µm diam, 310–360 µm high, subglobose, upright or lying horizontally on the host, dark brown to black, with brown, septate hairs 2.5–4 µm wide, sparsely covering the exposed sides and bottom. Neck central, 90–110 µm wide, up to 600 µm long, cylindrical, upright or decumbent, apex without sulcations. Ostiole periphysate. Ascumatal wall fragile to leathery, 32–45 µm thick, two-layered; outer layer consisting of thick-walled, brown, polyhedral cells of *textura prismatica* to *textura angularis* with opaque walls; cells tending to be darker towards the outside, becoming flattened and paler towards the interior. Inner layer consisting of several rows of thin-walled, hyaline, flattened cells. Paraphyses abundant, longer than the asci, becoming disintegrated with age, septate, slightly constricted at the septa, hyaline, 4.5–9 µm wide, tapering to ca. 3 µm. Asci (148–)152–186(–204) × 7.5–9 × 6–9 µm (mean ± SD = 168.3 ± 14.7 × 8.3 ± 0.5 µm), (107–)116–140(–162) µm (mean ± SD = 128.8 ± 11.8 µm) long in the sporiferous part, truncate at the apex, cylindrical, stipitate, with 8 uniseriate, ascospores; apical annulus 4–4.5 µm wide, 2.5–3 µm high. Ascospores (14.5–)15–18(–19) × 5.5–7 µm (mean ± SD = 15.8 ± 1.1 × 6.0 ± 0.3 µm), hyaline, ellipsoidal to fusiform, often flattened on one side, aseptate, wall 0.5–0.6 µm thick, smooth or with a thin fibrillar sheath visible in India ink or with the SEM, filled with one large or numerous small drops. *Asexual morph:* unknown.

Culture characteristics: Colonies on MLA 19–24 mm diam after 14 d (22–25 mm after 21 d, 26–29 after 28 d) at 25 °C, circular, raised. Aerial mycelium abundant, cottony, margins filamentous, colony surface olive-grey in the centre, dark olivaceous-grey towards margin; reverse black. Colonies on PCA 14–16 mm diam

after 14 d (16–18 mm after 21 d, 18–19 mm after 28 d) at 25 °C, circular, raised. Aerial mycelium abundant, cottony, margins filamentous, colony olive-grey with dark olivaceous-grey to almost black margin; reverse black. Sporulation not observed.

Specimens examined: **Czech Republic**, Southern Bohemia, Šumava Mts. National park, Železná Ruda, glacial cirque of the Černé jezero lake, on decaying wood of *Fagus sylvatica*, 13 Aug. 1999, M. Réblová M.R. 1586. **New Zealand**, South Island, West Coast, Buller Distr., Victoria Forest park, Palmer's Hut 18 km SW of Springs Junction on unpaved road, Lake Christabel track, on decaying wood of *Nothofagus* sp., 28 Feb. 2003, M. Réblová M.R. 2671/NZ 160; *ibid.*, Westland Distr., Saltwater Forest, Poerua River valley 28 km W of Hari Hari, on dried driftwood, 12 Mar. 2003, M. Réblová M.R. 2796/NZ 306 (PDD 110879, culture ICMP 15147).

Notes: The holotype was not accessible for study (pers. comm., Wenfeng Zhang, IFRD). The ascospores of *T. fibrosa* were described to have a thin fibrillar sheath visible in India ink or with the SEM (Hyde *et al.* 2000). The ascus apex and ascospores of *T. fibrosa* from a non-holotype specimen were studied by Lee *et al.* (2004) at the ultrastructural level. Some ascospores were surrounded by an electron-transparent mucilage-like matrix clearly visible towards the end of ascospores when they were still inside the ascus. Moreover, they detected an additional wall layer inside the mesosporium, which is also present in the ascospores of *T. biatriispora*, but absent in the morphologically similar genus, *Annulatascus*.

Our specimens from New Zealand and the Czech Republic fit well the description and illustration of *T. fibrosa* from Hong Kong, China, provided by Hyde *et al.* (2000), except that the ascospores do not possess a fibrillar sheath. The occurrence on water-saturated decayed wood (ICMP 15147, collected as dried driftwood on the shores of a river) is consistent with the ecology of other freshwater species classified in this genus. The material from the Czech Republic was collected in the glacial cirque in the Šumava Mts., a unique locality with specific microclimatic conditions. The ascumata in our collections were larger than ascumata in the type collection (135–255 µm diam *vide* Hyde *et al.* 2000). The material collected in New Zealand was isolated in axenic culture, but only sterile dematiaceous mycelium was produced.

Considering that cryptic speciation appears to be common in this lineage, the morphological differences in the ascospore wall, ecological differences, and the absence of molecular data from collections originating from the area of original description of *T. fibrosa*, the present collections are tentatively identified as this species, pending further investigations of accessions from the area of its description.

Torrentispora fusiformis Fryar & K.D. Hyde, Cryptog. Mycol. 25: 256. 2004.

Notes: For description and illustration see Fryar & Hyde (2004). This species is known only from Brunei on submerged wood in brackish and freshwater environments. *Torrentispora fusiformis* closely resembles *T. calembola* in the morphology of the ascospores and immersed ascumata with upright cylindrical necks, but differs in having longer ascospores exceeding 30 µm, and narrower asci.

Torrentispora novae-zelandiae Réblová & A.N. Mill., *sp. nov.* MycoBank MB821778. Fig. 25.

Fig. 23. *Torrentispora calembola* and *T. dubia*. **A–I.** *Torrentispora calembola*. **A–C.** Ascumata (with ascoma primordium on A). **D, E.** Asci. **F.** Longitudinal section of the ascumatal wall. **G.** Apical annulus. **H.** Paraphyses. **I.** Ascospores. **J–S.** *Torrentispora dubia*. **J–L.** Ascumata. **M, N.** Asci. **O.** Longitudinal section of the ascumatal wall. **P.** Apical annulus. **Q.** Ascogenous hyphae. **R, S.** Ascospores. **A–C** from PRA-12745, **D–I** from PRA-12744, **J–R** from PRA-12746, **S** from PAD. Scale bars: **A–C, J–L** = 250 µm, **D, E, H, M, N, Q** = 10 µm, **F, O** = 20 µm, **G, I, P, R, S** = 5 µm.



Fig. 24. *Torrentispora fibrosa*. A–D. Ascomata. E. Longitudinal section of the ascomatal wall. F–I. Asci (H, I in India ink). J. Apical annulus. K, L. Ascospores (L in India ink). M. Paraphyses. N, O. Colonies on MLA and PCA after 28 d. A–M from PDD 110879, N, O from ICMP 15147). Scale bars: A–D = 250 μ m, E = 20 μ m, F–I, M = 10 μ m, J, K, L = 5 μ m.

Etymology: Referring to New Zealand, the country where the fungus was collected.

Ascomata immersed, with only tips of necks protruding, solitary. Venter 350–450 μ m diam, 350–420 μ m high, subglobose, upright or lying horizontally on the host, dark brown to black, glabrous, with brown, septate hairs ca. 2.5 μ m wide, sparsely growing at the base. Neck central, 100–110 μ m wide, up to 600 μ m long, cylindrical, upright or slightly decumbent, apex without sulcations. **Ostiole** periphysate. **Ascomatal wall** fragile, 25–33 μ m thick, two-layered; outer layer consisting of thick-

walled, brown, polyhedral cells of *textura prismatica* with opaque walls; cells tending to be darker towards the outside, becoming flattened and paler towards the interior. Inner layer consisting of several rows of thin-walled, hyaline, flattened cells. **Paraphyses** abundant, longer than the asci, becoming disintegrated with age, septate, slightly constricted at the septa, hyaline, 4.5–6.5 μ m wide, tapering to 2–2.5 μ m. **Asci** (170–) 200–213(–225) \times 8.5–10.5 μ m (mean \pm SD = 203 \pm 18.3 \times 9.5 \pm 0.9 μ m), 140–167(–197) μ m (mean \pm SD = 166.3 \pm 18.6 μ m) long in the sporiferous part, truncate at the apex, cylindrical, stipitate with 8 uniseriate ascospores, apical annulus

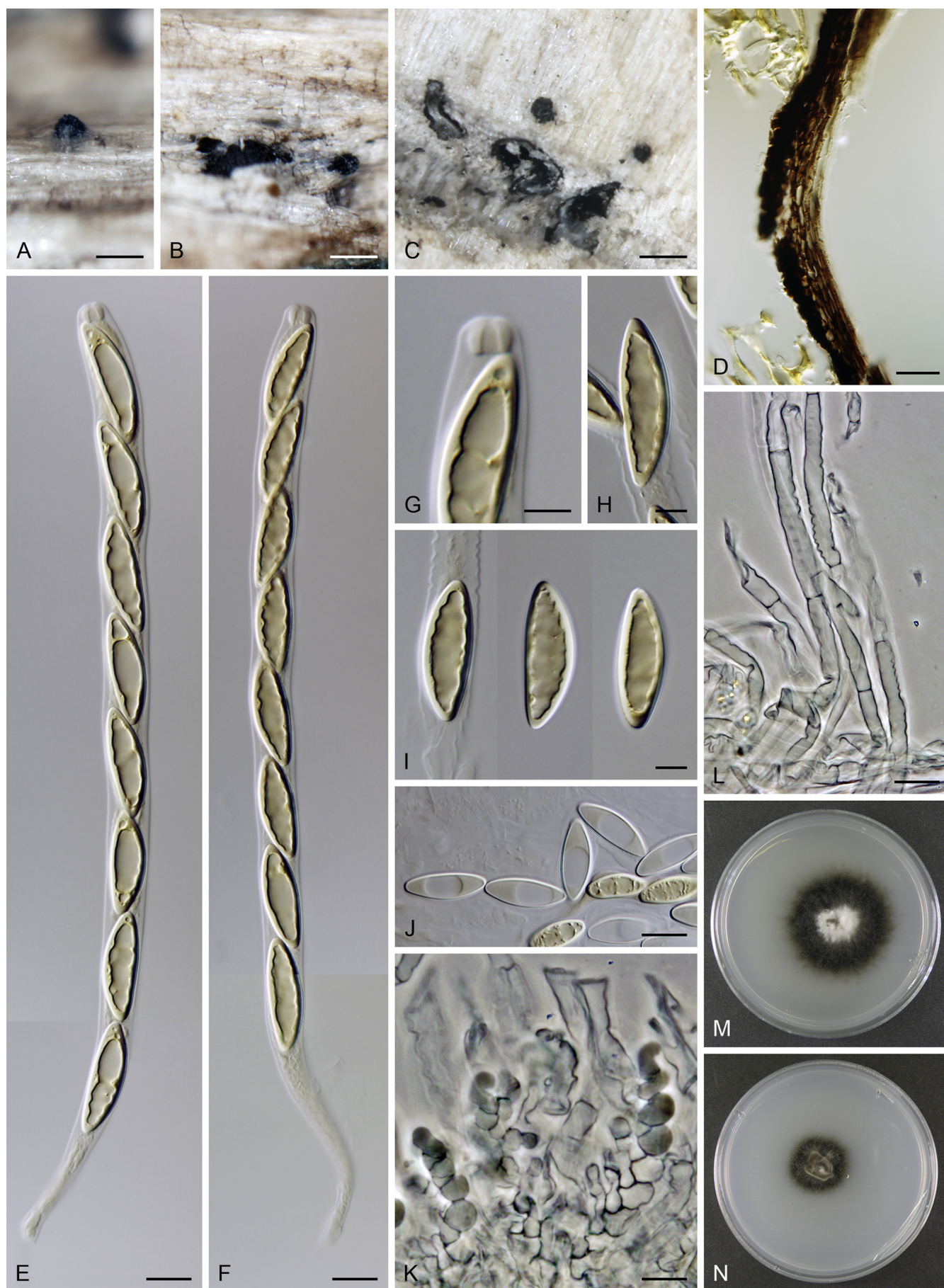


Fig. 25. *Torrentispora novae-zelandiae*. **A–C.** Ascomata. **D.** Longitudinal section of the ascomal wall. **E, F.** Asci. **G.** Apical annulus. **H–J.** Ascospores. **K.** Ascogenous hyphae. **L.** Paraphyses. **M, N.** Colonies on MLA and PCA after 28 d. **A–L** from PDD 110880, **M, N** from ICMP 18368. Scale bars: **A–C** = 250 μ m, **D** = 20 μ m, **E, F, J–L** = 10 μ m, **G–I** = 5 μ m.

5–5.5 µm wide, 4–4.5 µm high. Ascospores (17.5–)18–25(–26) × (6–)7–8.5 µm (mean ± SD = 22.9 ± 3.2 × 7.4 ± 0.7 µm), hyaline, fusiform, often flattened on one side, aseptate, smooth and thick-walled (0.5–0.6 µm), filled with a large drop or numerous small drops.

Culture characteristics: Colonies on MLA 20–23 mm diam after 14 d (24–26 mm after 21 d, 27–30 after 28 d) at 25 °C, circular, raised. Aerial mycelium abundant, present mostly in the centre of the colony, cottony, margins filamentous, colony surface pale grey to whitish in the centre, dark olivaceous-grey towards margin formed by substrate mycelium with a black hue; reverse black. Colonies on PCA 11–14 mm diam after 14 d (12–15 mm after 21 d, 15–18 mm after 28 d) at 25 °C, circular, raised. Aerial mycelium abundant, cottony, margins filamentous, colony surface beige-brown in the centre, dark olivaceous-grey towards margin; reverse black. Sporulation not observed.

Specimens examined: New Zealand, South Island, West Coast, Buller Distr., Victoria Forest Park, Big River Inangana track, 14 km SE of Reefton, on decaying wood, 5 Apr. 2005, M. Réblová M.R. 2956/NZ 719 (holotype, PDD 110880, culture ex-type ICMP 18368); *ibid.*, M.R. 3438/NZ 718.

Notes: *Torrentispora novae-zelandiae* is similar to *T. calembola* in having long-necked immersed ascomata and asci of similar length, but differs from the latter in narrower asci and shorter ascospores. The ascospores in the non-type collection (M.R. 3438/NZ 718) are 19–22 × (5.5–)6–7 µm, the asci are 199–210 × 8.5–9.5 µm.

Torrentispora pilosa Shearer & F.R. Barbosa, *Mycologia* 105: 339. 2013.

Notes: For description and illustration see Barbosa *et al.* (2013). *Torrentispora pilosa* is known from submerged wood in a tropical stream in Costa Rica and is similar to *T. fusiformis* in ascospore morphology, but differs from the latter in having larger, hairy ascomata, shorter asci and ascospores that can develop up to two septa.

DISCUSSION

Soon after *Ceratostomella* was established with the simple diagnosis “Perithecia et asci Ceratostomatis. Sporidia continua, hyalina” (Saccardo 1878a), it became a large, heterogeneous group of morphologically similar species whose highly polyphyletic nature was revealed with molecular data (e.g. Réblová 2006, 2011, Huhndorf & Fernández 2005, Huhndorf *et al.* 2008, 2009, Réblová & Štěpánek 2009, de Beer *et al.* 2013a, b, 2014, Réblová *et al.* 2015a, b). These studies have challenged the traditional divisions separating species in this fungal complex based on characters of ascoma anatomy, ascospore morphology (colour), branching pattern of ascogenous hyphae, and conidiogenesis. The “*Ceratostomella* phenotype” apparently represents an ecological adaptation, and so it has evolved numerous times throughout the *Sordariomycetes*.

Our efforts to clarify phylogenetic relationships among taxa in this fungal complex focused on those *Ceratostomella* species with hyaline or pale brown ascospores and persistent asci that show similarity to *Lentomitella* and *Torrentispora*. Based on revision of their holotypes, recently collected material, living cultures and novel DNA sequences, *Ceratostomella dubia*,

C. fuscolutea, *C. hyalostoma* and *C. subdenudata* were confirmed to be distantly related to *Ceratostomella* and were transferred to three other genera in this study. Furthermore, revision of holotypes of other *Ceratostomella* species resembling *Lentomitella*, i.e. *C. investita*, *C. maderensis*, *C. triseptata* and *C. vestita* var. *varvicensis*, confirmed their placement in *Lentomitella*. Other species such as *C. cirrhosa* and *C. crinigera* had already been allocated to *Lentomitella* (Réblová 2006). The taxonomic status of other *Ceratostomella* spp. with persistent asci, their published details, and where available, phylogenetic data, are listed below.

The combined six-gene phylogenetic analysis of these *Ceratostomella* spp., the ex-type strains of *Fusoidispora aquatica* and *Pseudodiplococcium ibericum*, non-type specimens of *Pseudoannulatuscus biatriisporus*, *Spadicoides bina* and *Xenospadicoides atra*, and several other undescribed taxa revealed a robust, strongly-supported monophyletic clade (Fig. 1). It represents the *Xenospadicoidales* and contains four genera, i.e. *Calyptosphaeria*, *Lentomitella*, *Spadicoides* and *Torrentispora*. It is embedded in a large subclade (70/0.99) within the *Sordariomycetidae* comprising *Atractosporales*, *Papulosaceae*, *Sporidesmiaceae* and numerous genera (as *incertae sedis*) with a prevailing mode of holoblastic conidiogenesis (Fig. 2).

Hernández-Restrepo *et al.* (2017) introduced *Xenospadicoidales* based on partial nuLSU sequence data for two monotypic dematiaceous hyphomycete genera *Xenospadicoides* and *Pseudodiplococcium*. A part of this order was introduced by Zhang *et al.* (2017) as the monotypic family *Lentomitellaceae* for *L. cirrhosa* and *L. crinigera* based on existing ITS, nuLSU, nucSSU and *rpb2* sequence data (Réblová 2006, Réblová *et al.* 2016). However, the sampling in both studies was insufficient, either members of *Lentomitella* or *Spadicoides* were absent from the phylogenetic analyses and the relationship between *Lentomitella* and *Torrentispora* (as *P. biatriisporus* and *F. aquatica*) in Zhang *et al.* (2017) was not statistically supported. Based on results of our ML and BI analyses of six- and three-gene datasets and in accordance with the principle of priority, the monotypic *Lentomitellaceae* (Zhang *et al.* 2017) is synonymised with the *Xenospadicoidaceae* (Hernández-Restrepo *et al.* 2017).

The *Xenospadicoidales* phylogenetic tree (Fig. 1) revealed a topology that is consistent with ascospore morphology and conidiogenesis shared by members of this order. These taxa are characterised by non-stromatic, dark ascomata with a central, cylindrical or rostrate neck with or without sulcations at the tip, persistent asci with a distinct, non-amyloid apical annulus and partially disintegrating paraphyses. The asexual morphs are dematiaceous hyphomycetes with sympodially proliferating holoblastic conidiogenous cells, phaeoisaria-like in *Lentomitella*, or with a tretic mode of asexual spore production in *Spadicoides* accompanied by holoblastic-denticulate conidiogenesis of the selenosporella-like synasexual morph. Other members of the order produce mostly sterile mycelium in axenic culture, but their ascospores often do not germinate *in vitro*. They are cosmopolitan and occur on decaying wood, bark and other plant material in freshwater and terrestrial habitats.

The morphology of ascospores, and to a certain extent also of the ascomatal neck, are the main diagnostic features to distinguish genera in the *Xenospadicoidales*. In *Calyptosphaeria* the ascospores are dull brown prior to discharge, smooth-walled, ellipsoidal to fusiform with a tendency to collapse within the

asci, while the ascomatal neck is sulcate or rarely roughened without sulcations. In *Lentomitella* the ascospores are hyaline, longitudinally striate, ellipsoidal or ellipsoidal-fusiform, and the neck is sulcate. In *Torrentispora* the ascospores are hyaline, smooth-walled or occasionally with a fibrillar sheath, distinctly thick-walled, fusiform or elongated fusiform, rarely cymbiform, and the neck is smooth or roughened without sulcations. The sexual morphs of *Spadicoides* have hyaline, ellipsoidal to ovoid ascospores; in species with verruculose ascospore walls the ascomatal neck is partly light fulvous to subhyaline without sulcations (*S. hyalostoma*), or the ascospores are smooth-walled and the ascomatal neck is dark and sulcate (*S. bina*, *S. fuscolutea*). In all genera except *Lentomitella* we observed a delayed formation of septa in aseptate ascospores within or outside the asci. In *Lentomitella* the ascospores are distinctly 1–3-septate early in ontogeny. In addition to the ascospore and ascomatal neck morphology, the apical annulus also appears to have taxonomic value. In all genera it is distinct, refractive, but differs in size. The relatively smallest apical ring occurs in *Lentomitella* (2.5–3 × 1.5–2 µm, width × height) and *Spadicoides* (2–3.5 × 1.5–2 µm), medium-sized apical rings occur in *Calyptosphaeria* (3–5 × 2.5–4.5 µm) and the largest apical rings are present in members of *Torrentispora* (4–8 × 3.5–4.5 µm).

Calyptosphaeria

Calyptosphaeria, typified with *C. tenebrosa*, is segregated from *Lentomitella* based on evidence from phylogenetic analyses and morphology of ascospores. The genus comprises three other species, i.e. *C. collapsa*, *C. subdenudata* (Peck 1879, Barr 1986, as *L. pallibrunnea* in Huhndorf et al. 2008) and *C. tropica* (as *L. tropica* in Huhndorf et al. 2008). The asexual morph is unknown and since the ascospores do not germinate *in vitro*, all sequence data were generated from DNA extracted directly from herbarium material (Huhndorf et al. 2008 and this study). Members of *Calyptosphaeria* inhabit decaying wood and bark and have been reported from terrestrial or rarely freshwater biotopes in tropical and temperate zones of southern and northern hemispheres.

Calyptosphaeria is closely related to *Lentomitella*, which differs by hyaline, longitudinally striate ascospores. *Calyptosphaeria* also shows a certain resemblance to *Xylomelasma* (Réblová 2006) in having ascomata with a sulcate neck and brown smooth-walled ascospores, but the latter genus differs by aseptate, slightly apiculate ascospores and presence of discrete ascogenous cells, which simultaneously produce several lateral and terminal dehiscent cells from which asci arise. Based on DNA sequence data, *Calyptosphaeria* and *Xylomelasma* are unrelated (Fig. 2).

Lentomitella

New collection data, living cultures and phylogeny based on novel DNA sequences of six nuclear ribosomal and protein-coding loci revealed a strongly supported *Lentomitella* clade (Fig. 1). Its members occur on decaying wood and bark in terrestrial habitats in temperate zones of both hemispheres. They are widely distributed on hardwoods, occasionally on wood of fruit trees (*L. conoidea*, Feltgen 1903) or senescent flower heads of *Protea lepidocarpodendron* (*L. unipretoriae*, Marincowitz et al. 2008), and some species like *L. crinigera* exhibit a clear preference for coniferous wood.

Routine sequencing of ITS and in-depth comparative analysis of the ITS2 2D structure revealed a novel genetic variation among *Lentomitella* isolates. Eleven species are accepted in the genus, nine of which are included in our phylogenies. No DNA sequence data or cultures of *L. investita* (Schweinitz 1832) and *L. unipretoriae* (Marincowitz et al. 2008) exist. Based on results from phylogenetic analyses and revision of morphological characters, three species are excluded from *Lentomitella*. *Lentomitella pallibrunnea* and *L. tropica* (Huhndorf et al. 2008) with pale brown, aseptate, smooth-walled ascospores are transferred to *Calyptosphaeria* as *C. subdenudata* and *C. tropica*, while *L. tomentosa* (Réblová 2006) with hyaline, aseptate and smooth-walled ascospores is transferred to *Spadicoides* as *S. fuscolutea*.

The asexual morphs of *Lentomitella* spp. are phaeoisaria-like dematiaceous hyphomycetes formed only *in vitro*. Interestingly, sporulation was observed only in collections of *L. investita*, *L. sulcata* and *Lentomitella* sp., all originating from New Zealand. *Lentomitella sulcata* and *Lentomitella* sp. belong to the same subclade and produce globose to ellipsoidal conidia on minute but conspicuous denticles. The asexual morph of *L. investita* produces clavate to obovate conidia on a long rachis containing numerous but indistinct denticles. The cultures derived from ascospores of European collections remain sterile.

The main diagnostic feature to distinguish among species of *Lentomitella* is the morphology of ascospores. The ascospores are 1–3-septate, often with a delayed formation of the second and third septum prior to discharge, which makes the correct identification sometimes difficult. Therefore, it is important to examine as many ascospores as possible and also look for old shrinking ascospores released from the asci, which may contain additional septa. Only *L. vestita*, the type species, has truly 1-septate ascospores. Other species such as *L. crinigera*, *L. magna*, *L. striatella*, *L. sulcata* and *L. unipretoriae* have ascospores 3-septate early in ontogeny. Alternatively, *L. conoidea*, *L. investita* and *L. tenuirostris* often develop 1(–2)-septate ascospores with the third septum delayed and sometimes not formed at all.

The presence of longitudinal ridges in ascospores is a good character to distinguish this genus from other morphologically similar taxa. The ridges are usually shallow, but well visible, however two interesting cases were observed. In ascospores of *L. investita* and *L. vestita* the individual ridges are more conspicuous than in other species and often can be seen protruding at the poles. In *L. magna* the longitudinal ridges sometimes become discontinuous giving the ascospore wall a reticulate appearance.

Ascomatal morphology is highly variable within collections of the same species and among collections of different species, and thus, is of limited value for distinguishing species. Ascomatal characters include the degree of immersion in the wood or bark, presence and abundance of hairs growing from the venter and elongation of the neck and its position (upright or slightly decumbent). These characters are often influenced by humid conditions; for example, longer necks often develop when ascomata grow in cracks in wood or are positioned under the bark. The neck can sometimes appear slightly wider at the tip, which is often caused by a rupture of the deeply sulcate ostiolium. In some cases, the sulcations may disappear upon aging, leaving the surface of the neck roughened.

The longitudinally striate, hyaline ascospores of *Lentomitella* resemble those of *Phomatospora* (Barr 1994, Cai et al. 2006), but the latter taxon differs by ascomata developed under a thin clypeus, aseptate ascospores and occurrence on damp or submerged wood or herbaceous material.

Lentomitella and the CBC species concept

The study of interspecific relationships of *Lentomitella* is corroborated by morphology, phylogenetic data and the ITS2 2D structure using the CBC species concept (Coleman 2000, 2003, 2007, Coleman & Vacquier 2002). A less conservative modification to this concept was proposed by Müller *et al.* (2007). According to these authors any CBC in the ITS2 is informative. Although the multicopy nature of ITS2 sequences may pose a potential danger of existence of intragenomic CBC and executing the CBC species concept, Wolf *et al.* (2013) demonstrated that the probability that there is no intragenomic CBC is ~0.99. Species delimited by CBCs are further characterised by hCBCs and non-CBCs. However, genotypes of two organisms differing by a single hCBC indicate that they can theoretically interbreed. The rapidly evolving hCBCs and short-lived non-CBCs substitutions occur more frequently than CBCs and may facilitate faster ecological adaptations of organisms followed by changes in morphology (Caisová *et al.* 2011, Réblová *et al.* 2013, 2015a).

The identification of canonical pairs that undergo reciprocal substitution (C=G ↔ G=C, A-U, U-A) in helices I–III aided us in discriminating among species of *Lentomitella*. The distinction of *Lentomitella* species is supported by seven CBCs (Figs 3, 4). The 14th base pair of the helix III of ITS2 is a particularly interesting site because changes among *Lentomitella* spp. occurring at this position include the full evolution of the reciprocal substitutions involving CBC, hCBC and non-CBC such as U-A → G/A → G/U → G=C. Furthermore, in search for hCBCs and non-CBCs we identified ten such events on helix II, all linked to species originating from New Zealand (*L. cirrhosa*, *L. magna*, *L. striatella*, *L. sulcata*) except one hCBC unique for *L. crinigera* and *L. obscura* both from European material.

The CBCs identified in helices I and III support the distinction of all *Lentomitella* species except the two species pairs, i.e. *L. conoidea* and *L. tenuirostris*, *L. cirrhosa* and *L. striatella*. They illustrate a situation when two closely related species are distinguished in the absence of a CBC between them. A close relationship between *L. conoidea* and *L. tenuirostris* is strongly supported by individual ITS, *tub2*, and *rpb2* sequence data and by the combined analysis of all six genes. There are only a few subtle characters of ascospores, asci, ascospores and macroscopic colony characters that distinguish these two species, which make their correct identification in the absence of molecular data challenging. Their ITS sequences show 94 % similarity, but the differences between their sequences are not associated with helices I–III of the ITS2. A second case was observed between *L. cirrhosa* and *L. striatella*, which also lack a CBC between them. Both species originate from New Zealand and are positioned at the base of the *Lentomitella* clade. *Lentomitella striatella* differs from *L. cirrhosa* in longer and wider asci and slightly longer 3-septate ascospores, while ascospores of *L. cirrhosa* are predominantly 1-septate and additional septa develop later and are rarely visible in old ascospores. Their ITS sequences show 96 % similarity.

The third interesting case concerns three morphologically highly similar species, *L. obscura*, *L. sulcata* and *Lentomitella* sp. that form a monophyletic clade, which is delimited from other species by a CBC on the 8th base pair of the helix III of the ITS2 (Fig. 4). Although *L. obscura* and *L. sulcata* are further distinguished by a unique CBC between them, the distinction between *L. obscura* represented by three European strains and *Lentomitella* sp. based on a single New Zealand strain is not supported

by any CBC. Their ITS sequences show 97 % similarity. The only difference between them is the occurrence of a non-CBC in the 13th base pair of the helix III in the ITS2.

Spadicoides

Spadicoides, typified by *S. bina*, was introduced by Hughes (1958) for a group of dematiaceous hyphomycetes occurring as saprobes on decaying wood or plants remnants. For the first time we show the sexual-asexual morph relationship between *Spadicoides* and perithecial ascomycetes. Hughes (1958) considered unbranched conidiophores as one of the key diagnostic characters to separate *Spadicoides* from the morphologically similar *Diplococcium*. His concept was adopted by Ellis (1963, 1971), Holubová-Jechová (1982) and Wang (1976). Sinclair *et al.* (1985) considered the formation of single vs. catenate conidia as the main diagnostic criterion, superior to the simple/branched conidiophores, to distinguish *Spadicoides* from *Diplococcium*. He abandoned the generic concept of *Spadicoides* sensu Hughes (1958) and transferred four *Spadicoides* species with conidia formed regularly or occasionally in short chains to *Diplococcium*.

Using partial nuLSU sequences, Shenoy *et al.* (2010) suggested that *Spadicoides* and *Diplococcium* are polyphyletic and unrelated to each other. In the same nuLSU phylogeny (Shenoy *et al.* 2010), the strain CBS 113708 of *S. bina* (nuLSU sequence EF204507) occurred in the *Cordanales* as sister to *Cordana pauciseptata* (as *Porosphaerella cordanophora*, the sexual morph; strain M.R. 1150, nuLSU sequence AF178563) with 100 % bootstrap support, while morphologically similar *Spadicoides atra* CBS 489.77 was shown as sister to *Lentomitella*. *Spadicoides bina* and *C. pauciseptata* share 1-septate, brown, ellipsoidal conidia of comparable size born terminally or laterally on upright, macronematous, dematiaceous conidiophores, but they differ in the mode of conidiogenesis. It is tetric in *Spadicoides* while in *Cordana* conidia are borne on minute denticles from intercalary and terminal swellings. The examination of a specimen [Sweden, Uppland, Dalby par., Jerusalem, on decaying wood of *Picea abies*, 17 Apr. 1986, K. & L. Holm 3980, F-540504 (UPS)], used for isolation of the “*S. bina*” strain CBS 113708 and preparation of the dried culture [(1992.02) F-540502 (UPS)] revealed that the fungus present on the wood and in the dried culture is *C. pauciseptata* (Fig. 26). It is obvious that the fungus was originally misidentified, which was merely followed by Shenoy *et al.* (2010) and Hernández-Restrepo *et al.* (2017), who segregated *S. atra* from *Spadicoides* into *Xenospadicoides*. It was distinguished from morphologically similar *Pseudodiplococcium* by arrangement of conidia, solitary in *Xenospadicoides* and catenate in *Pseudodiplococcium*.

Spadicoides bina was recently recollected and obtained in axenic culture (CBS 137794) from isolated ascospores of an undescribed *lentomitella*-like species (PRA-13420). A strongly supported *Spadicoides* clade containing *S. bina*, *S. fuscolutea*, *S. hyalostoma* and *X. atra* was recovered in our six-gene phylogeny (Fig. 1) and ITS-nuLSU analysis (Supplementary Fig. 1), which included also *P. ibericum*. Based on molecular DNA data and morphology of conidia, conidiogenous cells and conidiophores, *X. atra* and *P. ibericum* are accepted in *Spadicoides*; a new combination is proposed for the later species, and *Pseudodiplococcium* and *Xenospadicoides* are synonymised with *Spadicoides*. Based on these results, the generic description

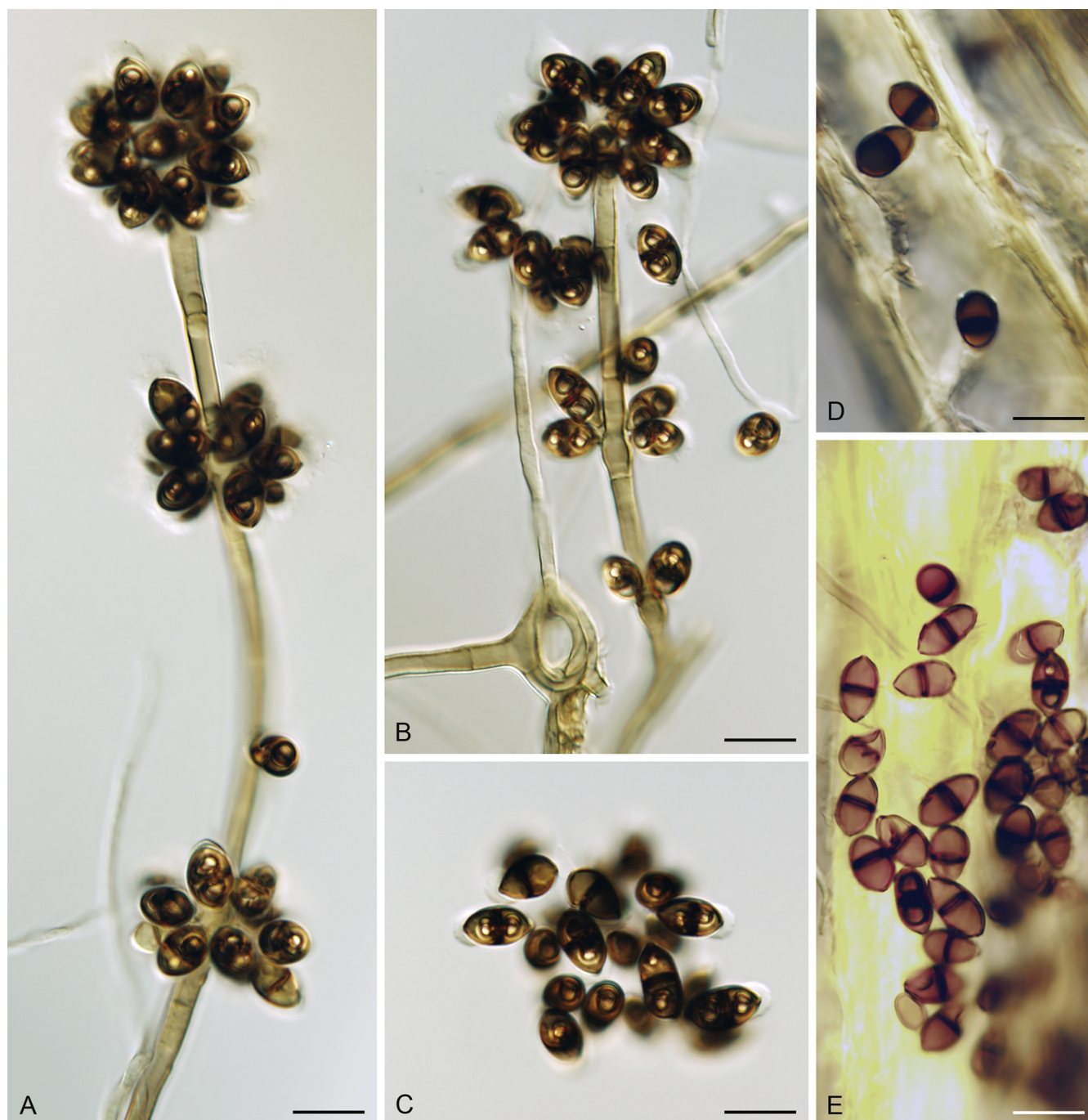


Fig. 26. *Cordana pauciseptata*. A, B. Conidiophores. C–E. Conidia. A–C from dried culture F-540502 (UPS), D, E from F-540504 (UPS). Scale bars: A–E = 10 μ m.

of *Spadicoides* is emended to include both sexual and asexual morphs. The genus is characterised by ascomata with long necks, hyaline, aseptate or 1-septate, delicately verruculose or smooth-walled ascospores, unbranched or branched conidiophores and dark brown conidia formed singly or in a chain, and the selenosporella-like synasexual morph.

Selenosporella is a hyphomycete genus (*Sordariomycetes*, *incertae sedis*) with pale brown to subhyaline conidiophores producing usually clavate, fusiform, obclavate to falcate, hyaline conidia (MacGarvie 1968). However, the exact mode of conidiogenesis has been the subject of a broad discussion. Although MacGarvie (1968) described the conidiogenesis of *S. curvispora*, the type species, as holoblastic-denticulate with conidia arising sympodially in basipetal succession from minute denticles, Ellis (1971) and Hughes (1979) interpreted the conidiogenesis as phialidic or possibly phialidic based on study of other

Selenosporella and selenosporella-like species. Onofri & Castagnola (1982) studied *S. curvispora* with electron microscopy and concluded that the conidiogenesis is holoblastic-denticulate. It is likely that selenosporella-like asexual morphs or synasexual morphs occurring in various taxonomic groups have different modes of conidiogenesis, which is difficult to observe with light microscopy.

The selenosporella-like synasexual morph observed in 4–8-wk-old axenic cultures of *S. bina* and *S. fuscolutea* also was reported for other species of *Spadicoides*, i.e. *S. heterocolorata* (Castañeda *et al.* 1997), *S. obclavata* (Kuthubutheen & Nawawi 1991a) and *S. wufengensis* (Li *et al.* 2010). Furthermore, it was described as a synasexual morph of dematiaceous hyphomycetes such as *Ceratosporium* (Hughes 1964), *Teratosperma* (Hughes 1951, Matsushima 1975), and also *Diplococcium*, e.g. *D. hughesii* (Wang & Sutton 1998), *D. dimorphosporum* and

D. singulare (Hernández-Restrepo *et al.* 2012). The selenosporella-like synasexual morph was reported also for *Endophragmiella*, e.g. *E. dimorphospora* (Awao & Udagawa 1974, Matsushima 1975), *E. subolivacea* (Matsushima 1975), and *E. theobromae* (Hughes 1979), including *Endophragmiella* spp. linked with sexual morphs such as *Echinospaeria canescens* and *Lasiosphaeria punctata* (Hughes 1979, Sivanesan 1983) or *Ruzenia spermoides* (Gams 1973, Miller & Huhndorf 2004b). *Oxydothis selenosporellae* (Samuels & Rossman 1987) and *Iodosphaeria* (Samuels *et al.* 1987) are additional sexual morphs linked with a selenosporella-like asexual morph. Fungi with a selenosporella-like phenotype were described as part of the life cycle of several other dematiaceous hyphomycetes such as *Acrodactys bambusicola* (Matsushima 1975), *Arachnophora excentrica* (Hughes 1979), *Polytretophora calcarata* (= *Spadicoides calcarata*, Kuthubutheen & Nawawi 1991b) and *Quadracea mediterranea* (Lunghini *et al.* 1996).

The position of *Spadicoides verrucosa* (Rao & de Hoog 1986) is in agreement with Shenoy *et al.* (2010). In our analysis this species is also placed in the *Sordariomycetidae* but in a separate clade near members of the *Phomatosporales* and *Magnaporthales*. According to Shenoy *et al.* (2010) *Spadicoides xylogena* is related to *Curvularia brachyspora* (ATCC 58872) (*Pleosporales*, *Dothideomycetes*); these fungi show remarkable similarity. Considering the obvious polyphyly of *Spadicoides*, the genus requires taxonomic revision.

The asexual morph of *Spadicoides* is most similar to *Diplococcium* in pigmented, macronematous conidiophores, polyretic conidiogenous cells and dark conidia, but it differs in having mostly unbranched or rarely branched conidiophores and is linked to morphologically different sexual morphs. *Diplococcium* has been linked to five *Helminthosphaeria* species (*Helminthosphaeriaceae*, *Sordariomycetes*) as a presumed asexual morph based on juxtaposition of conidiophores and ascomata (Samuels *et al.* 1997, Réblová 1999), while *Diplococcium spicatum*, the type species, was positioned in the *Helotiales* (*Leotiomycetes*) based on molecular DNA data (Shenoy *et al.* 2010).

Torrentispora

Torrentispora, typified by *T. fibrosa*, was erected as a monotypic genus in the *Annulatascaceae* based on its massive, non-amyloid apical annulus (Hyde *et al.* 2000). It was introduced for taxa morphologically similar to *Annulatascus*, but distinct in ascomatal wall having irregular rows of cylindrical cells in surface view and smaller ascospores (< 20 µm) vs. *textura epidermoidea* in surface view and larger ascospores (> 20 µm) in *Annulatascus* (Hyde 1992). *Torrentispora* was further distinguished from *Annulatascus* by morphology of the ascospores at the ultrastructural level; the ascospores of *Torrentispora* lack episporial verrucose ornamentation and possess an additional wall layer inside the mesosporium (Lee *et al.* 2004).

In the phylogeny based on three nuclear markers (Fig. 2), *Torrentispora* is shown unrelated to *Annulatascus*, but forms a monophyletic, strongly supported subclade nested in the *Xenospadicoidales*. To date, the genus comprises four species mostly from freshwater habitats from subtropical, tropical and temperate zones, i.e. *T. crassiparietis*, *T. fibrosa*, *T. fusiformis*

and *T. pilosa* (Hyde *et al.* 2000, Fryar & Hyde 2004, Barbosa *et al.* 2013). Based on the evidence from DNA sequence data we introduce *T. calembola* and *T. novae-zelandiae* as new species mainly from terrestrial habitats and we propose three new combinations (*T. aquatica*, *T. biatriispora* and *T. dubia*).

Torrentispora fibrosa was originally collected on submerged wood in streams in Hong Kong, China where the climate is subtropical tending towards temperate for nearly half of the year (Hyde *et al.* 2000, Ho *et al.* 2001). Other collections have been reported from Florida USA (Raja *et al.* 2003), but no states north of Florida (Shearer 1993, 2001). Our collections originate from temperate zones of Europe and New Zealand, but differ from the type species by absence of the fibrillar sheath in ascospores. Ingold (1966) speculated on the latitudinal distribution of aquatic hyphomycetes by examining aquatic spores in samples of stream foam at a distance of every 15° latitude. Conversely, it has been supported by molecular data that some freshwater ascomycetes are not restricted to a certain latitude, e.g. collections of the freshwater species *Annulasmagnus triseptatus* (*Annulatascales*) from Canada, France, Hong Kong and Venezuela form a strongly supported monophyletic clade (Campbell & Shearer 2004, Dayarathne *et al.* 2016).

Pseudoannulatascus was introduced as a monotypic genus (Luo *et al.* 2015) to include *Annulatascus biatriisporus* (Hyde 1995) based on partial nuLSU sequence data. *Pseudoannulatascus biatriisporus* is most similar to *Torrentispora* in the morphology of ascomata, asci and ascospores. Their close relationship was revealed in our phylogeny using DNA sequences from a non-type collection of *P. biatriisporus* from Costa Rica [specimen A 464-3, Raja *et al.* (2003)], our collection of *T. fibrosa* from New Zealand (ICMP 15147) and other *Torrentispora* species. Therefore, *Pseudoannulatascus* is synonymised with *Torrentispora*.

The monotypic genus *Fusoidispora* was described for a freshwater lignicolous species, *F. aquatica* (Vijaykrishna *et al.* 2005). We analysed the partial nuLSU sequence of *F. aquatica* [AY780365, holotype HKU(M) 17484, Vijaykrishna *et al.* (2005)] in the nuLSU (not shown) and six-gene (Fig. 1) phylogenies. This species was nested in the *Torrentispora* clade with high statistical support. Despite the obvious difference in the ascospore morphology, the DNA sequence data of the holotype suggest that *F. aquatica* is a member of *Torrentispora* and therefore a new combination is proposed.

Torrentispora aquatica is most similar to *Pisorisporium cymbiforme* (*Pisorisporiales*, *Sordariomycetidae*) (Réblová *et al.* 2015c) in morphology and size of ascomata, which lie horizontally on the host, ascomatal wall, asci and morphology of long-fusoid to cymbiform, thin-walled ascospores, including the numerous guttules arranged in a chain within ascospores like peas in a pod. It differs from *P. cymbiforme* in ascospores with globose mucilaginous pads at both ends and the non-amyloid apical annulus. The DNA of *T. aquatica* was extracted directly from herbarium material (Vijaykrishna *et al.* 2005). However, we do not exclude the possibility that the DNA was extracted from another fungus. It is well known that different species of aquatic fungi occur close to each other on the same substrate; we often encountered ascomata of *Lentomitella*, *Spadicoides* and *Torrentispora* next to each other on the natural substrate.

REVISION OF *CERATOSTOMELLA* SPP. WITH PERSISTENT ASCI

Species of *Ceratostomella* with evanescent asci that were transferred to members of *Microascales* and *Ophiostomatales* are listed in [de Beer et al. \(2013b, 2014\)](#). The following list includes revised *Ceratostomella* species with persistent asci in three categories: as accepted species of *Ceratostomella* s. str., species excluded from *Ceratostomella* and described in other genera and species of uncertain status. Names in bold refer to the currently accepted classification and are accompanied by short notes, reference to full synonymy and additional published details.

Species accepted in *Ceratostomella* s. str.

Ceratostomella cuspidata (Fr.) Réblová, Mycologia 98: 77. 2006.

Basionym: *Sphaeria cuspidata* Fr., Syst. mycol. 2(2): 474. 1823.
Synonym: *Ceratostoma cuspidatum* (Fr.) Sacc., Syll. fung. 1: 220. 1882.

Ceratostomella pyrenaica Réblová & J. Fourn., in Réblová, Mycologia 98: 78. 2006.

Ceratostomella rhynchophora (De Not.) Réblová, Mycologia 98: 78. 2006

Basionym: *Sordaria rhynchophora* De Not., Comm. Soc. crittog. Ital. 2, Fasc. 3: 480. 1867.

Ceratostomella rostrata (Tode : Fr.) Sacc., Syll. fung. 1: 408. 1882.

Basionym: *Sphaeria rostrata* Tode, Fung. mecklenb. sel. 2: 14. 1791 : Fr., Syst. Mycol. 2: 473. 1823.

Notes: For full synonymy, descriptions, illustrations, phylogeny, discussion, nomenclatural notes on *C. rostrata* and key to *Ceratostomella* s. str. see [Réblová \(2006\)](#).

Species excluded from *Ceratostomella* and described in other genera

Barbatosphaeria barbirostris (Dufour : Fr.) Réblová, Mycologia 99: 727. 2007.

Basionym: *Sphaeria barbirostris* Dufour, Turp. Icon. fig. 1. 1820: Fr., Syst. Mycol. 2: 473. 1823.

Synonyms: *Ceratostomella barbirostris* (Dufour : Fr.) Sacc., Syll. Fung. 1: 410. 1882.

Ceratostomella trichina (Pers.) Sacc., Syll. fung. 1: 410. 1882.

Ceratostomella dispersa (P. Karst.) Sacc., Syll. Fung. 1: 411. 1882.

Specimens examined: **Germany**, Rhineland, Vosges, Wasgau, on decaying wood of *Quercus* sp. (**syntype** of *S. trichina* Pers. in Litt., Mougeot & Nestier, Stirp. Crypt. Voges. No. 666, K 147294; C. Roumeguère Fung. Sel. Gal. Exs. No. 187, K 147310).

Notes: Revision of the holotypes of *Ceratostomella barbirostris* and *C. dispersa* revealed that these species are conspecific and were transferred to the new genus *Barbatosphaeria* as *B. barbirostris* ([Réblová 2007](#)). For full synonymy, description, illustration, holotype and other material examined see [Réblová \(2007\)](#), for phylogeny, additional illustrations and key to *Barbatosphaeria* spp. see [Réblová et al. \(2015b\)](#).

Recently, two collections labelled *Sphaeria trichina*, with the same locality and host information, were located in the Kew fungarium. The specimen labelled as syntype, K 147294, matches the description of *Barbatosphaeria barbirostris*. The other specimen, K 147310, although from the same host, contains a different piece of wood containing empty ascomata.

Calyptosphaeria subdenudata (Peck) Réblová & A.N. Mill.

Basionym: *Sphaeria subdenudata* Peck, Ann. Rep. N.Y. St. Mus. nat. Hist. 32: 52. 1880 (1879).

Synonym: *Ceratostomella subdenudata* (Peck) M.E. Barr, Bull. N.Y. St. Mus. 459: 44. 1986.

Notes: This study; for full synonymy see above.

Ceratosphaeria lampadophora (Berk. & Broome) Niessl, Verh. nat. Ver. Brünn 14: 203. 1876.

Basionym: *Sphaeria lampadophora* Berk. & Broome, Ann. Mag. nat. Hist., Ser. 3. 3: 372. 1859.

Synonym: *Ceratostomella lampadophora* (Berk. & Broome) Cooke, Grevillea 17: 49. 1889.

Notes: For description, illustration and phylogeny of *C. lampadophora* see [Huhndorf et al. \(2008\)](#), for notes on its harpophora-like asexual morph and additional phylogenetic data see [Réblová \(2006\)](#) and [Réblová et al. \(2011\)](#). *Ceratosphaeria*, based on *C. lampadophora*, is a member of the *Magnaporthales* (*Sordariomycetes*).

Chaetosphaeria longispora (Sacc.) P.M. Kirk, Index Fung. 120: 1. 2014.

Basionym: *Ophioceras longisporum* Sacc., Syll. fung. 2: 360. 1883.

Synonyms: *Sphaeria longispora* Ellis, Bull. Torrey bot. Club 6: 135. 1877 non Currey 1859 nec Karsten 1873. (Nom. illegit., Art. 53.1)

Ceratostomella longispora (Sacc.) Cooke, Grevillea 17: 50. 1889.

Lasiosphaeria ellisii M.E. Barr, Mycotaxon 46: 48. 1993.

Chaetosphaeria ellisii (M.E. Barr) Huhndorf & F.A. Fernández, Fung. Diver. 19: 27. 2005.

Notes: For synonymy see [Barr \(1993\)](#), for description, illustration and phylogeny see [Huhndorf & Fernández \(2005\)](#). *Sphaeria longispora* (Ellis 1877) is a later homonym of *S. longispora* Curr. 1859 and *S. longispora* Karst. 1873. Two replacement names were published for *S. longispora*. [Barr \(1993\)](#) introduced *Lasiosphaeria ellisii* for this fungus, later transferred to *Chaetosphaeria* by [Huhndorf & Fernández \(2005\). \[Kirk \\(2014\\)\]\(#\) considered the first combination of *S. longispora* in *Ophioceras* by \[Saccardo \\(1883\\)\]\(#\) as the earliest legitimate name of the taxon in the same rank \(Art. 41.3\) in order to replace *Sphaeria longispora* Ellis. *Ophioceras longisporum* Sacc. therefore becomes a basionym for all future combinations. \[Kirk \\(2014\\)\]\(#\) proposed a new combination of *O. longisporum* in the genus *Chaetosphaeria* but erroneously cited *S. longispora* as the basionym. However, it does not affect the valid publication of this new combination \(Art. 41.8c\).](#)

Chaetosphaeria myriocarpa (Fr.) C. Booth, Mycol. Pap. 68: 5. 1957.

Basionym: *Sphaeria myriocarpa* Fr., Syst. mycol. 2(2): 459. 1823.

Synonym: *Ceratostomella stevensonii* (Berk. & Broome) Sacc., Syll. fung. 1: 412. 1882.

Notes: For full synonymy, description, illustration and revision of the holotype see [Booth \(1957\)](#).

Clohiesia corticola K.D. Hyde, *Nova Hedw.* 61: 126. 1995.
Synonym: *Ceratostomella hyalocoronata* Inderb., *Mycoscience* 41: 167. 2000.

Specimen examined: **China**, Guangdong Province, Wu Gui Shan, 15 km S of Zhongshan, on decaying branch submerged in a small stream, 8 Nov. 1998, E. M. Leaño & P. Inderbitzin (holotype, UBC F13874).

Notes: The examination of the holotype of *C. hyalocoronata* ([Inderbitzin 2000](#)) revealed a fungus that fits well in the description of *Clohiesia* ([Hyde 1995](#)) and is conspecific with the generic type *C. corticola*. Using nuLSU partial sequence data, *Clohiesia*, originally treated as a member of the *Annulatascaceae*, is related to the *Sordariales* ([Raja et al. 2003](#)) and currently placed there ([Kirk et al. 2008](#)).

Daruvedia bacillata (Cooke) Dennis, *Belarra* 2: 25. 1988.
Basionym: *Sphaeria bacillata* Cooke, *Handb. Brit. Fungi* 2: 879. 1871.
Synonym: *Ceratostomella bacillata* (Cooke) Cooke, *Grevillea* 17: 50. 1889.

Notes: [Dennis \(1988\)](#) proposed a new monotypic genus, *Daruvedia*, for *Sphaeria bacillata* ([Cooke 1871](#)). Although he did not find any ascomata in the holotype, Cooke's habit sketches and drawings of the ascomata, ascus and ascospores, the only surviving original elements, enabled him to identify his fresh material as *S. bacillata*. [Hu et al. \(2010\)](#) designated Dennis's material as epitype and provided full synonymy and detailed description of the species based on additional material. In the absence of DNA sequence data, *Daruvedia* is either placed in the *Pyrenulaceae* (*Pyrenulales*, *Eurotiomycetes*) (as *Pleurotremataceae* *vide* [Barr 1994](#), [Lumbsch & Huhndorf 2010](#)) or is classified in *Dothideomycetes incertae sedis* ([Eriksson 2006](#), [Kirk et al. 2008](#)).

Jattaea echinella (Ellis & Everh.) Réblová, *Fung. Diver.* 49: 182. 2011.
Basionym: *Ceratostomella echinella* Ellis & Everh., *N. Amer. Pyren.* p. 195. 1892.

Notes: For description, illustration and revision of the holotype see [Réblová \(2011\)](#). *Jattaea* is a member of the *Calosphaeriales*, well-distinguished from *Ceratostomella* by hyaline, allantoid ascospores in clavate asci lacking an apical annulus and ascomata usually arranged in small valsoid formations.

Jattaea tumidula (Sacc.) Réblová, *Fung. Diver.* 49: 186. 2011.
Basionym: *Calosphaeria tumidula* Sacc., *Atti Soc. Veneto-Trent. Sci. Nat. Padova* 4: 77–100 (*Fungi Ven. novi Ser.* 4: 20) 1875.
Synonym: *Ceratostomella mali* Ellis & Everh., *Proc. Acad. Nat. Sci. Philad.* 42: 225. 1890.

Notes: For full synonymy, description, illustration and holotype information see [Réblová \(2011\)](#).

Lentomitella cirrhosa (Pers.: Fr.) Réblová, *Mycologia* 98: 82. 2006.
Basionym: *Sphaeria cirrhosa* Pers., *Syn. Meth. Fung.* p. 59. 1801 : [Fries](#), *Syst. Mycol.* 2: 475. 1823.
Synonym: *Ceratostomella cirrhosa* (Pers.) Sacc., *Syll. fung.* 1: 408. 1882.

Notes: See [Réblová \(2006\)](#) and this study; for full synonymy see above.

Lentomitella crinigera (Cooke) Réblová, *Mycologia* 98: 83. 2006.

Basionym: *Sphaeria crinigera* Cooke, *Grevillea* 1: 156. 1873.
Synonyms: *Ceratostomella crinigera* (Cooke) Cooke, *Grevillea* 17: 49. 1889.
Ceratostomella triseptata Petr., *Annls mycol.* 23: 135. 1925.

Notes: See [Réblová \(2006\)](#) and this study; for full synonymy see above.

Lentomitella investita (Schw.) Réblová
Basionym: *Sphaeria investita* Schw., *Trans. Amer. Phil. Soc.* 2, Vol. 4: 216. 1834.
Synonyms: *Ceratostomella investita* (Schw.) Starbäck, *Bih. Kongl. Svenska Vet.-Akad. Handl.* 19(2): 26. 1894.
Ceratostomella vestita Sacc. var. *varvicensis* Grove, *J. Bot.* 23: 131. 1885.
Ceratostomella maderensis Petr., *Bot. Jahrb., Beibl.* 142: 98. 1929.

Notes: This study; for full synonymy see above.

Lentomitella vestita (Sacc.) Höhn., *Annls mycol.* 3: 548. 1906.
Basionym: *Ceratostomella vestita* Sacc., *Michelia* 1: 370. 1878.

Notes: This study; for full synonymy see above.

Natantiella ligneola (Berk. & Broome) Réblová, *Mycol. Res.* 113: 996. 2009.
Basionym: *Sphaeria ligneola* Berk. & Broome, *Ann. Mag. nat. Hist., Ser. 3.* 3: 372. 1859
Synonyms: *Ceratostomella ligneola* (Berk. & Broome) Cooke, *Grevillea* 17: 49. 1889.
Ceratostomella ampullasca (Cooke) Sacc., *Syll. Fung.* 1: 409. 1882.
Ceratostomella similis Kirschst., *Krypt. Flora Brandenb.* 7: 245. 1911.

Notes: Revision of the holotypes of *Ceratostomella ampullasca*, *C. ligneola* and *C. similis* revealed that these species are conspecific ([Réblová & Štěpánek 2009](#)). They were transferred to a monotypic genus *Natantiella* supported by DNA sequences. *Natantiella ligneola* is common on strongly decaying wood and occurs in temperate zones in the northern and southern hemispheres. The genus is placed in *incertae sedis* position in the *Sordariomycetes*. In phylogenetic analysis, *Natantiella* forms a monophyletic, strongly supported clade with members of the *Ophiostomatales* (this study), and is unrelated to *Ceratostomella* s. str. For full synonymy, description, illustration, phylogeny and holotype and other material examined see [Réblová & Štěpánek \(2009\)](#).

Phaeoacremonium leptorrhynchum (Durieu & Mont.) D. Gramaje et al., *Fung. Biol.* 119: 768. 2015.
Basionym: *Sphaeria leptorrhyncha* Durieu & Mont., *Expl. Sci. Alg., Fl. Algér.* 1 (livr. 13). p. 510. 1848.
Synonym: *Ceratostomella leptorrhyncha* (Durieu & Mont.) Sacc., *Syll. fung.* 1: 412. 1882.

Notes: For full synonymy, illustration and holotype examination see [Réblová \(2011\)](#). *Phaeoacremonium leptorrhynchum*, known only from Algeria on *Chamaerops humilis*, is one of the few *Phaeoacremonium* species that are known only in their sexual morph and only from herbarium material. Based on the revision of the holotype, [Réblová \(2011\)](#) suggested that *C. leptorrhyncha* and *Phaeoacremonium novae-zelandiae* (as *Togninia*) are

conspecific and proposed a new combination as *Togninia leptorrhyncha*, later transferred to *Phaeoacremonium* by Gramaje *et al.* (2015), the correct name for the holomorph. We prefer to keep both species separate until representative material of *P. leptorrhynchum* is recollected, isolated in axenic culture and subjected to phylogenetic analysis. Evidence gathered during our current research calls for caution, when morphologically highly similar material from different continents is compared.

Phomatospora helvetica H. Wegelin, Mitt. thürgau. naturf. Ges. 12: 173. 1894.

Synonyms: *Ceratostomella hydrophila* Mouton, Bull. Soc. R. Bot. Belg. 26: 171. 1887.

Phomatospora moravica Petr., Anns mycol. 22: 55. 1924.

Phomatospora luteotagens J. Fourn. & Lechat, Mycosphere 1: 40. 2010.

Specimen examined: Belgium, Beaufays near Liège, on submerged decorticated wood in a stream (**holotype**, BR 93866-67).

Notes: Based on characters of immersed to partially erumpent, globose to conical ascomata 500–650 µm diam under a thin black clypeus and with a flattened base, cylindrical asci 121–134 × 8–9 µm, 100–120 µm in the sporiferous part, and uniseriate, ellipsoidal, hyaline, aseptate, longitudinally striate ascospores (11.5–)12–13.5 × 5–6 µm, this species fits well the description of *Phomatospora helvetica* and *P. moravica* (von Hammer & Scheuer 2008). It was later redescribed as *P. luteotagens* by Fournier & Lechat (2010). The yellow stain of the woody substrate was observed in the holotype of *P. luteotagens* and is consistently present in other collections from France and Spain of this species.

To date, the genus *Phomatospora* includes 120 epithets according to Index Fungorum. It comprises fungi from freshwater, marine and terrestrial habitats on herbaceous debris but also on wood. The ascospores are hyaline, usually aseptate with longitudinally striate walls and often with a mucilaginous sheath and/or bipolar appendages (Barr 1994, Cai *et al.* 2006). Based on the habitat and characters of ascospores with and without mucilaginous appendages or sheaths, the genus might be heterogeneous. There has been no monographic study on *Phomatospora* and very little is known about its asexual morphs (Rappaz 1992). Although *C. hydrophila* is the oldest name for this species, we refrain from making any formal changes until the genus *Phomatospora* can be revised.

Pseudorhynchia polyrrhyncha (Penz. & Sacc.) Höhn., Sber. Akad. Wiss. Wien, Math.-naturw. Kl., Abt. 1. 118: 1206. 1909.

Basionym: *Ceratostomella polyrrhyncha* Penz. & Sacc., Malpighia 11: 408. 1897.

Notes: This tropical species was originally described from Java on *Elletaria* sp. in a monotypic genus. Höhnelt (1909) recollected this taxon in the same locality and on the same host as the type. The third collection was reported by Samuels & Barr (1997) from Venezuela on a dead leaf of *Heliconia* sp. Samuels & Barr (1997) transferred the genus to the Niessliaceae (*Hypocreales*). For description and illustration of the type and other representative material see Höhnelt (1909), Müller & von Arx (1962) and Samuels & Barr (1997).

Spadicoides fuscolutea (Rehm) Réblová

Basionym: *Ceratostomella fuscolutea* Rehm, Anns mycol. 6: 320. 1908.

Notes: This study; for full synonymy see above.

Spadicoides hyalostoma (Munk) Réblová

Basionym: *Endoxyla hyalostoma* Munk, Bot. Tidsskr. 61: 62. 1965.

Synonym: *Ceratostomella hyalostoma* (Munk) Unter., Mycologia 85: 307. 1993.

Notes: This study.

Togniniella microspora (Ellis & Everh.) Réblová, Fung. Diver. 49: 193. 2011.

Basionym: *Ceratostomella microspora* Ellis & Everh., Proc. Acad. nat. Sci. Philad. 45: 444. 1894.

Notes: For description, holotype information, discussion and comparison with the morphologically similar *Flabellascus* see Réblová (2011) and Réblová *et al.* (2004, 2015a).

Torrentispora dubia (Sacc.) Réblová & A.N. Mill.

Basionym: *Ceratostomella dubia* (Sacc.) Sacc., Syll. fung. 1: 410. 1882.

Notes: This study; for full synonymy see above.

Wallrothiella congregata (Wallr.) Sacc., Syll. Fung. 1: 455. 1882.

Basionym: *Sphaeria congregata* Wallr., Fl. crypt. Germ. 4: 786. 1833.

Synonym: *Ceratostomella sphaerosperma* (Fuckel) Sacc., Syll. fung. 1: 412. 1882.

Specimen examined: Germany, Johannisberg, on decaying wood of *Pinus sylvestris*, spring (**holotype**, Fungi Rhen Exs. No. 2013, G).

Notes: For synonymy, description, illustration and phylogeny see Réblová & Seifert (2004) and Huhndorf *et al.* (2009). Based on molecular data, *Wallrothiella* was placed by Huhndorf *et al.* (2009) in the *Amplistromataceae* (*Sordariomycetes*).

***Ceratostomella* species of uncertain status**

Ceratostomella albocoronata (Ellis) Sacc., Syll. fung. 2, Add. xxx. 1883.

Basionym: *Ceratostoma albocoronata* Ellis, Am. Nat. 17: 318. 1883.

Specimen examined: USA, New Jersey, Newfield, Gloucester County, on rotten wood, Jun. 1882 (**holotype**, NY).

Notes: The holotype contained several empty ascomata of a lentomitella-like fungus. They were immersed with short, protruding but mostly broken necks and dark hairs growing from the venter. According to the protologue (Ellis 1883), asci are cylindrical 35 × 7 µm with eight ellipsoidal, hyaline ascospores 7.5–9.5 × 3–3.5 µm with 1–2 drops (as 1–2 nucleate). The dematiaceous hyphomycete mentioned by Ellis (1883), associated with ascomata and scattered over the wood, produces obovate, 2–3-septate, 11.5 × 7.5 µm conidia borne singly on the apices of upright, brown conidiophores. Only a few conidia and remnants of conidiophores were present and they belong to *Spadicoides obovata* (Cooke & Ellis 1876, Ellis 1963). Based on the description, *C. albocoronata* does not match any known species of *Lentomitella*. On the other hand, ascospore morphology and the presence of *Spadicoides* conidia and conidiophores suggest its relationship with species of the latter

genus. For an accurate systematic placement, it would be necessary to collect representative material to generate DNA sequences and experimentally prove the connection between the two morphs. To date, the sexual morph of *S. obovata* is unknown.

Ceratostomella bambusina Höhn., Sber. Akad. Wiss. Wien, Math.-naturw. Kl., Abt. 1: 118: 337. 1909.

Specimen examined: **Western Malaysia**, Indonesia, Java Barat (W. Java), Tjibodas, on decaying bamboo culm, 1907–1908 (**holotype**, FH 00258773).

Notes: The material contained several non-stromatic, partially erumpent, solitary ascomata with a cylindrical upright neck, persistent, stipitate asci with a non-amyloid apical annulus and eight globose, hyaline, aseptate ascospores. Similar ascospores are a diagnostic feature of *Amplistroma* and *Wallrothiella* (*Amplistromatales*) (Huhndorf et al. 2009) and also occur in *Woswasia atropurpurea* (*incertae sedis*) (Jaklitsch et al. 2013), both members of the *Sordariomycetidae*. While the latter taxon and *Amplistroma* produce large stromata, *Wallrothiella* is non-stromatic. However, it has a thick, three-layered ascomatal wall and long-necked ascomata that are solitary or most often confluent. *Ceratostomella bambusina* can be compared to *Wallrothiella congregata*, the type species, in characters of ascospores, asci and partly ascomata, but differs in smaller ascomata that develop individually on the substrate and much thinner, two-layered ascomatal walls. DNA sequence data of this species are necessary to confirm its systematic placement.

Ceratostomella canulata (Preuss) Sacc., Syll. fung. 1: 412. 1882. *Basionym:* *Sphaeria canulata* Preuss, Linnaea 26: 714. 1855.

Specimen: **Germany**, Hoyerswerda, on decaying wood (**holotype**).

Notes: The type material could not be located in B (pers. comm., B. Hein). The fungus is described with immersed globose ascomata, protruding cylindrical necks with hyphae growing at the base, cylindrical asci and hyaline aseptate ascospores. Based on its description it is not possible to identify the fungus or convincingly suggest its relationship.

Ceratostomella capillaris (Ellis) Sacc., Syll. fung. 2, Add. xxx. 1883.

Basionym: *Ceratostoma capillare* Ellis, Bull. Torrey bot. Club 9: 20. 1882.

Specimen examined: **USA**, New York, Gloucester County, on decaying sterile catkins of *Alnus serrulata*, 28 Jun. 1881 (**holotype**, NY).

Notes: Based on morphology of minute, globose ascomata with a filiform neck, and asci with a partly evanescent wall containing eight 2–3-seriate, hyaline to subhyaline, fusiform, slightly curved, aseptate ascospores with gelatinous appendages at both end, this species resembles members of *Ophiostoma*.

Ceratostomella capilliformis E. Bommer, M. Rousseau & Sacc., Syll. fung. 9: 573. 1891.

Specimen examined: **Belgium**, Groenendaal, on decaying wood of *Carpinus betulus* (**holotype**, PAD).

Notes: The type material contained empty ascomata 200 µm diam with cylindrical, upright or decumbent necks ca. 250–300 µm long. According to the protologue (Saccardo 1891), the asci are 30–36 × 6–9 µm, clavate, slightly swollen at the base, paraphyses are present, and ascospores are 8 × 3 µm, ellipsoidal and later curved. Given the morphology of ascomata, asci and ascospores this species resembles species of the genera *Barbatosphaeria* and *Jattaea*. The swollen base of the asci may

be interpreted as discrete cells arising from ascogenous hyphae, which is one of the diagnostic features of *Barbatosphaeria* (Réblová et al. 2015b). The bulbous base of the ascus stipe also occurs in members of *Jattaea* but it is of a different origin (Réblová et al. 2015a). Given the size and especially the width of ascospores, *C. capilliformis* resembles *B. dryina* (Réblová et al. 2015b), but the latter taxon differs by larger ascomata 400–600 µm diam, longer asci and 1-septate ascospores. Other species of *Barbatosphaeria* have usually 1–2 µm wide ascospores. Among *Jattaea* species, *C. capilliformis* can be compared to *J. discreta* (Réblová 2011) in morphology and size of ascomata with a venter 230–400 µm diam, asci (30–) 35–45(–50) × 6.5–8 µm and aseptate, subballantoid ascospores (6–) 6.5–8 × 1.5–2 µm, which are, however, narrower than those of *C. capilliformis*. Fresh material that would match the holotype is needed to confirm a systematic placement of this taxon.

Ceratostomella conica (Ellis & Everh.) M.E. Barr, Mycotaxon 46: 60. 1993.

Basionym: *Ceratostoma conicum* Ellis & Everh., Proc. Acad. nat. Sci. Philad. 42: 226. 1890.

Specimen examined: **USA**, New Jersey, Newfield, on decaying wood of a pine log, 1888 (**holotype**, NY).

Notes: The fungus is characterised by immersed to partially erumpent ascomata with a rostrate ostiolum, cylindrical, short-stipitate asci with a massive, non-amyloid apical annulus and fusiform, hyaline 1–3-septate, smooth-walled ascospores. It resembles *Chaetosphaeria*, but differs in the morphology of the apical annulus, which is relatively small and shallow in the latter genus. In order to find a correct systematic placement for this species, fresh material should be collected and DNA sequence data generated.

Ceratostomella coprogena Masee, Bull. Misc. Inf., Kew: 105. 1913.

Specimen: **Singapore**, botanical garden, on animal dung, Burkill (**holotype**).

Notes: The type material could not be located at Kew (pers. comm., B. Aguirre-Hudson). The coprophilous habitat is rather atypical and it does not occur in any members of the *Xenospadicoidales* or in other species described in *Ceratostomella*.

Ceratostomella cyclospora Kirschst., Verh. bot. Ver. Prov. Brandenb. 48: 52. 1907.

Synonym: *Calosphaeria cyclospora* (Kirschst.) Petr., Anns mycol. 22: 74. 1924.

Specimen: **Germany**, Grünauer forest near Rathenow, on decaying wood of *Pinus* sp., 3 Jul. 1904, W. Kirschstein (**holotype**).

Notes: The holotype is apparently lost (pers. comm., E. Gerhardt, B). According to the protologue (Kirschstein 1907) and a later study of the holotype by Petrak (1924), the ascomata are rarely solitary, mostly congregated in pairs of two or in a valsoid formation, partially or entirely immersed in bark or decorticated wood, 700–900 µm diam with elongated necks, asci 30–40 × 4–6 µm, 20–25 µm long in the sporiferous part, cylindrical-clavate and tapering at base, thick-walled and containing eight hyaline, aseptate ascospores that are cylindrical, strongly curved, 4 × 1 µm. Petrak (1924) concluded that this species is better placed in *Calosphaeria* and proposed a new combination in the latter genus. The species fits the description of *Barbatosphaeria hippocrepida* (Réblová & Štěpánek 2009, Réblová et al. 2015b), known only from New Zealand, apart from the size of ascomata and asci. It is

likely that *C. cyclospora* represents a species closely related to *B. hippocrepida*. Without studying the holotype or other representative material we refrain from making any formal changes.

Ceratostomella debaryana (Auersw.) Sacc., Syll. fung. 1: 409. 1882.

Basionym: *Gnomonia debaryana* Auersw., Mycol. eur. Abbild. Sämmtl. Pilze Eur. 5–6: 23. 1869.

Specimen: **Germany**, Inselsberge, on decaying wood of *Fagus sylvatica*, Fleischhak (**holotype**).

Notes: The type material of *C. debaryana* could not be located in B (pers. comm., E. Gerhardt). According to the protologue and illustration (Auerswald 1869), the ascomata are immersed, globose, 140 µm diam with subcylindrical protruding necks, cylindrical short-stipitate asci 68 × 6 µm and eight uniseriate, ellipsoidal, hyaline, aseptate ascospores with granulose content. The size of ascomata is too small to match the size of any genus of *Xenospadicoideales*.

Ceratostomella echinata Ellis & Everh., N. Amer. Pyren. p. 195. 1892. (nom. nud., Art. 32.1).

Notes: Although Index Fungorum lists this name among species of *Ceratostomella*, this species was not described; page 195 in Ellis & Everhart (1892) refers to *C. echinella* (see above). No type or authentic material is preserved in NY (pers. comm., B.M. Thiers).

Ceratostomella excelsior Mouton, Bull. Soc. R. Bot. Belg. 36: 12. 1897.

Synonym: *Endoxyla excelsior* (Mouton) Munk, Bot. Tidsskr. 61: 66. 1965.

Specimen examined: **Belgium**, Beaufays near Liège, on decaying wood of *Fraxinus* sp., V. Mouton (**holotype**, BR-93865-66).

Notes: The species bears a certain resemblance to *Jattaeta* based on the morphology of ascomata, ascospores and tapering asci without a visible apical annulus and with a bulbous base attached to ascogenous hyphae. However, it does not fit the description of any known species of that genus (Damm et al. 2008, Réblová 2011). Munk (1965) transferred the fungus to the broadly perceived *Endoxyla* (Untereiner 1993). Representative material should be collected and subjected to phylogenetic analysis in order to correctly classify this taxon.

Ceratostomella hystricina (Cooke) Sacc., Syll. fung. 2, Add. xxx. 1883.

Basionym: *Ceratostoma hystricina* Cooke, Grevillea 11: 109. 1883.

Specimen examined: **USA**, South Carolina, Aiken, on bark of *Ficus* sp., H.W. Ravenel 2676 (**syntypes**, ex herb. M.C. Cooke, K 147286, K 147288); *ibid.*, H.W. Ravenel Fungi Amer. Exs. No. 674 (K 147290).

Notes: The protologue of *C. hystricina* and representative herbarium material do not refer to the same fungus. Examination of the three specimens from K cited above revealed a fungus that is in agreement with observations of Ellis & Everhart (1892) and a fungus distributed in Ellis & Everhart's N. Amer. Fungi. Exs. Ser. II. No. 2349 (not seen). These specimens contain a fungus with globose, immersed to superficial, densely aggregated ascomata covered with a dark pink to brown crustose layer, with a cylindrical, upright, glabrous neck and minute, hyaline, aseptate, allantoid ascospores 4–4.5 × 1–1.5 µm. Asci are present but indistinct and visible merely as bundles of ascospores. However,

in the protologue, the fungus is described with ellipsoidal-lanceolate ascospores 16–18 × 6 µm (Cooke 1883) and the same illustration is made on the envelope of the syntype (K 147286). Cooke based his description of *C. hystricina* on H.W. Ravenel Fungi Amer. Exs. No. 674. The fungus present in the examined collections is best placed in the *Diaporthales*; a species of *Valsa* *vide* Ellis & Everhart (1892).

Ceratostomella leiocarpa Sacc. [as 'leiocarpa'], Michelia 1: 370. 1878.

Specimen: **Italy**, Cansiglio, on decaying wood of *Fagus sylvatica* (**holotype**, PAD).

Notes: The type material could not be located in PAD (pers. comm., R. Marcucci). Based on characters of the ascomata, asci and ascospores cited in the protologue by Saccardo (1878a), this species fits best the description of *Lentomitella cirrhosa*.

Ceratostomella multirostrata (Fuckel) Sacc., Syll. fung. 1: 411. 1882.

Basionym: *Ceratostoma multirostratum* Fuckel, Jb. nassau. Ver. Naturk. 23–24: 129. 1870.

Specimen examined: **Germany**, Budenheimer Forest, on decaying wood of *Pinus sylvestris*, spring (**holotype**, Fungi Rhen. Exs. No. 771, G).

Notes: The holotype contains empty ascomata that are superficial, confluent, with 1–4 cylindrical upright necks and accompanied by a coelomycete forming stromatic conidiomata with monostichous loculi. Based on the protologue (Fuckel 1870) and illustration accompanying the type material, we cannot conclusively attribute this species to any known genus.

Ceratostomella mycophila Rick, Brotéria, sér. bot. 5: 48. 1906.

Specimen: **Brazil**, Rio Grande do Sul, in hymenophore of *Poria* sp., 1905 (**holotype**, PACA 12733).

Notes: The type material is deposited in Herbarium Anchieta but was not available to our study (pers. comm., M. S. Marchioreto, PACA). According to the protologue (Rick 1906), the fungus fits well the description of *Ceratostomella* s. str. It resembles *C. rostrata* in habitat, size and morphology of cylindrical, pale brown ascospores, but differs in shorter asci 25 × 6 µm vs. (26–) 30–39 × 5–6 µm in *C. rostrata* (Réblová 2006). However, some collections of *C. rostrata* can rarely have shorter asci, e.g. Sclerom. Suec. Exs. No 116, PRM 666367 with asci 23–32 × 5–6 µm. This collection is old, the ascus stipe is partly disintegrated and asci appear slightly wrinkled and therefore shorter. Recollection of fresh material of *C. mycophila* from its original locality is recommended before it can be accepted in *Ceratostomella* or confirmed as conspecific with *C. rostrata*.

Ceratostomella nyssicola (Berk. & M.A. Curtis) Sacc. [as 'nys-saecola'], Syll. fung. 1: 412. 1882.

Basionym: *Sphaeria nyssicola* Berk. & M.A. Curtis, [as 'nys-saecola'] Grevillea 4: 143. 1876.

Specimen examined: **USA**, Pennsylvania, wood of *Nyssa* sp., Michener 5166 (**holotype**, K 155069).

Notes: The holotype is in poor condition and apart from mostly damaged ascomata, only a few pale brown, ellipsoidal and slightly apiculate, aseptate, smooth-walled ascospores 9.5–10.5 × 4.5–5 µm, which have a minute germ pore at each end and a large drop inside, are present. Based on these characters the fungus belongs in *Xylomelasma* (Réblová 2006), and it is likely an earlier name for *X. sordida*, the type species.

Ceratostomella rhenana (Auersw.) Sacc., Syll. fung. 1: 409. 1882.

Basionym: *Gnomonia rhenana* Auersw., Myc. Europ. Pyren. 5–6: 23. 1869.

Specimen examined: Germany, Nassau, on decaying wood, Fuckel ex Herb. Barbey-Boissier No. 603 (K 84430, Fungi Rhen. Exs. No. 1804).

Notes: The type material of *C. rhenana* is apparently lost (pers. comm., B. Hein, B). Winter (1887) based his description of *C. rhenana* on a part of Fuckel's exsiccate collection (Fungi Rhen. Exs. No. 1804, pro parte). Our revision of this specimen from Fuckel's herbarium in G revealed *Lentomitella vestita*, but a fungus *sensu* Auerswald (1869) and Winter (1887) was not found. However, a specimen of Fungi Rhen. Exs. No. 1804 deposited in Kew (K 84430) contained the fungus, which is in agreement with the protologue of *Gnomonia rhenana* (Auerswald 1869). The material in Kew is not suitable for typification due to its poor condition and lack of asci. The systematic placement of this fungus is unknown. Other parts of Fungi Rhen. Exs. No. 1804 need to be studied and fresh material of this fungus needs to be recollected to investigate the relationship of *C. rhenana* with *Ceratospaeria* and other morphologically similar taxa. For a detailed discussion on this species and revision of available representative material see Réblová (2009).

Ceratostomella rostrata var. *levirostris* Sacc., Syll. fung. 1: 408. 1882.

Notes: No type or authentic material of *Ceratostomella rostrata* var. *levirostris* could be found in PAD (pers. comm., R. Marcucci). Saccardo (1882) mentioned this taxon briefly in a discussion of *C. rostrata*: 'Var. *levirostris* rostro non v. vix sulcato. Cum specie.' *Ceratostomella stricta* (Pers.) Sacc., Syll. fung. 1: 410. 1882. *Basionym:* *Sphaeria stricta* Pers., Syn. meth. fung. 1: 59. 1801.

Notes: The holotype could not be located in L (pers. comm., G. Thijssse). *Sphaeria stricta* is distributed in Fries's Sclerom. Suec. Exs. No. 148, but this collection was not examined. The fungus was described with just a few words (Persoon 1801), and later redescribed by Saccardo (1882) based on various materials from European localities. Based on Saccardo's description of non-stromatic densely aggregated, globose, glabrous ascomata with a cylindrical neck, cylindrical-clavate asci with a slender stipe and hyaline, subcylindrical, curved ascospores, the fungus would be best placed in *Calosphaeria* or *Jattaea* in *Calosphaeriales*.

Ceratostomella stricta var. *cingulata* (Fr.) Sacc., Syll. fung. 12: 83. 1897.

Basionym: *Sphaeria stricta* var. *cingulata* Fr., Syst. mycol. 2: 474. 1823.

Notes: We could not locate any authentic material for this study.

Ceratostomella stricta var. *majuscula* Schulzer & Sacc., Hedwigia 23: 42. 1884.

Synonym: *Ceratostomella majuscula* (Schulzer & Sacc.) Mussat, in Saccardo, Syll. fung. 15: 84. 1901. (Nom. inval., Art. 36.1a, c)

Specimen: Hungary, Vinkovce, on decaying wood of *Populus* sp. (holotype).

Notes: Type material could not be located in W. The species is described with hyaline ascospores 12–14 × 3 µm with 2–3 guttules (Schulzer & Saccardo 1884). The description is insufficient to transfer this fungus to any known genus. The fungus was also illustrated in Schulzer (1869), cited in Saccardo & Schulzer (1884) as Ill. Fung. Slav. no 845. In the absence of

the holotype, the illustration is the only surviving element, which should serve as a lectotype. Schulzer's manuscript with illustrations is deposited at the Hungarian Academy in Budapest. Unfortunately, the illustration could not be located (pers. comm., G. Tóth, Dept. of Manuscripts & Rare Books).

Ceratostomella stylophora (Berk. & Broome) Cooke, Grevillea 17: 49. 1889.

Basionym: *Sphaeria stylophora* Berk. & Broome, Ann. Mag. nat. Hist., Ser. 3, 7: 453. 1861.

Specimen: UK, Scotland, Mossburnford, on bark of *Acer platanoides*, A. Jerdon (holotype, K 84425).

Notes: The type material contained non-stromatic, ovoid ascomata densely aggregated in small groups and erumpent through the thin bark of a twig, with upright, cylindrical, partly flattened necks. The asci were mostly disintegrated, only remnants of the upper half with a distinct apical annulus could be seen. The ascospores are hyaline, fusiform, slightly curved, 1-septate with short appendages at each end. The fungus is better placed in the *Diaporthales*.

Ceratostomella subpilosa (Fuckel) Sacc., Syll. fung. 1: 411. 1882.

Basionym: *Ceratostoma subpilosum* Fuckel, Jb. Nassau. Ver. Naturk. 23–24: 128. 1870.

Specimen examined: Germany, Grünau, on decaying wood of *Salix alba* (holotype, Fungi Rhen. Exs. No. 2251, G).

Notes: The type material is overmature. The ascomata are subglobose, glabrous with a fragile crumbling wall, immersed with only necks emerging, ascospores 8–9 × 4–5 µm, ellipsoidal slightly tapering towards the ends, hyaline, aseptate, smooth-walled, although some ascospores were observed to be verruculose. Given the poor condition of the specimen, the fungus could not be properly identified.

Ceratostomella subsalsa (P. Crouan & H. Crouan) Sacc., Syll. fung. 1: 412. 1882.

Basionym: *Sphaeria subsalsa* P. Crouan & H. Crouan, Florule Finistère p. 25. 1867.

Specimen: France, Finistère, on decaying wood of *Obione* sp. (holotype).

Notes: The holotype material deposited in CO was not examined. The identity and placement of this fungus is unknown; it was described with globose, greenish ascomata 1–2 mm diam, thick-walled clavate asci and ovoid, hyaline ascospores.

Ceratostomella unedonis Fabre, Anns Sci. Nat., Bot., Sér. 6. 15: 34. 1883.

Specimen: France, Vaucluse, on decaying wood of *Arbutus unedo* (holotype).

Notes: The holotype material deposited in FABR was not examined. The identity and placement of this lignicolous fungus is unclear. Based on the description of Saccardo (1883) the ascomata are sparse, solitary, globose, ca. 330 µm diam, with an upright central neck, short-stipitate asci 70–80 × 8 µm with eight uniseriate, hyaline, aseptate, ovoid ascospores 8–10 × 5 µm. The description is insufficient to identify this taxon.

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APPENDIX A. SUPPLEMENTARY DATA

Supplementary data related to this article can be found at <https://doi.org/10.1016/j.simyco.2017.11.004>.

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