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Phylogenetic relationships of five uncommon species of *Lasiosphaeria* and three new species in the Helminthosphaeriaceae (Sordariomycetes)

Andrew N. Miller[1]
Illinois Natural History Survey, University of Illinois, Champaign, Illinois 61820

Sabine M. Huhndorf
Botany Department, The Field Museum, Chicago, Illinois 60605

Jacques Fournier
Las Muros, F-09420 Rimont, France

Abstract: In an ongoing effort to monograph the genus *Lasiosphaeria*, it is desirable to obtain estimates of the phylogenetic relationships for five uncommon species, *L. coacta*, *L. munkii*, *L. punctata*, *L. sphagnorum* and *L. stuppea.* Three additional species previously placed in *Lasiosphaeria*, *Echinosphaeria canescens*, *Hilberina caudata* and *Ruzenia spermoides*, also were included in this study as well as three undescribed species. These species were believed to have relations elsewhere based on various ambiguous morphological characters, so an independent dataset from one or more genes was used to resolve their phylogenetic affinities. Sequences from the nuclear ribosomal 28S large subunit (LSU) and β-tubulin genes were generated for these taxa. Maximum likelihood and Bayesian analyses indicated these taxa form a well supported monophyletic group with members of the Helminthosphaeriaceae and therefore, should be transferred out of *Lasiosphaeria.* Except for *Helminthosphaeria gibberosa*, *Hilberina elegans*, *Ruzenia spermoides* and *Synaptospora plumbea*, all taxa within this clade possess ascomata with distinct thick-walled setae. Based on a combination of morphological and molecular data, *Helminthosphaeria tomaculum*, *Helminthosphaeria triseptata* and *Hilberina robusta* are described as new and four new combinations are proposed: *Helminthosphaeria ludens*, *Hel. stuppea*, *Hilberina punctata* and *H. sphagnorum.* Ten new combinations are proposed based on morphological data: *Echinosphaeria heterostoma*, *Helminthosphaeria flavocompta*, *Hel. gibberosa*, *Hel. heterotricha*, *Hilberina breviseta*, *H. elegans*, *H. foliicola*, *H. meznaensis*, *H. moseri* and *H. rhynchospora. Lasiosphaeria coacta* is placed in synonymy with *Hel. ludens* and the previous transfer of *Hilberina munkii* is accepted. *Synaptospora plumbea* was found to belong in the family. Illustrations are provided for most Helminthosphaeriaceae taxa seen in this study.

Key words: Ascomata, β-tubulin, *Echinosphaeria*, *Helminthosphaeria*, *Hilberina*, LSU rDNA, phylogeny, *Ruzenia*, *Synaptospora*

Introduction

The genus *Lasiosphaeria* Ces. & de Not. historically has been an agglomeration of various morphologically diverse taxa but recently has been emended to include a monophyletic group of taxa possessing tomentose ascomata and yellow centrum pigments (Miller and Huhndorf 2004a, b). However, numerous species, which do not possess these characters, still reside within the genus and after careful study need to be transferred elsewhere. Several species previously placed in *Lasiosphaeria* have been transferred to other genera (Miller and Huhndorf 2004a, Huhndorf et al. 2005, Huhndorf and Fernández 2005), but many uncommon or rarely collected taxa remain in the genus. This study employs phylogenetic analyses of partial gene sequences of LSU and β-tubulin to determine the taxonomic placement for five uncommonly collected species of *Lasiosphaeria*: *L. coacta* Kirschst. (JF04126), *L. munkii* R. Hilber & O. Hilber (SMH1531), *L. punctata* Munk (SMH4825), *L. sphagnorum* (P. Crouan & H. Crouan) Sacc. (Buck49156) and *L. stuppea* Ellis & Everh. (JF04120, TL11998) as well as three undescribed species (represented by SMH2485, JF02048, JF04015, SMH3054). The latter include two species from the tropics and one from temperate areas that possess unique combinations of morphological characters. Type collections were studied for eight additional species, and new combinations are made based on morphological data. Three additional new combinations are made based on morphological data in the literature.

Materials and methods

Taxon sampling.—GenBank accession numbers for taxa in this study are provided (Table I). Because the taxonomic placement of these taxa was unknown, representatives from several orders throughout the Sordariomycetes were included in these analyses. Two members of the Xylariales, *Anthostomella* sp. and *Eutypa* sp., were used as outgroup taxa. Two sequences identified as *H. caudata* (Miller and Huhndorf 2004a) are omitted from the analyses because

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[1] Corresponding author: amiller@inhs.illinois.edu

TABLE I. Taxa used in this study. GenBank numbers in boldface indicate new sequences

Taxon	Source[a]	GenBank accession no. LSU	GenBank accession no. β-tubulin
Anthostomella sp.	SMH3101	AY780050	AY780084
Camarops tubulina	SMH4614	AY346266	AY780095
Camarops ustulinoides	SMH1988	AY346267	AY780096
Chaetosphaeria ovoidea	SMH2605	AF064641	AF466057
Coniochaetidium savoryi	TRTC 51980	AY346276	AY780114
Diaporthe phaseolorum	FAU458	AY346279	AY780115
Echinosphaeria canescens	JHC97-006	**KF765604**	**KF765622**
Echinosphaeria canescens	SMH4666	**KF765605**	**KF765623**
Echinosphaeria canescens	SMH4791	AY436403	—
Echinosphaeria canescens	TL5730	AY436404	**KF765624**
Eutypa sp.	SMH3580	AY346280	AY780117
Fusarium ambrosium	SMH1999	AY780077	AY780137
Helminthosphaeria carpathica	SMH3903	**KF765606**	**KF765625**
Helminthosphaeria clavariarum	ANM Acc.17	—	**KF765626**
Helminthosphaeria corticiorum	JF04225	**KF765607**	**KF765627**
Helminthosphaeria hyphodermiae	SMH4192	**KF765608**	**KF765628**
Helminthosphaeria ludens	JF04126	—	**KF765629**
Helminthosphaeria mammillata	ANM986	**KF765609**	**KF765630**
Helminthosphaeria odontiae	ANM928	**KF765610**	**KF765631**
Helminthosphaeria cf. *stuppea*	JF04120	**KF765611**	**KF765632**
Helminthosphaeria cf. *stuppea*	TL11998	**KF765612**	**KF765633**
Helminthosphaeria tomaculum	SMH2485	**KF765613**	**KF765634**
Helminthosphaeria triseptata	JF02048	—	**KF765635**
Helminthosphaeria triseptata	JF04015	**KF765614**	**KF765636**
Hilberina caudata	SMH1542	**KF765615**	**KF765637**
Hilberina munkii	SMH1531	**KF765616**	**KF765638**
Hilberina punctata	SMH4825	—	**KF765639**
Hilberina robusta	SMH3054	—	**KF765640**
Hilberina sphagnorum	Buck49156	**KF765617**	**KF765641**
Lasiosphaeria ovina	SMH1538	AF064643	AF466046
Melanochaeta hemipsila	SMH2125	AY346292	AF466049
Neurospora crassa	MUCL 19026	AF286411	M13630
Poroconiochaeta discoidea	SANK 12878	AY346297	AY780134
Ruzenia spermoides	ANM163	**KF765618**	**KF765642**
Ruzenia spermoides	CBS 101621	AY436321	**KF765643**
Ruzenia spermoides	SMH4606	AY436422	**KF765644**
Ruzenia spermoides	SMH4655	**KF765619**	**KF765645**
Synaptospora plumbea	ANM963	**KF765620**	**KF765646**
Synaptospora plumbea	SMH3962	**KF765621**	**KF765647**
Valsa ceratosperma	AR3426	AF408387	AY780144
Valsonectria pulchella	SMH1193	AY346304	AY780145

[a] CBS = Centraalbureau voor Schimmelcultures; MUCL = Mycothèque de l'Université catholique de Louvain; SANK = Sankyo Research Laboratories; TRTC = Royal Ontario Museum; ANM = Andrew N. Miller; AR = Amy Rossman; Buck = William Buck; FAU = Francis A. Uecker; JF = Jacques Fournier; JHC = J. Heilman-Clausen; SMH = Sabine M. Huhndorf; TL = Thomas Læssøe.

they were identified incorrectly. These sequences (AY436405 and AY436406) have been removed from GenBank. Taxa within the Helminthosphaeriaceae are difficult or impossible to obtain in culture due to lack of ascospore germination (Réblová 1999b). Except in the case of *Ruzenia spermoides* (Hoffm.) O. Hilber, attempts to obtain species in culture with the techniques of Huhndorf et al. (2004) were unsuccessful. All voucher specimens are deposited in the Field Museum Mycology Herbarium (F) or the Illinois Natural History Survey Fungarium (ILLS). Examination of morphological characters follows Promputtha and Miller (2010) and Mugambi and Huhndorf (2010). Additional species information can be found at: http://www-s.life.illinois.edu/pyrenos/

DNA extraction, PCR amplification, sequencing and sequence alignment.—Detailed protocols for the extraction, amplification and sequencing of DNA and methods for the alignment of LSU and β-tubulin sequences are fully described in Miller and Huhndorf (2005) and Promputtha and Miller (2010). Because ascospores of the Helminthosphaeriaceae taxa did not germinate in culture, DNA was extracted directly from ascomata, except in the case of *Ruzenia spermoides*, in which DNA was extracted from cultures.

Phylogenetic analyses.—Separate alignments were made for each of the two datasets. Portions of the 5′ and 3′ ends of each dataset were excluded due to missing data in most taxa (93 bp in LSU, 45 bp in β-tubulin). In addition, eight ambiguously aligned regions representing 164 bp were excluded from the LSU dataset due to alignment difficulties caused by indels. No ambiguously aligned regions occurred in the β-tubulin dataset. Modeltest 3.7 (Posada and Crandall 1998) determined the best-fit model of evolution for each dataset to be general time reversible (GTR). The aligned LSU and β-tubulin datasets were analyzed separately and their clade support compared for conflict. Independent maximum likelihood (ML) analyses were conducted on each dataset with PhyML with Seaview 4.2 (Galtier et al. 1996) under these parameters: GTR model was implemented with four rate classes, invariable sites and across site variation were optimized, and 1000 bootstrap replicates were performed from a BioNJ starting tree employing the best of NNI and SPR branch swapping. Clades with bootstrap support ≥ 70% were considered strongly supported (Wiens 1998). Because no conflict existed between strongly supported clades, the two datasets were concatenated into a single combined dataset (TreeBASE: S14893). A ML analysis on the combined dataset was performed with 100 stepwise random addition replicates, TBR branch-swapping and a reconnection limit of 12 under the GTR model with PAUP* 4.0b10 (Swofford 2002). In addition, a PhyML ML analysis of the combined dataset was performed as above. Finally, a third ML analysis was conducted with RAxML 7.2.6 (Stamatakis et al. 2006) using the CIPRES 3.1 web portal (Miller et al. 2009, 2010). The data were divided into four partitions corresponding to the LSU and each of the three codon positions of the β-tubulin gene. Bootstrap replicates were performed 1000 times under the GTR model employing GAMMA model of rate heterogeneity and the rapid bootstrapping option (Stamatakis et al. 2008).

Bayesian analyses were performed on the combined, partitioned data under the GTR model with MrBayes 3.0b4 (Huelsenbeck and Ronquist 2001) as an additional means of assessing branch support. Ten million generations were sampled every 1000th generation, resulting in 10 000 total trees. The Markov chain always achieved stationarity after the first 100 000 generations (= 100 trees), so the first 1000 trees, which extended well beyond the burn-in phase of each analysis, were discarded. Posterior probabilities were determined from a consensus tree generated with the remaining 9000 trees using PAUP* 4.0b10. This analysis was repeated twice, starting from different random trees to ensure trees from the same tree space were being sampled during each analysis.

RESULTS

Phylogenetic analyses.—The LSU dataset consisted of 36 taxa and 920 characters, while the β-tubulin dataset consisted of 40 taxa and 606 characters. The combined dataset comprised 41 taxa, 35 of which were common to both datasets, and 1526 characters. Each of the three ML analyses (PAUP, PhyML, RAxML) produced trees with identical topologies. The single most likely tree generated from the PhyML analysis of the combined LSU and β-tubulin dataset is illustrated (FIG. 1).

The family Helminthosphaeriaceae occurs as a highly supported monophyletic group encompassing the five *Lasiosphaeria* species (represented by Buck49156, JF04120, JF04126, SMH1531, SMH4825, TL11998) and the three undescribed species (represented by SMH2485, JF02048, JF04015, SMH3054). Both *Helminthosphaeria* Fuckel and *Hilberina* Huhndorf & A.N. Mill. are polyphyletic with their type species (*Hel. clavariarum* (Desm.) Fuckel and *H. caudata* (Fuckel) Huhndorf & A.N. Mill.) occurring as sister species on an unsupported branch. Two morphologically similar specimens of an undescribed species of *Helminthosphaeria* (JF04015 and JF02048) occurred within an unsupported clade with *Hel. odontiae* Höhn. and *Hel. hyphodermiae* Samuels, Cand. & Magni, but did not group as a monophyletic unit. Three species represented by multiple specimens (*Echinosphaeria canescens* (Pers.) A.N. Mill. & Huhndorf, *Ruzenia spermoides*, *Synaptospora plumbea* Huhndorf, F.A. Fern. & Cand.) were monophyletic and highly supported. The relationship between *H. caudata* and *L. punctata* (SMH4825) is moderately supported as is the relationship between *Lasiosphaeria* cf. *stuppea* JF04120 and *Helminthosphaeria* JF04126. The other two larger supported clades contain species with no obvious morphological characters that would unite them at a higher taxonomic rank. Until further analyses that sample more taxa and include additional genes can be conducted to better clarify phylogenetic relationships within this family, the five species described as *Lasiosphaeria* and the three undescribed species are placed in existing genera rather than creating additional, new monotypic genera with unresolved relationships.

TAXONOMY

Images of these sequenced taxa are included for comparison of morphological characteristics: *Echinosphaeria canescens* (FIG. 2), *Helminthosphaeria carpathica* Réblová (FIG. 3), *Hel. clavariarum* (FIG. 4), *Hel. corticiorum* Höhn. (FIG. 5), *Hel. hyphodermiae* (FIG. 6), *Hel. odontiae* (FIG. 7), *Hel. mammillata*

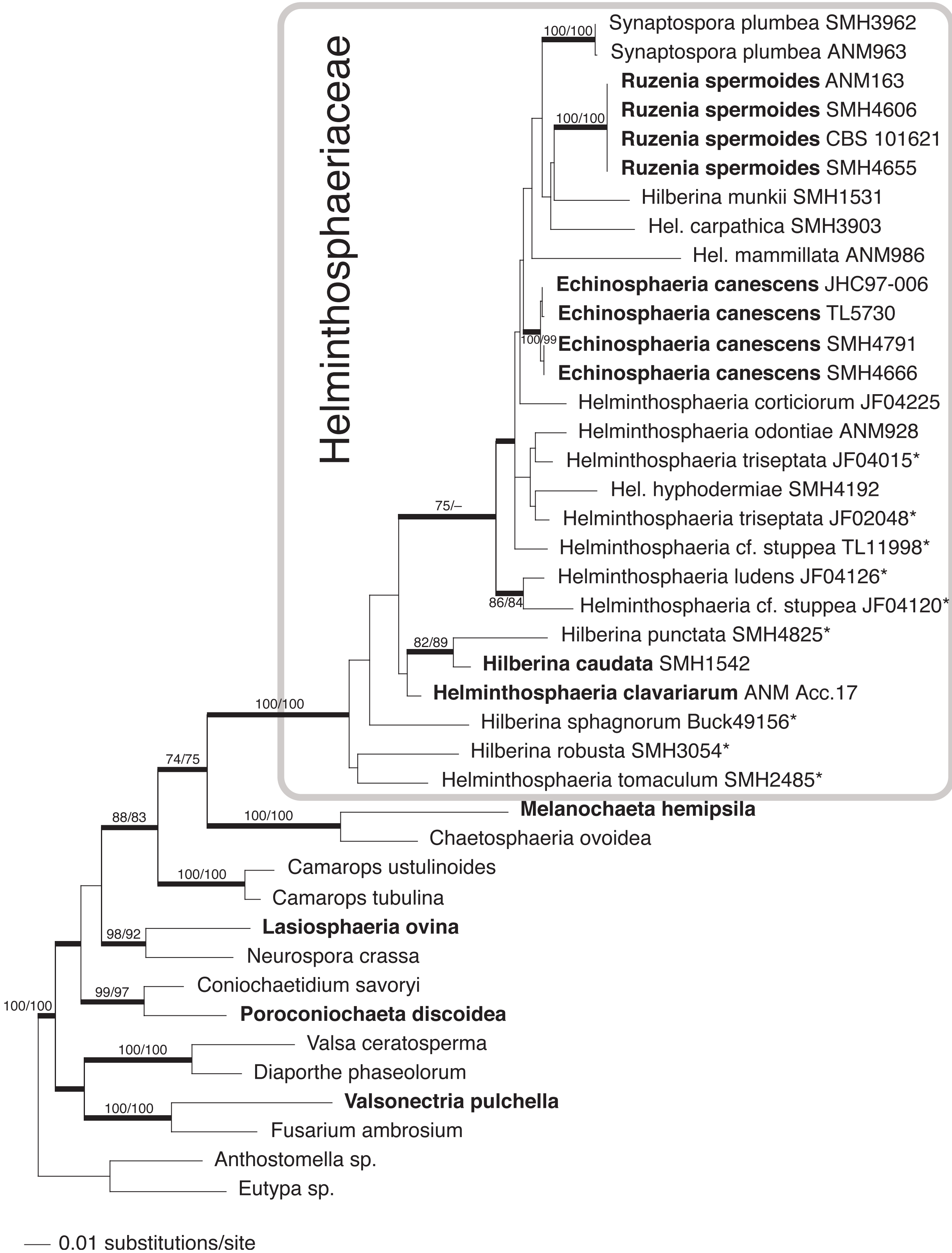


FIG. 1. Phylogeny of *Helminthosphaeriaceae*. The single most-likely tree generated from a PhyML analysis of combined LSU and β-tubulin sequence data for 41 taxa (L = 10212.28). Thickened branches indicate Bayesian posterior probabilities ≥ 95%, while numbers above or below branches refer to PhyML/RAxML bootstrap values ≥ 70%. Two species in the *Xylariales* are outgroups. Taxon names in boldface indicate type species and names with an asterisk indicate new taxa.

Réblová (FIG. 8), *Hilberina caudata* (FIG. 9), *H. munkii* (R. Hilber & O. Hilber) Declercq (FIG. 10), *Ruzenia spermoides* (FIG. 11) and *Synaptospora plumbea* (FIGS. 12, 13). The following taxonomic combinations are made based on molecular and morphological data or morphological data obtained from type specimens.

Echinosphaeria heterostoma (P. Karst.) Huhndorf & A.N. Mill., comb. nov. FIG. 14
MycoBank MB805973

≡ *Lasiosphaeria heterostoma* P. Karst., *Bidr. Känn. Finl. Nat. Folk* 23:162, 1873 (basionym).

Ascomata subglobose to ovoid, brown to dark brown, 375–500 μm diam, 450–550 μm high, superficial, with a smooth, densely setose surface, occurring densely clustered, on sparse, subicular hyphae. Setae ca. 150 μm long, straight, rigid, with acute apex, brown, similar color as ascoma but appearing shiny black in macroscopic view, thick-walled with a narrow lumen. Ascomatal apex composed of thick palisade of hyaline, blunt-ended setae, papillate, ostiole with periphyses. Ascomatal wall of textura globosa in surface view; in longitudinal section two-layered, cells of inner layer hyaline, flattened, outer layer composed of pale brown, globose to angular pseudoparenchymatic cells that give rise to setae. Centrum with numerous, narrow, paraphyses. Asci cylindrical, short stipitate, spore-bearing part 60–90 × 11–15 μm, with a narrow, shallow, refractive apical ring, with eight biseriately arranged ascospores. Ascospores cylindrical, curved or distinctly bent in the middle, both ends rounded, pale brown to brown, 1–5 septate, 34–38 × 4–5 μm.

Habitat: on dead wood.

Known distribution: Finland, known only from the type collection.

Specimen examined: FINLAND. Tavastia australis, Tammela, Mustiala, ad lign. Pin. 5-IX-1866, leg. et det. *P.A. Karsten, No. 4583* (HOLOTYPE H).

Echinosphaeria heterostoma resembles *E. canescens* in having abundant, rigid, pointy setae covering the entire ascomata and cylindrical, curved ascospores. It differs, however, in having a thick palisade of hyaline, blunt-ended setae covering the ascomatal apex and in having ascospores that are pale brown and become multiseptate.

Helminthosphaeria flavocompta (Berk. & M.A. Curtis) Huhndorf & A.N. Mill., comb. nov. FIG. 15
MycoBank MB805977

≡ *Sphaeria flavocompta* [as ''*flavido-compta*''] Berk. & M.A. Curtis, *Grevillea* 31:189, 1876 (basionym).

Ascomata ovoid, dark brown to black, ca. 160 μm diam, 250 μm high, erumpent to superficial, with a slightly warted, sparsely setose surface, occurring scattered or loosely clustered, on sparse, subicular hyphae. Setae at least 125 μm long, brown, paler than ascoma, thick-walled with a narrow, septate lumen, acute to rounded apex, wall surface roughened. Ascomatal apex papillate, ostiole with periphyses. Centrum with numerous, narrow, paraphyses. Asci probably cylindrical, short stipitate, spore-bearing part ca. 70 × 15 μm, with a narrow, shallow, refractive apical ring, with eight biseriately arranged ascospores. Ascospores ellipsoid, three-septate, pale brown, 15–17 × 6.5–7.5 μm.

Habitat: on dead wood.

Known distribution: United States (South Carolina), known only from the type collection.

Specimens examined: UNITED STATES. SOUTH CAROLINA: Society Hill, on *Cyrilla* wood, Oct 1855, *No. 5021* (ISOTYPE FH; HOLOTYPE K).

Helminthosphaeria flavocompta is one of four *Helminthosphaeria* species with three or more septate ascospores. Its ascospore sizes are in the range of *Hel. triseptata* from which it differs by having eight ascospores in a biseriate arrangement in the ascus and less abundant ascomatal setae. It differs from *Hel. mamillata* by having paler brown setae and slightly larger ascospores. *Helminthosphaeria ludens* has slightly larger ascospores than *Hel. flavocompta*.

Helminthosphaeria gibberosa (Munk) Huhndorf & A.N. Mill., comb. nov. FIG. 16
MycoBank MB 805978

≡ *Lasiosphaeria gibberosa* Munk, *Dansk Bot. Ark.* 17:115, 1957 (basionym).

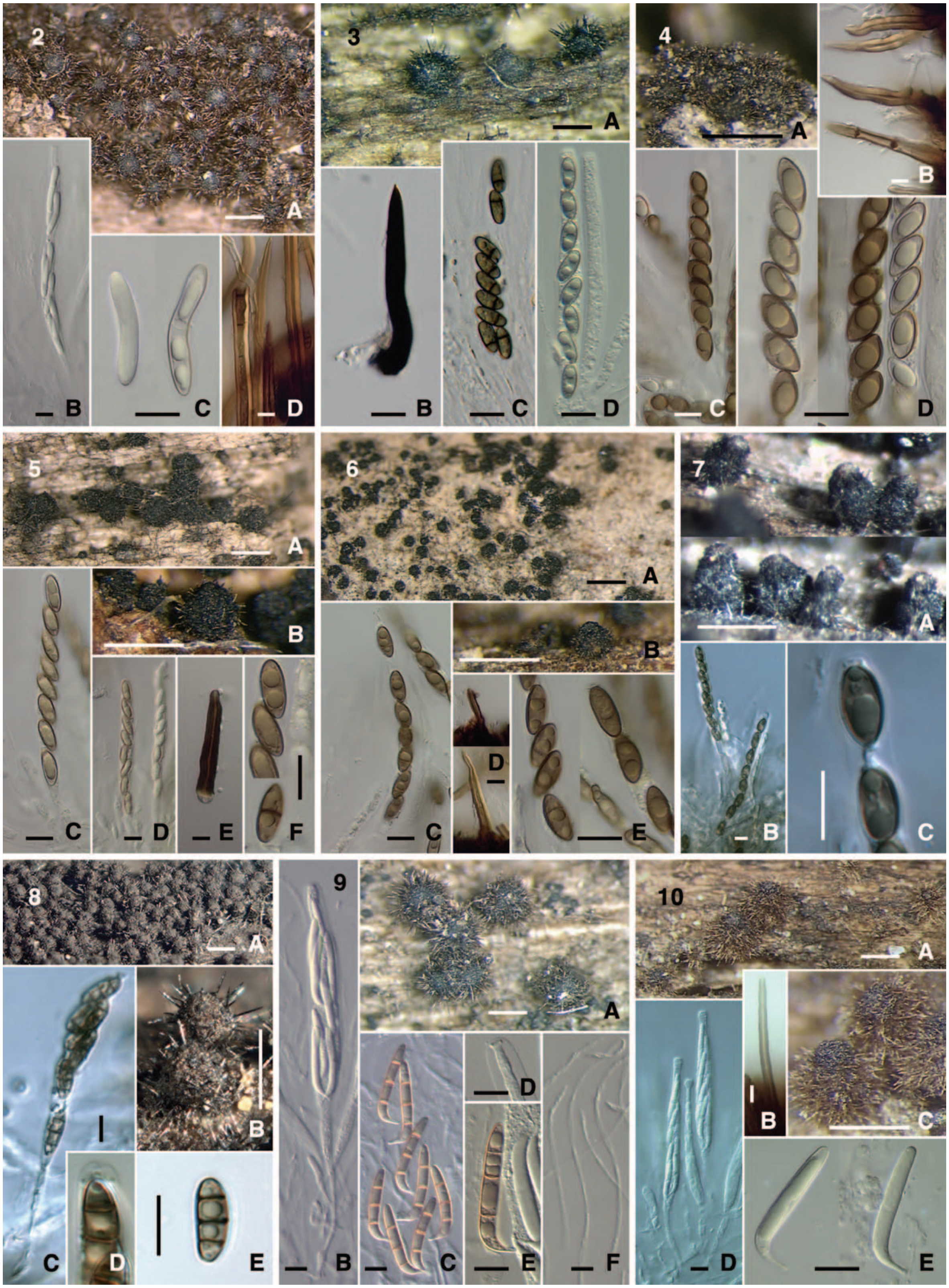
Ascomata subglobose to ovoid, dark brown to black, ca. 410 μm diam, 425 μm high, erumpent to superficial, with a strongly warted, glabrous surface, occurring scattered or loosely clustered on sparse, subicular hyphae. Ascomatal apex papillate, sulcate, ostiole with periphyses. Centrum with numerous, narrow, paraphyses. Asci cylindrical, short stipitate, 80–90 × 8–10 μm, with a narrow, shallow, refractive apical ring, with 4–8 uni- or biseriately arranged ascospores, often only four becoming mature. Ascospores ellipsoid, one-celled, brown, surface roughened, coarsely punctate, 12–16 × 6–7 μm.

Habitat: on dead wood.

Known distribution: Denmark, known only from the type collection.

Specimen examined: DENMARK. Jylland, Lysbro Skov, near Silkeborg, on rotten *Betula* wood, Sep 1953, *A. Munk* (HOLOTYPE C).

Helminthosphaeria gibberosa is distinguished by its ascomata with a roughened surface, lack of ascomatal setae and its pale brown ascospores with a roughened wall. Only *Hel. odontiae* occurring on resupinate basidiomycetes has similar ascomata but differs in



FIGS. 2–10. 2. *Echinosphaeria canescens (SMH4666)*. A. Ascomata. B. Ascus. C. Ascospores. D. Setae. 3. *Helminthosphaeria carpathica* (*SMH3903*). A. Ascomata. B. Seta. C, D. Asci and ascospores. 4. *Helminthosphaeria clavariarum* (*SMH4609*). A. Ascomata. B. Seta. C. Ascus. D. Ascospores. 5. *Helminthosphaeria corticiorum* (*JF04225*). A, B. Ascomata. C, D. Asci. E. Seta. F. Ascospores. 6. *Helminthosphaeria hyphodermiae* (*SMH4192*). A, B. Ascomata. C. Ascus. D. Seta. E. Ascospores. 7.

having a pale apex composed of densely packed, hyaline to pale setae and in having darker brown, smooth ascospores. In *Hel. gibberosa*, as in some other members of the genus, the asci have 4–8 ascospores, often with only four becoming mature.

Helminthosphaeria heterotricha (Munk) Huhndorf & A.N. Mill., comb. nov. FIG. 17

MycoBank MB805979

≡ *Lasiosphaeria heterotricha* Munk, *Friesia* 9:151, 1969 (basionym).

Ascomata subglobose to ovoid, dark brown to black, ca. 210–280 μm diam, 250–350 μm high, erumpent to superficial, with a slightly warted, sparsely setose surface, occurring scattered or loosely clustered on sparse, subicular hyphae. Setae 150+ μm long, brown, paler than ascoma, thick-walled with a narrow, septate lumen, apex acute. Ascomatal apex papillate, ostiole with periphyses. Centrum with numerous, narrow, paraphyses. Asci cylindrical, short stipitate, 65–80 × 7–8 μm, with a narrow, shallow, refractive apical ring, with 4–8 uni- or biseriately arranged ascospores, often only four becoming mature. Ascospores ellipsoid, one-celled, hyaline, 8–12 × 5–6 μm.

Habitat: on dead wood.

Known distribution: Denmark, known only from the type collection.

Specimen examined: DENMARK. Sjaelland, Oyrehaven, on rotten *Fagus* stump, 3-XII-1963 (HOLOTYPE C).

Helminthosphaeria heterotricha is one of eight wood inhabiting *Helminthosphaeria* species that differs from the others by having long, pale brown setae sparsely covering the ascomata and having ascospores that are hyaline and one-celled. As in some other members of the genus, the asci have 4–8 ascospores, often with only four becoming mature.

Helminthosphaeria ludens (Morgan) Huhndorf & A.N. Mill., comb. nov. FIGS. 18–20

MycoBank MB805980

≡ *Chaetosphaeria ludens* Morgan, *Journal of Mycology* 11:105, 1905 (basionym).

= *Lasiosphaeria coacta* Kirschst., *Krypt. Fl. Brandenb.* VII:234, 1911.

Ascomata ovoid, dark brown to black, ca. 250–325 μm diam, 250–300 μm high, erumpent to superficial, with a slightly warted, sparsely setose surface, occurring scattered or loosely clustered, on sparse, subicular hyphae. Setae 150+ μm long, brown, paler than ascoma, thick-walled with a narrow, septate lumen, apex acute to rounded. Ascomatal apex papillate, ostiole with periphyses. Ascomatal wall of textura globosa in surface view; in longitudinal section two-layered, cells of both layers composed of flattened to angular pseudoparenchymatic cells, inner layer hyaline, outer layer dark brown. Centrum with numerous, narrow, paraphyses. Asci cylindrical, short stipitate, 95–130 × 8–17 μm, with a narrow, shallow, refractive apical ring, with 4–8 uni- or biseriately arranged ascospores, often only four becoming mature. Ascospores ellipsoid, brown, 1–3(–4)-septate, often unevenly distributed, 17–26 × 7–9 μm.

Habitat: on dead wood of trees and woody stem of heather.

Known distribution: France, Germany, United States (Ohio).

Specimens examined: FRANCE. Aude, Camurac, Forêt de Niave, 1200 m, on rotten wood of *Abies alba*, 14-V-2004, *J. Fournier, JF04126* (F, ILLS). GERMANY. Lake Kleinbehnitz, on twigs of *Calluna vulgaris*, leg. *Kirschstein* (HOLOTYPE of *L. coacta*, B). UNITED STATES. OHIO: Preston, on *Acer* wood, 1897, *APM 210* (LECTOTYPE designated here, IA).

Helminthosphaeria ludens is found in USA and Europe. The type collection has ascomata with setae on the entire surface and asci with only four of the eight ascospores maturing and becoming brown and forming three more or less irregularly distributed septa. *Lasiosphaeria coacta* is a synonym of this species with setae seen mostly on the basal half of the ascomata in the type collection. While no asci were found in the type collection, *L. coacta* is described as having 4–8-spored asci and this is what is also found in collection JF04126 from France. In collection JF04126, the septa are late to form and the spores mostly remain hyaline and non-septate. In *Hel. ludens*, ascospore septation can be irregular as in the type collection and in the type of *L. coacta* or more regular as in collection JF04126. *Helminthosphaeria ludens* has larger ascospores than the other three multiseptate species.

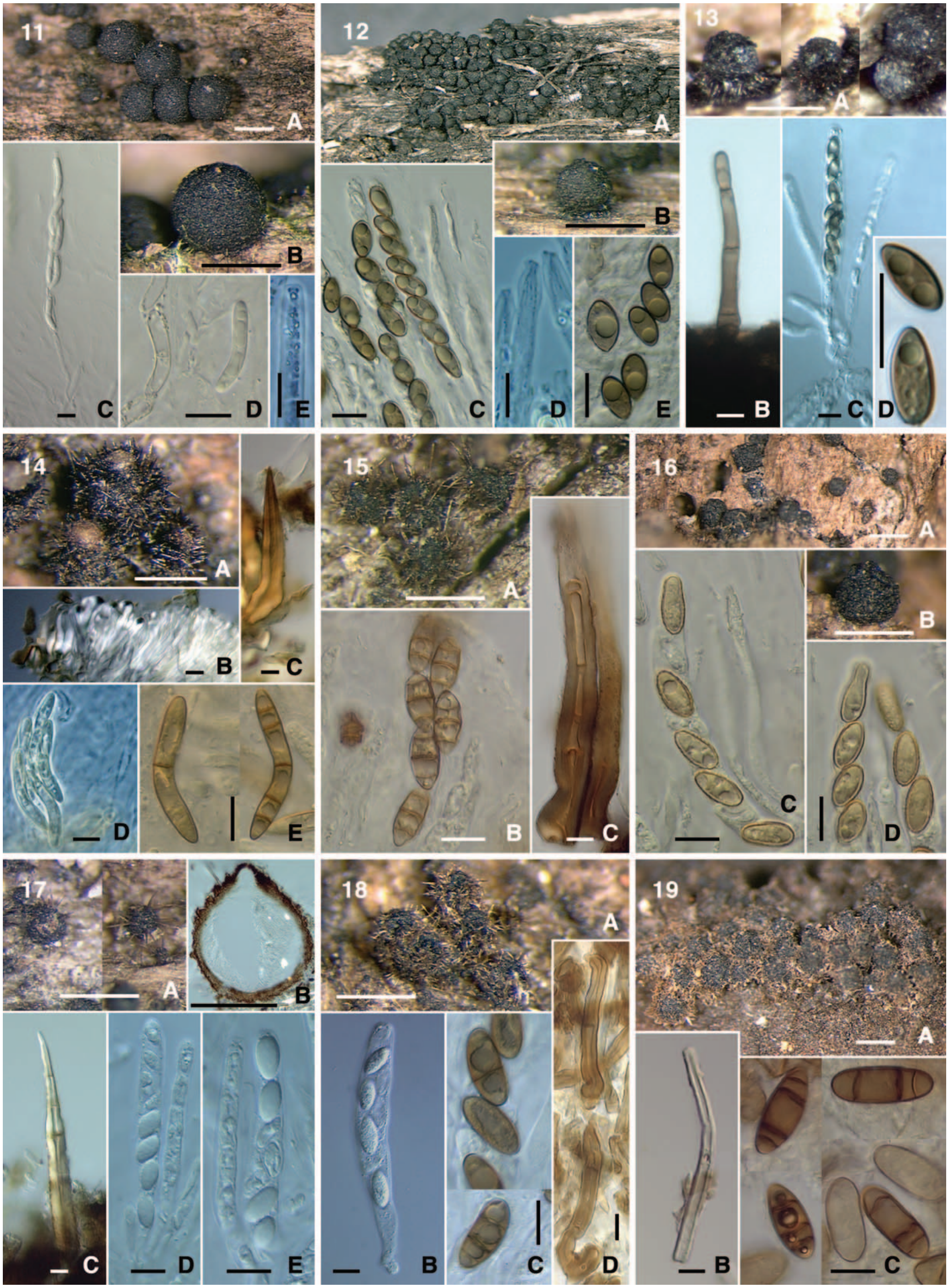
Helminthosphaeria stuppea (Ellis & Everh.) A.N. Mill., Huhndorf & J. Fourn., comb. nov. FIGS. 21–23

MycoBank MB805981

≡ *Lasiosphaeria stuppea* Ellis & Everh., *Bull. Wash. Coll. Lab. Nat. Hist.* 1:4, 1884 (basionym).

←

Helminthosphaeria odontiae (*ANM928*). A. Ascomata. B. Ascus. C. Ascospores. 8. *Helminthosphaeria mammillata* (*ANM986*). A, B. Ascomata. C. Ascus. D. Ascus apex. E. Ascospores. 9. *Hilberina caudata* (*SMH1542*). A. Ascomata. B. Ascus. C, E. Ascospores. D. Ascus apex. F. Paraphyses. 10. *Hilberina munkii* (*SMH1531*). A, C. Ascomata. B. Seta. D. Ascus. E. Ascospores. Ascomata = 500 μm; asci, ascal apices, ascospores, paraphyses, setae = 10 μm.



FIGS. 11–19. 11. *Ruzenia spermoides* (*SMH4606*). A, B. Ascomata. C. Ascus. D. Ascospores. E. Ascus apex. 12. *Synaptospora plumbea* (*SMH3962*). A, B. Ascomata. C. Ascus. D. Ascus apex. E. Ascospores. 13. *Synaptospora plumbea* (*ANM963*). A. Ascomata. B. Seta. C. Ascus. D. Ascospores. 14. *Echinosphaeria heterostoma* (HOLOTYPE, H). A. Ascomata. B. Ascomatal apex. C. Seta. D. Ascus. E. Ascospores. 15. *Helminthosphaeria flavo-compta* (HOLOTYPE, K). A. Ascomata. B. Ascus. C . Seta. 16.

Ascomata subglobose, brown to dark brown, ca. 520 μm diam, 520 μm high, superficial, with a smooth, densely setose surface, occurring scattered or loosely clustered on sparse, subicular hyphae. Setae 75+ μm long, brown, lighter than ascoma, thick-walled with a narrow lumen, septations not seen, apex acute to rounded. Ascomatal apex papillate, sulcate, ostiole with periphyses. Centrum with numerous, narrow, paraphyses. Asci cylindrical, short stipitate, 150–175 × 20–25 μm, with a wide, shallow, refractive apical ring, with eight biseriately arranged ascospores. Ascospores reniform to allantoid, slightly curved, hyaline, one-celled, 30–35 × 8–10 μm.

Habitat: on dead wood.

Known distribution: Denmark, France, United States (Colorado, Washington).

Specimens examined: DENMARK. Copenhagen, Valbyparken ved bsevdueforeningen, on herbaceous stems of *Rosa canina*, 2-VI-2005, *T. Læssøe, TL11998* (F, ILLS). FRANCE. Ariège, Riverenert, Col de la Crouzette, Foret de Soulan, ca. 1200 m, on rotten wood of *Abies alba*, 3-VI-2004, *J. Fournier, JF04120* (F, ILLS) (both specimens above from Denmark and France are putatively identified as this species). UNITED STATES. COLORADO: Arrow, on *Pinus* sp., 14 Jul 1905, *E. Bethel* (BPI-600271). WASHINGTON: Adams County, Mount Paddo, on dead wood of *Tsuga pattoniana*, Sep 1883, *W.N. Suksdorf 115* (HOLOTYPE NY); King County, North Bend, on dead wood, Aug 1892, *A.M. Parker 111* (NY).

Helminthosphaeria stuppea is a striking species with ascomata that have a thick covering of long flexuous hairs. There are three morphologically identical collections of this species from USA, one of which is in poor condition. It is found on decaying coniferous wood at higher elevation in western USA where it probably is common but easily overlooked. The European collections putatively identified as this species have smaller ascomata with fewer hairs and ascospores that are similar in shape but overall smaller. Fresh collections from USA should be sought to compare molecular data.

Helminthosphaeria tomaculum Huhndorf & A.N. Mill. sp. nov. FIG. 24
MycoBank MB805982

Etymology: tomaculum (L.) = kind of sausage, referring to the sausage-shaped, allantoid ascospores.

Ascomata subglobose to wide ovoid, dark brown to black, 400–530 μm diam, 375–475 μm high, superficial, with a warted, sparsely setose surface, occurring scattered or loosely clustered on sparse, subicular hyphae. Setae 150+ μm long, brown, similar to the ascoma, thick-walled with a narrow, septate lumen, apex acute to rounded. Ascomatal apex papillate, sulcate, ostiole with periphyses. Ascomatal wall of textura globosa in surface view; in longitudinal section two-layered, cells of both layers composed of flattened to angular pseudoparenchymatic cells, inner layer hyaline, outer layer dark brown. Centrum with numerous, narrow, paraphyses. Asci clavate to ventricose, short stipitate, 125–130 × 10–17 μm, with a narrow, shallow, refractive apical ring, with eight biseriately arranged ascospores. Ascospores curved cylindrical to allantoid, hyaline to pale brown, one-celled, 20–28 × 6–8.5 μm.

Habitat: on dead wood.

Known distribution: Costa Rica, known only from the type collection.

Specimen examined: COSTA RICA. San Jose, Perez Zeledon, Catie Experimental Forest, Villa Mills, 2850 m, [9.55, -83.6833], on 10 cm log, 15-V-1996, *S.M. Huhndorf, F..A. Fernández, SMH2485* (HOLOTYPE F).

Helminthosphaeria tomaculum is the second species in the genus to have allantoid to somewhat reniform ascospores. The temperate species, *Hel. stuppea*, differs in having ascomata covered in dense, paler setae and a prominent darker papillate apex. The warted ascomata of *Hel. tomaculum* resemble those of *Lasiosphaeris hirsuta* (Fr.) A.N. Mill. & Huhndorf, which differs in its long, cylindrical geniculate ascospores and thin-walled, darker brown ascomatal setae.

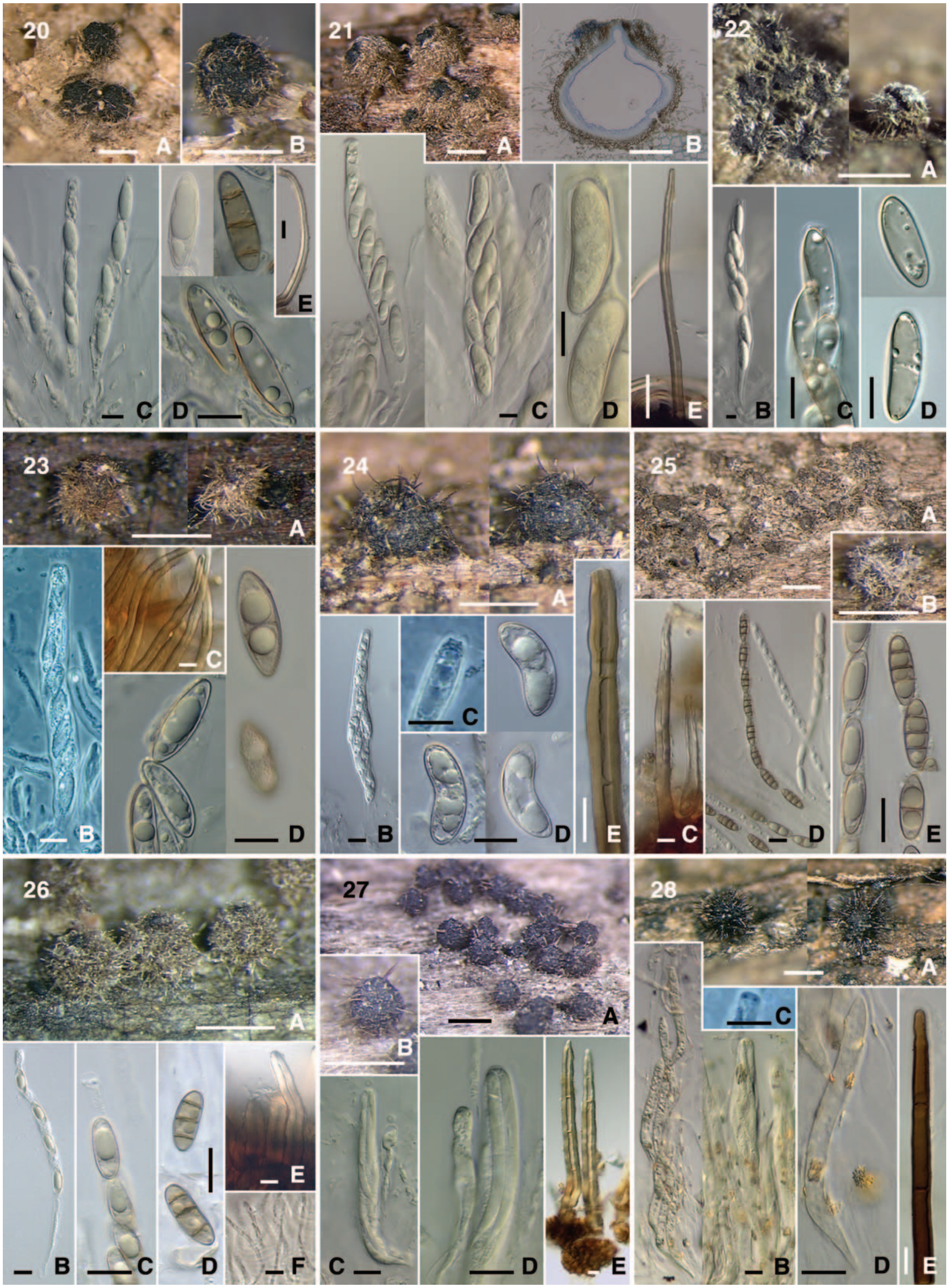
Helminthosphaeria triseptata A.N. Mill., Huhndorf & J. Fourn., sp. nov. FIGS. 25–26
MycoBank MB805983

Etymology: referring to the ascospore septation.

Ascomata subglobose to ovoid, brown to dark brown, 375–425 μm diam, 375–475 μm high, superficial, with a smooth, densely setose surface, occurring densely clustered on sparse, subicular hyphae. Setae 100+ μm long, brown, paler than ascoma, thick-walled with a narrow, septate lumen, apex acute to rounded.

←

Helminthosphaeria gibberosa (HOLOTYPE, C). A, B. Ascomata. C. Ascus. D. Ascospores. 17. *Helminthosphaeria heterotricha* (HOLOTYPE, C). A. Ascomata. B. Ascomatal section. C. Seta. D. Asci. E. Ascospores. 18. *Helminthosphaeria ludens* (HOLOTYPE, IA). A. Ascomata. B. Ascus. C. Ascospores. D. Setae. 19. *Helminthosphaeria ludens* (HOLOTYPE of *Lasiosphaeria coacta*, B). A. Ascomata. B. Seta. C. Ascospores. Ascomata = 500 μm; ascomatal section = 100 μm. Asci, ascal apices, ascospores, setae = 10 μm.



FIGS. 20–28. 20. *Helminthosphaeria ludens* (*JF04126*). A, B. Ascomata. C. Ascus. D. Ascospores. E. Seta. 21. *Helminthosphaeria stuppea* (HOLOTYPE, NY). A. Ascomata. B. Ascomatal section. C. Asci. D. Ascospores. E. Seta. 22. *Helminthosphaeria stuppea*-like (*JF04120*). A. Ascomata. B. Ascus. C. Ascus apex. D. Ascospores. 23. *Helminthosphaeria stuppea*-like (*TL11998*). A. Ascomata. B. Ascus. C. Seta. D. Ascospores. 24. *Helminthosphaeria tomaculum* (*SMH2485*). A. Ascomata. B. Ascus. C. Ascus apex. D. Ascospores.

Ascomatal apex papillate, ostiole with periphyses. Ascomatal wall of textura globosa in surface view; in longitudinal section two-layered, cells of both layers composed of flattened to angular pseudoparenchymatic cells, inner layer hyaline, outer layer dark brown. Centrum with numerous, narrow, paraphyses. Asci cylindrical, short stipitate, 100–170 × 6–7 μm, with a narrow, shallow, refractive apical ring, with 4–8 uniseriately arranged ascospores, often only four becoming mature. Ascospores ellipsoid, pale brown, 0–3-septate, 13–17 × 5–6.5 μm.

Habitat: on dead wood.

Known distribution: France.

Specimens examined: FRANCE. Ariège, Rimont, Las Muros, 470 m, on wood of *Robinia pseudoacacia*, 10-II-2004, *J. Fournier, JF04015, ILLS71110* (HOLOTYPE ILLS, ISOTYPE F); Ariège, Rimont, trail from Grillou to Sourroque, 500 m, on wood of *Corylus avellana*, 3-I-2002, *J. Fournier, JF02048* (F, ILLS).

The two collections of *Hel. triseptata* do not have identical LSU sequence data and differ slightly in morphology. Collection JF02048 often has four-spored asci and ascospores that are late to become septate, whereas collection JF04015 has eight-spored asci and the spores readily turn brown and become three-septate in the ascus. Additional collections may show that there is more than one species involved. In *Hel. triseptata*, the cylindrical ascus, uniseriate arrangement of the spores, spore size and pattern of septation differ from *Hel. ludens* and *Hel. flavocompta*.

Hilberina breviseta (P. Karst.) Huhndorf & A.N. Mill., comb. nov. FIG. 27

MycoBank MB805984

≡ *Lasiosphaeria breviseta* P. Karst., *Hedwigia* 23:57, 1884 (basionym).

Ascomata ovoid, brown to dark brown, 360–380 μm diam, 425–450 μm high, superficial, with a smooth, sparsely setose surface, occurring scattered to loosely clustered on sparse, subicular hyphae. Setae 175+ μm long, brown, paler than ascoma, thick-walled with a narrow, septate lumen, apex acute. Ascomatal apex papillate, indistinct. Asci cylindrical, spore-bearing part 75–85 × 8–11 μm, with a narrow, shallow, refractive apical ring, with eight biseriately arranged ascospores. Ascospores cylindrical, lower one-fourth curved in obtuse angle, basal end attenuate and acerose, hyaline to yellowish, septations not seen, (described as 3–5 septate in Hilber and Hilber 1983), 38–45 × 3–3.5 μm.

Habitat: on dead wood.

Known distribution: Finland, United States (North Carolina) (also reported from Austria, France and Germany by Hilber and Hilber 1983).

Specimens examined: FINLAND. Tavastia australis. Tammela, Mustiala, ad lign., 21-IX-1866, leg. et det. *P.A. Karsten No. 928* (LECTOTYPE H). UNITED STATES. NORTH CAROLINA: Swain County, Great Smoky Mountains National Park, Indian Gap, Appalachian Trail, 35°36′33.7″N, 83°26′48″W, 1615 m, 4-XI-2007, *A.N. Miller, S.M. Huhndorf, J.L. Crane, T.J. Atkinson, I. Promputtha, M. Grief, G.K. Mugambi, P. Chaudhary ANM1418* (ILLS).

The type collection from Finland consists of several wood fragments with a number of ascomata in fair condition. Hilber and Hilber (1983) recognize the species from several collections from Europe and report the ascospores as 4–6-celled. Ascospore septations were not seen in the type or North Carolina collections, but it is possible that they are present in the other reported collections not seen by us. We include it as an aseptate species in the following key to the Helminthosphaeriaceae. The species differs from other aseptate *Hilberina* species in ascospore length and setae length and morphology.

Hilberina elegans (Mouton) Huhndorf & A.N. Mill., comb. nov. FIG. 28

MycoBank MB805985

≡ *Lasiosphaeria elegans* Mouton, *Mém. Soc. Roy. Bot. Belgique* 26:184, 1887 (basionym).

Ascomata ovoid to obpyriform, dark brown to black, 600–625 μm diam, 725–750 μm high, superficial, with a smooth, densely setose surface, occurring scattered to loosely clustered on sparse, subicular hyphae. Setae 150+ μm long, dark brown, thin-walled, with a wide, septate lumen, apex rounded. Ascomatal apex papillate. Asci clavate to ventricose, spore-bearing part 120–175 × 17–19 μm, with thin refractive apical ring, with eight biseriately arranged ascospores. Ascospores cylindrical, lower one-fourth curved in obtuse angle, basal end attenuate and acerose, hyaline, one-celled, 65–70 × 4–5.5 μm.

←

E. Seta. 25. *Helminthosphaeria triseptata* (*JF04015*). A, B. Ascomata. C. Seta. D. Asci. E. Ascospores. 26. *Helminthosphaeria triseptata* (*JF02048*). A. Ascomata. B. Ascus. C. Ascus apex. D. Ascospores. E. Seta. F. Paraphyses. 27. *Hilberina breviseta* (HOLOTYPE, B). A, B. Ascomata. C. Ascus. D. Ascospores. E. Setae. 28. *Hilberina elegans* (HOLOTYPE, BR). A. Ascomata. B. Asci. C. Ascus apex with ring. D. Ascospores. E. Seta. Bars: Ascomata = 500 μm. Ascomatal section = 100 μm. Asci, ascal apices, ascospores, paraphyses, setae = 10 μm.

Habitat: on dead branches.

Known distribution: Belgium, known only from the type collection.

Specimen examined: BELGIUM. In ramulis *Ulicis*, coll. *V. Mouton, 96786.77* (LECTOTYPE designated here, BR).

Hilberina elegans differs from other aseptate species by its ascomatal setae and ascospore size. The dark brown, thin-walled setae are different from the pale brown, thick-walled setae of *H. breviseta* and most other *Hilberina* species. The ascospores are longer than those of *H. breviseta*.

Hilberina foliicola (O. Hilber & R. Hilber) Huhndorf & A.N. Mill., comb. nov.

MycoBank MB805986

≡ *Lasiosphaeria foliicola* O. Hilber & R. Hilber, in Hilber et al., *Mycotaxon* 30:281. 1987 (basionym). Holotype: United States. Virginia, Giles County, Cascades, near Little Stony Creek, on dead leaves of *Quercus* sp., 1-X-1985, leg. O. Hilber (BPI, n.v.).

Ascomata ovate, 300–400 μm diam × 600 μm high, solitary or in small groups, densely covered by hairs; ascomatal hairs long, flexuous, thin-walled (described as thick but appearing thinner in the illustration) and dark brown; ascospores cylindrical, basal end curved in obtuse angle, attenuate and acerose, hyaline, one-celled, 40–45 × 3.7–4.6 μm (described as having a sheath when young).

Habitat: on dead *Quercus* leaves.

Known distribution: UNITED STATES (Virginia), known only from the type collection.

Specimens examined: no collections were seen.

The description is adapted from Hilber et al. (1987a), and the species is included in the following key to Helminthosphaeriaceae. The species differs from others in the genus by the substratum of dead leaves and distinctive long, flexuous ascomatal hairs.

Hilberina meznaensis (R. Hilber) Huhndorf & A.N. Mill., comb. nov.

MycoBank MB805987

≡ *Lasiosphaeria meznaensis* R. Hilber, *Sydowia* 36:111, 1983 (basionym). Holotype: Tschechoslowakei: Nordböhmen, Ceskosaské, Svycarsko, Mesná bei Hrensko, auf *Alnus glutinosa*-Ast, 12.8.1971, leg. Podlahová, (PRM731570, n.v.).

Ascomata ovate to obpyriform, 450–550 μm diam × 650–800 μm high, densely setose, setae dark brown, septate, thin-walled, lumen not thickened; ascospores cylindrical, basal end curved in obtuse angle, at times curving s-like, attenuate and acerose, hyaline to pale brown, 5–9-septate, 62–90 × 4.5–6 μm.

Habitat: on dead wood and bark.

Known distribution: Czechoslovakia, Germany.

Specimens examined: no collections were seen.

The description is adapted from Hilber and Hilber (1983), and the species is included in the following key to Helminthosphaeriaceae. Hilber and Hilber (1983) suggested that the ascomata of this species could be confused with those of *Lasiosphaeris hispida* (Tode) Clem., both being densely covered with thin-walled, dark brown setae. The ascospores of course differ in the morphology of the basal end, with *L. hispida* having the curved, geniculate, rounded end found in typical *Lasiosphaeris* Clem. species. The species differs from other *Hilberina* species in its longer and more septate ascospores.

Hilberina moseri (O. Hilber) Huhndorf & A.N. Mill., comb. nov.

MycoBank MB805988

≡ *Lasiosphaeria moseri* O. Hilber, *Sydowia* 36:114, 1983 (basionym).

Ascomata ovate to obpyriform, 400–700 μm diam × 650–900 μm high, wall tuberculate, sparsely setose, setae pale brown, thick-walled with narrow lumen, septate; ascospores cylindrical, lower one-fourth bent geniculate in obtuse angle, basal end rounded, dark brown, 3–4-septate, 42–55 × 4–4.5 μm.

Habitat: on burned wood.

Known distribution: Germany, known only from the type collection.

Specimen examined: GERMANY, Bayern, Regensburg-Ost, NSG-Keilstein-West (MTB 6938), auf fast verwachsenem Brandplatz, an einem nahezu verkohlten Laubholzzweig, 21-IX-1981, *O. Hilber* (HOLOTYPE M).

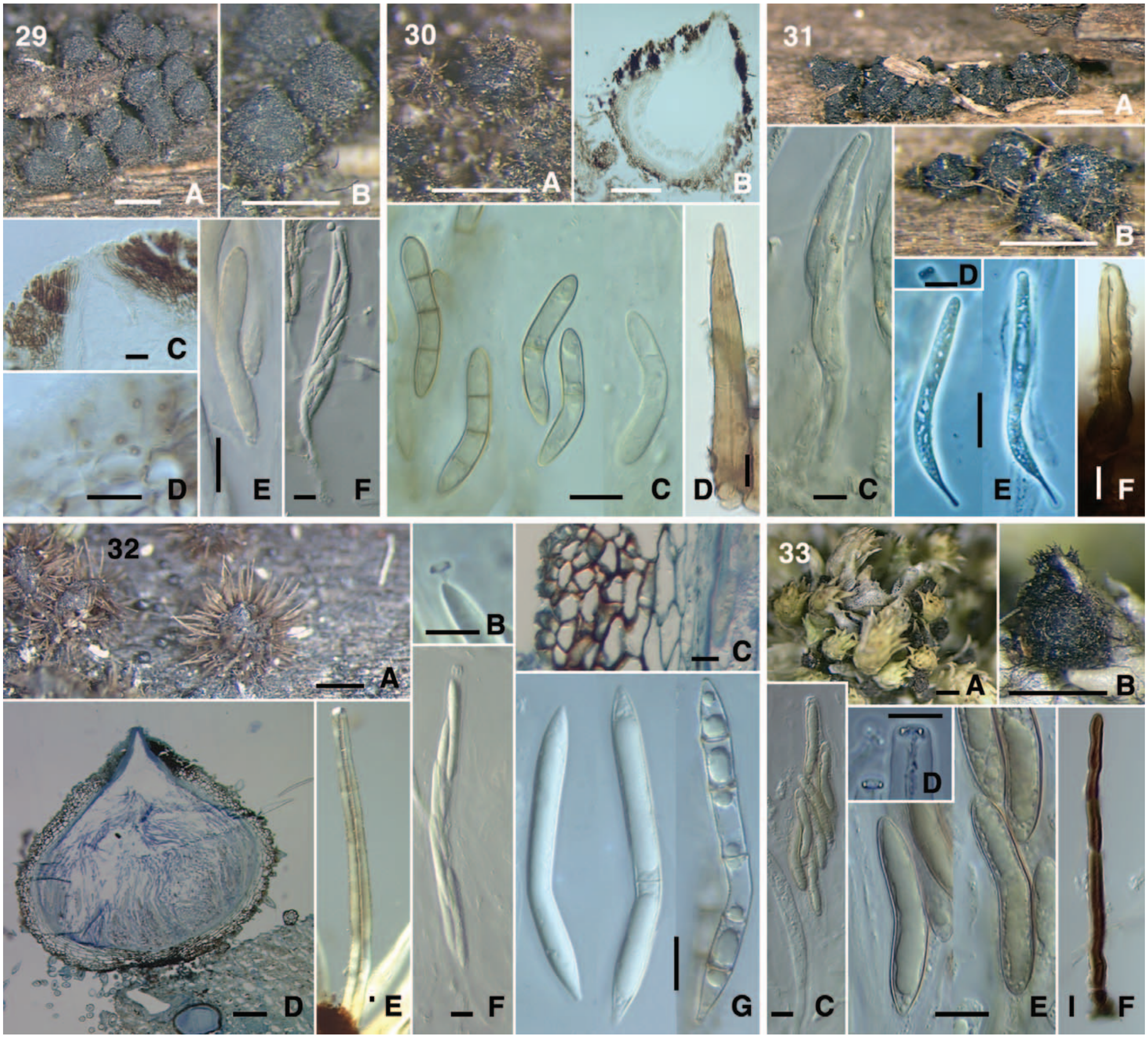
The description is adapted from Hilber and Hilber (1983), and the species is included in the following key to Helminthosphaeriaceae. The type collection was seen but was in marginal condition and not illustrated here; however it matches the illustration given in Hilber and Hilber (1983). The thick-walled ascomatal setae in this species match those found in many *Hilberina* species. The ascospores lack the attenuate basal tip but instead have a bent basal end with a rounded tip, similar to that of some *Lasiosphaeris* species, according to the illustration.

Hilberina punctata (Munk) A.N. Mill. & Huhndorf, comb. nov. FIGS. 29–30

MycoBank MB805989

≡ *Lasiosphaeria punctata* Munk, *Dansk Bot. Ark.* 17:114, 1957 (basionym).

Ascomata ovoid to obpyriform, not collapsing when dry, dark brown to black, 325–400 μm diam, 500–525 μm high, superficial, with a papulose, sparsely setose surface, occurring densely clustered on sparse or abundant, subicular hyphae. Setae 85+ μm long, brown, lighter than ascoma, thick-walled with a narrow lumen, apex acute. Ascomatal wall cells with Munk pores. Asci cylindrical to ventricose, short stipitate,



FIGS. 29–33. 29. *Hilberina punctata* (HOLOTYPE, C). A, B. Ascomata. C. Ascomatal neck. D. Ascomatal wall cells with Munk pores. E. Ascospore. F. Ascus. 30. *Hilberina punctata* (*SMH4825*). A. Ascomata. B. Ascomatal section. C. Ascospores. D. Seta. 31. *Hilberina rhynchospora* (HOLOTYPE BR). A, B. Ascomata. C. Ascus. D. Ascus apex with ring. E. Ascospores. F. Seta. 32. *Hilberina robusta* (*SMH3054*). A. Ascomata. B. Ascus apex with ring. C. Ascomatal wall section. D. Ascomatal section. E. Seta. F. Ascus. G. Ascospores. 33. *Hilberina sphagnorum* (*Buck49156*). A, B. Ascomata. C. Ascus. D. Ascus apex with ring. E. Ascospores. F. Seta. Bars: Ascomata = 500 μm; ascomatal sections = 100 μm. Ascomatal walls, neck, asci, ascal apices, ascospores, setae = 10 μm.

130–140 × 10–13 μm, with a narrow, shallow, refractive apical ring, with eight bi- or triseriately arranged ascospores. Ascospores cylindrical, curved or distinctly bent in the middle, both ends rounded, hyaline to pale brown; spores mostly one-celled but can become three-septate, wall roughened, 28–40 × 4–5.5 μm.

Habitat: on dead wood.

Known distribution: Denmark, France.

Specimens examined: DENMARK. Vallø Skorskov, on rotten *Fagus*, Sep 1953, *A. Munk* (HOLOTYPE C). FRANCE. Midi-Pyrénées, Ariège, Las Muros, Rimont, Ruisseau de Peyrau, 400 m, on 5 cm dead branch, 25-IX-2002, *A.N. Miller, J. Fournier, A.M. Stchigel, & M. Calduch, SMH4825* (F).

Hilberina punctata differs from other *Hilberina* species by its roughened ascospores that are rounded at both ends and curved or bent in the middle. The ascospores lack the pointed, attenuate basal tip common in other species. The sparsely setose ascomata occur on a sparse subiculum in the type species, but in recent collections the subiculum can be abundant.

Hilberina rhynchospora (Mouton) Huhndorf & A.N. Mill., comb. nov. FIG. 31

MycoBank MB805990

≡ *Lasiosphaeria rhynchospora* Mouton, *Mém. Soc. Roy. Bot. Belgique* 26:183, 1887 (basionym).

Ascomata ovoid, dark brown to black, 300–400 µm diam, 350–450 µm high, erumpent becoming superficial, with a smooth, sparsely setose surface, occurring densely clustered in small groups on sparse, subicular hyphae. Setae ca. 75 µm long, brown, paler than ascoma, thick-walled with a narrow, septate lumen, apex rounded. Ascomatal apex papillate, indistinct. Asci clavate to ventricose, spore-bearing part 80–100 × 10–13 µm, with thin refractive apical ring, with eight biseriately arranged ascospores. Ascospores cylindrical, lower one-fourth curved in obtuse angle, basal end attenuate and acerose, hyaline, one-celled, 40–47 × 3–4 µm.

Habitat: on dead wood.

Known distribution: Belgium, France, United States (North Carolina).

Specimens examined: BELGIUM. In ligno putrido, Beaufays, coll. *V. Mouton*, *96848.42* (LECTOTYPE designated here, BR). FRANCE. Limousin, Department of Haute-Vienne, Roussac, banks of La Crouze river, 46°4′47.86″N, 1°11′59.36″E, 300 m, 22-IV-2011, *A.N. Miller*, *S.M. Huhndorf*, *J. Fournier*, *A. Brissard ANM2388* (ILLS). UNITED STATES. NORTH CAROLINA: Macon County, Highlands Biological Station, Highlands, 21-VII-1997, *F.A. Fernández*, *SMH3314* (F).

This species is similar to *H. breviseta*, differing only by slightly longer ascospores and shorter setae. The ascospores are three-septate and 50–55 × 5 µm in Mouton 1887, but the notes on the type packet describe the ascospores as aseptate and 40 × 3 µm, which is in line with what we observed. In both species, the ascomata occur in small clusters and are sparsely setose. Recent collections of *H. rhynchospora* and *H. breviseta* were too sparse for successful DNA extraction so additional fresh collections are necessary to determine whether the two species are synonymous.

Hilberina robusta Huhndorf & A.N. Mill., sp. nov. FIG. 32

MycoBank MB805991

Etymology: referring to the large ascomata.

Ascomata wide ovoid to obpyriform, dark brown to black, 750–800 µm diam, 700–750 µm high, superficial, with a smooth, densely setose surface, occurring scattered or loosely clustered. Setae 400+ µm long, brown, lighter than ascoma, thick-walled with a narrow lumen, apex acute to rounded. Ascomatal apex papillate, slightly sulcate, ostiole with periphyses. Ascomatal wall of textura globosa in surface view; in longitudinal section three-layered, cells of inner layer hyaline, flattened, middle layer composed of pale brown, globose to angular pseudoparenchymatic cells, cells of outer layer smaller, globose. Centrum with numerous, narrow, paraphyses. Asci cylindrical, short stipitate, 170–220 × 12–17 µm, with a narrow, shallow, refractive, double apical ring, with eight biseriately arranged ascospores. Ascospores fusiform, lower one-third distinctly bent geniculate, both ends lanceolate, basal end with slight bulbous swelling, one-celled and hyaline for a long time, with age becoming five-septate and pale brown with prominent guttules and cell contents adhering to septa, 55–72 × 5–6.5 µm.

Habitat: on dead wood.

Known distribution: Brazil, Costa Rica, Ecuador, Panama, United States (Puerto Rico).

Specimens examined: BRAZIL. BAHIA: Santa Teresinha, Serra da Jibóia, on dead branches, 10 May 2013, *D.A.C. Almeida & A.N. Miller* (HUEFS 192206). COSTA RICA. ALAJUELA: Parque Nacional Volcan Arenal, La Fortuna de San Carlos, Pilón trail, 10.4419, -84.7167, 15-VII-2001, *S.M. Huhndorf*, *F.A. Fernández*, *A.N. Miller*, *M.P. DaRin*, *SMH4554* (F). ECUADOR. ORELLANA: Yasuni National Park, Garza trail, 5-III-2001, *F.A. Fernández*, *A.N. Miller*, *R. Briones*, *SMH4353* (F). PANAMA. Barro Colorado Island National Monument, Donato trail, 9°10′N, 79°50′W, 50–150 m, on 20 cm log, 16-IX-1997, *S.M. Huhndorf & F.A. Fernández*, *SMH3438*; Thomas Barbour trail, 9°10′N, 79°50′W, 50–150 m, on 25 cm log, 18-IX-1997, *S.M. Huhndorf & F.A. Fernández SMH3502* (F). UNITED STATES. PUERTO RICO: Luquillo Mountains, El Verde Research Station, 16-hectare grid, 18°19′27″N, 65°48′58″W, 388 m, on log of *Croton poecilanthus*, 10-VI-1995, *S.M. Huhndorf*, *SMH1453.1*; 18°19′41″N, 65°49′2″W, 342 m, on 25 cm log of *Casearia arborea*, 8-X-1995, *S.M. Huhndorf*, *SMH1799.1*; 18°19′39.7″N, 65°48′58.9″W, 362 m, on 15 cm wood fragment, 12-I-1997, *S.M. Huhndorf & F.A. Fernández*, *SMH2897* (F); 18°19′26.7″N, 65°49′0.3″W, 382 m, on 50 cm log, 20-I-1997, *S.M. Huhndorf & F.A. Fernández*, *SMH3054* (HOLOTYPE F).

Hilberina robusta has distinctive large ascomata with abundant, long, pale setae. It is recognized by sharply bent ascospores that are pointed at each end but not attenuate at the basal end. The ascospores turn pale brown and form septations and distinct guttulations and thickenings at the septa as they age. It is a common species on decaying wood in moist tropical forests and is readily identifiable.

Hilberina sphagnorum (P. Crouan & H. Crouan) A.N. Mill. & Huhndorf, comb. nov. FIG. 33

MycoBank MB805992

≡ *Sphaeria sphagnorum* P. Crouan & H. Crouan, *Florule Finistère* 24, 1867 (basionym). Type: France, Kergontes en Gouesnou, n.v.

Ascomata obpyriform, dark brown to black, 425–475 µm diam, 600–700 µm high, superficial, with a smooth, densely setose surface, occurring loosely clustered on sparse, subicular hyphae. Setae 150+ µm long, dark brown, same color as the ascoma, thick-walled with a narrow lumen, apex rounded. Ascomatal apex papillate. Asci clavate to ventricose, long stipitate, spore-bearing part 100–110 × 15–22 µm, with a narrow, shallow, refractive, double apical ring, with eight bi- or triseriately arranged ascospores. Ascospores cylindrical, curved or distinctly bent in the middle, both ends rounded, one-celled, pale brown, 33–40 × 6–8 µm.

Habitat: on leaves of *Sphagnum*.

Known distribution: France, United States (Vermont); probably widely distributed wherever the host grows.

Specimen examined: UNITED STATES. VERMONT: Orleans County, Craftsbury, Atlas Timberlands, S. of Eden Mountain Road, 44°39′53″N, 72°27′27″W, 425 m, on *Sphagnum*, 16-V-2005, *W.R. Buck 49156* (NY, F).

This species occurs on *Sphagnum* leaves and stems, which aids in distinguishing it from other species, and is probably relatively abundant although not commonly collected. The ascospores resemble those of *H. punctata* and also lack the attenuate, pointed basal end present in other species of *Hilberina*. The type collection was requested from the CR herbarium but was not located at that institution.

KEY TO THE ACCEPTED SPECIES IN THE HELMINTHOSPHAERIACEAE (EXPANDED AND REVISED FROM SAMUELS ET AL. 1997, HUHNDORF ET AL. 1999, RÉBLOVÁ 1999B, 2002)

1. Ascospores ellipsoid, short allantoid, or reniform . . . 2
1. Ascospores long allantoid, cylindrical, fusiform, lanceolate, or acerose, often bent or curved 20
   2. Ascospores short allantoid or reniform 3
   2. Ascospores ellipsoid 4
3. Ascospores reniform, hyaline to pale brown, (25)30–35 µm long, ascomatal hairs sparse or abundant, pale . . . . *Helminthosphaeria stuppea* (the two sequenced collections differ in their smaller, less setose ascomata and smaller ascospores)
3. Ascospores short allantoid, hyaline, 20–28 µm long, ascomatal setae sparse, blunt-ended. . . . . *Helminthosphaeria tomaculum*
   4. Substrate a member of the Basidiomycota . . 5
   4. Substrate other (most often wood) 8
5. Substrate a member of the Clavariaceae. . . . . *Helminthosphaeria clavariarum*
5. Substrate a resupinate basidiomycete 6
   6. Ascospores longer than 12 µm, often becoming 2–3-septate . . . . . *Helminthosphaeria corticiorum*
   6. Ascospores averaging shorter than 12 µm, remaining aseptate or becoming apiosporous. 7
7. Ascospores 0(–1–2)-septate, septum eccentric when single, 8–10 × 4–6 µm. . . . . *Helminthosphaeria odontiae*
7. Ascospores one-celled, 9–12 × 4.2–5.5 µm. . . . . *Helminthosphaeria hyphodermiae*
   8. Ascospores remaining one-celled 9
   8. Ascospores becoming one or more septate . . . 13
9. Ascospores in the ascus sticking or fusing together in groups of two to five 10
9. Ascospores not fusing together 11
   10. Ascomata setose, with circular basal stroma in the substrate, ascospores 7.5–9 × 5–6 µm . . . . *Synaptospora setosa* Huhndorf, F.A. Fern. & Cand. (see Huhndorf et al. 1999)
   10. Ascomata roughened, not setose, with or without basal mycelium, ascospores 6–11 × 5–6 µm . . . *Synaptospora petrakii* Cain (see Cain 1957)
11. Ascomata setose, asci 4–8-spored, ascospores remaining hyaline, 8–12 × 5–6 µm. . . . . *Helminthosphaeria heterotricha*
11. Ascomata roughened, not setose, with or without basal mycelium 12
   12. Ascomata shiny black to metallic gray, with circular basal stroma in the substrate, ascospores brown, 8–11 × 4.5–5.5 µm . . . . *Synaptospora plumbea* (see Huhndorf et al. 1999)
   12. Ascomata strongly roughened, dark brown to black, lacking a basal stroma, ascospores pale brown, 12–16 × 6–7 µm, surface coarsely punctate . . . . *Helminthosphaeria gibberosa*
13. Ascospores developing one septum 14
13. Ascospores developing 1–3 septa 17
   14. Septum eccentric in the lower third (apiosporous), ascospores 11.5–12.5 × 5–6 µm. . . . . *Helminthosphaeria carpathica* (see Réblová 1999b)
   14. Septum median 15
15. Ascospores becoming fused obliquely in pairs, 5–6 × 3.5–4.5 µm . . . . *Synaptospora olandica* Réblová (see Réblová 2002)
15. Ascospores not fusing 16
   16. Ascomatal setae stiff, spine-like and dark brown, ascospores 9.5–12.5 × 5–5.5 µm . . . . *Helminthosphaeria pilifera* Réblová (see Réblová 1999b)
   16. Ascomatal setae curly, blunt-ended and hyaline to pale brown, ascospores 10–12 × 5–6 µm. . . . . . . *Echinosphaeria cincinnata* A.E. Bell (see Bell 2010)
17. Asci 4(–8)-spored, ascospores pale brown, aseptate for a long time, eventually becoming 1–3-septate, 17–26 × 7–9 µm . . . . . *Helminthosphaeria ludens* (*L. coacta* is a synonym whose type specimen forms more than three septa that are unevenly placed)
17. Asci eight-spored, ascospores < 17 µm long 18
   18. Ascomatal setae stiff, spine-like, aseptate and dark brown, ascomata on basal subiculum, ascospores ellipsoid, 13.5–15.5 × 5–6 µm, 1–3-septate . . . . *Helminthosphaeria mammillata* (see Réblová 1999b)
   18. Ascomatal setae thick-walled, septate, pale brown to brown 19

19. Asci eight-spored, clavate, ascospores brown, three-septate, 15–17 × 6.5–7.5 μm. . . . . *Helminthosphaeria flavocompta*
19. Asci (4–)8-spored, cylindrical, ascospores pale brown, three-septate, 13–17 × 5–6.5 μm . . . . . *Helminthosphaeria triseptata* (a second collection of this species has asci that form only four mature spores)
    20. Ascospores cylindrical, often bent or curved, or long allantoid 21
    20. Ascospores often distinctly bent or curved in the basal one-forth portion, basal end often attenuate, bluntly or sharply pointed, lanceolate or acerose 26
21. Ascomata lacking setae . . . . *Ruzenia spermoides* (see Miller and Huhndorf 2004a)
21. Ascomatal setae thick-walled, septate, dark brown to pale brown, blunt-ended or pointed 22
    22. Ascomatal setae with ends pointed, brown to pale brown, sparse or abundant 23
    22. Ascomatal setae blunt-ended, straight or curly, dark or pale brown 25
23. Ascomatal setae sparse, flexuous with ends pointy, subiculum sometimes present . . *Hilberina punctata*
23. Ascomatal setae abundant, covering entire ascomata in stiff, pointy, pale brown spines 24
    24. Ascospores hyaline to pale brown, aseptate or becoming one-septate . . . . *Echinosphaeria canescens* (see Miller and Huhndorf 2004a) (the species as accepted here has both long and short ascospores, however, the synonymy of *E. strigosa* (Alb. & Schwein.) Declercq is currently under investigation)
    24. Ascospores brown, becoming five-septate. . . . . *Echinosphaeria heterostoma*
25. Ascomatal setae orange brown to pale brown, forming a thick curly entanglement on the ascoma, ascospores long allantoid, one-septate, found on dead wood . . . . *Echinosphaeria medusa* A.E. Bell & Mahoney (see Bell and Mahoney 2008)
25. Ascomatal setae dark brown, flexuous, ascospores cylindrical, slightly curved, aseptate, found on bryophyte hosts . . . . *Hilberina sphagnorum*
    26. Ascospores fusiform, lower one-third distinctly bent geniculate, with both ends pointed . . . . *Hilberina robusta*
    26. Ascospores cylindrical, lower one-forth curved in obtuse, right or acute angle, with only basal end pointed 27
27. Substrate leaves or grass culms 28
27. Substrate dead wood or bark 29
    28. Ascomata found on dead leaves, ascospores hyaline, aseptate . . . . *Hilberina foliicola*
    28. Ascomata found on dead grass culms, ascospores hyaline to pale brown, three-septate . . . . *Hilberina dactylina* (J. Webster) Declercq (see Hilber et al. 1987b and Declercq 2009)
29. Ascomatal hairs or setae dark brown 30
29. Ascomatal setae pale or reddish brown 31
    30. Ascospores hyaline, aseptate . . . . *Hilberina elegans*
    30. Ascospores hyaline to brown, 5–7-septate . . . . *Hilberina meznaensis*
31. Ascospores with basal end often sharply curved in right to acute angle 32
31. Ascospores with basal end curved or bent in obtuse angle 33
    32. Ascospores hyaline, aseptate, with basal end attenuate and acerose with a small, knob-like, enlarged tip . . . . *Hilberina munkii* (see Hilber et al. 1987a)
    32. Ascospores brown, three-septate, with basal end attenuate and bluntly pointed or acerose . . . . *Hilberina caudata*
33. Ascomata rust brown, densely setose . . . . *Hilberina rufa* (Cand., J. Fourn. & Magni) Declercq (see Candoussau et al. 2001)
33. Ascomata dark brown or black in color, sparsely setose 34
    34. Ascospores brown, 3–4-septate, with basal end slightly attenuate and bluntly pointed . . . . *Hilberina moseri*
    34. Ascospores hyaline, aseptate, with basal end attenuate and acerose 35
35. Ascospores 38–45 × 3–3.5 μm . . . . *Hilberina breviseta*
35. Ascospores 40–47 × 3–4 μm . . . . *Hilberina rhynchospora*

DISCUSSION

All five species previously residing in *Lasiosphaeria* along with the three newly described species occur in the well supported Helminthosphaeriaceae (FIG. 1), however *L. coacta* is recognized as being synonymous with *Hel. ludens*. Because most of the species in this family are uncommon and rarely collected, all Helminthosphaeriaceae species in the tree are illustrated here, many for the first time (FIGS. 2–33). When the family was established for species of *Helminthosphaeria*, only taxa with ellipsoid, brown ascospores were included (Samuels et al. 1997). Réblová (1999a) suggested that the three-septate-spored *Tengiomyces* Réblová might be a member of the group, but no recent specimens are available for obtaining molecular sequence data. Taxa with other ascospore types (*Echinosphaeria* A.N. Mill. & Huhndorf and *Ruzenia* O. Hilber) were added to the family based on LSU data (Miller and Huhndorf 2004a). This study confirms the placement of these two genera and adds *Hilberina* and *Synaptospora* to the family. *Helminthosphaeria* species initially were thought to be primarily fungicolous (Samuels et al. 1997), but species occurring on dead wood were added (Réblová 1999b) and wood is the primary substrate for *Echinosphaeria*, *Ruzenia* and *Synaptospora* species. Wood, leaves, grass culms and bryophytes are the known substrates for species of *Hilberina*.

Genera.—*Echinosphaeria* now contains seven named species with one, *E. strigosa*, considered by us to be a synonym but with further investigations underway. *Echinosphaeria macrospora* Puja, Bhat & K.D. Hyde and *E. pteridis* S. Dharg. & Bhat lack the ascomatal characteristics unique to the genus and should be considered as belonging elsewhere. The cultures obtained of both of these species (Puja et al. 2006, Dhargalkar and Bhat 2009) should be used to generate molecular sequence data to determine their proper phylogenetic placement. *Echinosphaeria cincinnata* and *E. medusa* both possess a distinctive pale, curly entanglement of setae on the ascomata (Bell and Mahoney 2008, Bell 2010) by which they differ from *E. canescens* and *E. heterostoma*. *Echinosphaeria cincinnata* further differs from the other three by possessing ellipsoid ascospores and possibly belongs in *Helminthosphaeria*. *Echinosphaeria heterostoma* differs from *E. canescens* by possessing multiseptate ascospores and an apex composed of a thick palisade of hyaline and blunt-ended setae (FIG. 14B). The type species of the genus, *Echinosphaeria canescens*, remains the only species represented by sequence data, and by virtue of the inclusion of multiple representative specimens it is also one of only a few strongly supported clades in the family (FIG. 1).

Helminthosphaeria contains 14 species, with only four (*Hel. flavocompta*, *Hel. gibberosa*, *Hel. heterotricha*, *Hel. pilifera*) missing from the phylogenetic analyses. As suggested by Munk (1957), *Helminthosphaeria* is a better place for *L. coacta* (= *Hel. ludens*) because of the similar ascomatal hairs and ascospores. The identifications of several specimens of *Hel. stuppea* are given as somewhat tentative due to differences between our collections and the published data. The genus is polyphyletic with taxa scattered throughout the Helminthosphaeriaceae, and species boundaries are unresolved for two taxa (*Hel. triseptata*, *Hel. stuppea*) (FIG. 1). Sampling additional genes and specimens may increase branch support and help clarify generic and specific boundaries within *Helminthosphaeria*.

Hilberina contains 13 species, nine of which are transferred to the genus herein based primarily on ascospore characteristics. Five species, including the type (*H. caudata*), were included in the phylogenetic analyses. After DNA extraction directly from ascomata of *H. caudata* and subsequent sequencing, two sequences identified as *H. caudata* (Miller and Huhndorf 2004a), which were derived from cultures, were determined to be contaminates. These sequences (AY436405 and AY436406) have been removed from GenBank. Although the genus is currently polyphyletic, all species in this genus possess ascomata with thick-walled setae (except *H. elegans*) and most species possess ascospores that are distinctly bent or curved in the basal portion with the basal end often attenuate, bluntly or sharply pointed, lanceolate or acerose.

Ruzenia is a monotypic genus with *R. spermoides* as its type species. Three collections from Europe (Czech Republic, Denmark, Spain) and one collection from USA (Tennessee) formed a strongly supported clade in the molecular analyses (FIG. 1). While common throughout western Europe, this species is rare in USA. It is distinguished by large, globose ascomata that lack setae and occur in large clusters. The elongate, curved ascospores resemble those of *E. canescens* or *H. punctata*.

Synaptospora contains four species, one of which (*S. plumbea*) was included in the phylogenetic analyses. Species of *Synaptospora* can have either setose (*S. olandica*, *S. setosa*) or glabrous ascomata (*S. petrakii*, *S. plumbea*) and a basal stroma may be present or lacking. The most distinctive feature in the group is the tendency of ascospores to stick together in groups of 2–6 within the ascus, prominent in all the species except *S. plumbea*.

Characters.—Helminthosphaeriaceae is expanded to contain taxa possessing a variety of ascospore shapes. Brown, ellipsoid ascospores are found in *Synaptospora* species, and ascospores that are brown or hyaline occur in *Helminthosphaeria* species. Many species have one-celled ascospores, but several have one or more septations (e.g. *Hel. ludens* FIGS. 18, 19, *Hel. triseptata* FIGS. 25, 26). In *Helminthosphaeria*, variation occurs in the number of ascospores that mature in an ascus. In several species (e.g. *Hel. gibberosa*, *Hel. heterotricha*, *Hel. ludens*, *Hel. triseptata*) only 4–6 ascospores fully develop, a characteristic that can be useful for species identification. In several *Synaptospora* species, ascospores within the ascus tend to stick together in groups (Cain 1957, Huhndorf et al. 1999, Réblová 2002). Ascospores that are cylindrical and curved, either hyaline or pale brown, are seen in species of *Echinosphaeria*, *Hilberina* and *Ruzenia*. Ascospores that are curved in the basal portion with an attenuate, pointy basal end are seen in species of *Hilberina*.

Although subfamilial relationships are unclear, most taxa share a unique morphological character in possessing thick-walled ascomatal setae (e.g. FIGS. 2, 10, 15, 18). Notable exceptions are *Hel. gibberosa*, *R. spermoides* and *S. plumbea*, all lacking any ascomatal vestiture, and *H. elegans*, which has thin-walled setae. The setae most distinguishable are those that are paler than the ascomata and in which the lumen is narrow and sometimes separated by septa (these septations are referred to as ''trabeculae'' by Bell and Mahoney 2008 and Bell 2010, but this term is not used here). Pale setae are prominent in many species in the family and can vary in shape (e.g. straight in *Hel. heterotricha*, curly in *E. cincinnata*), length (e.g. long in *H. robusta*, short in *E. heterostoma*) and shape of the end or apex (e.g. pointed in *Hel. clavariarum* and *Hel. heterotricha*, rounded in *H. rhynchospora*). Dark brown setae that are somewhat thinner-walled also are present in a number of species in the family (e.g. *Hel. carpathica*, *H. elegans*). One unique character is an ascomatal apex composed of a thick palisade of hyaline, blunt-ended setae (*E. heterostoma*, FIG. 14).

The taxa in this family have ascomata that are erumpent or superficial on the substrate. Subicular hyphae may be prominent (some collections of *H. punctata*, not illustrated), present and darkening the substrate (*Synaptospora*, FIG. 12) or visibly absent (*Hel. gibberosa*, FIG. 16). In most taxa however, the subiculum is present to some degree but not extensive. The asci can be cylindrical or clavate with some measure of a stipe. An apical ring is often present but the variability does not appear to be phylogenetically informative and offers no help for identification purposes.

Anamorphs.—In general, members of the Helminthosphaeriaceae do not grow in culture so the study of anamorphs in this group is not extensive. Similar anamorphs and synanamorphs have been reported in some species in the Helminthosphaeriaceae. A *Diplococcium* Grove anamorph is believed to be associated with five of the 14 species of *Helminthosphaeria* (i.e. *Hel. clavariarum*, *Hel. corticiorum*, *Hel. mammillata*, *Hel. odontiae*, *Hel. pilifera*) (Samuels et al. 1997, Réblová 1999b). *Echinosphaeria canescens* and *H. punctata* are reported to be associated with *Endophragmiella* B. Sutton and *Selenosporella*-like synanamorphs (Hughes 1979, Sivanesan 1983). We observed in this study a *Selenosporella*-like anamorph in several cultures of *R. spermoides*, confirming an illustration by Gams (1973, FIG. 6) of what appears to be a *Selenosporella*-like anamorph germinating from ascospores of this species. A species of *Diplococcium*, *D. hughesii* C.J.K. Wang & B. Sutton, was described with a *Selenosporella* G. Arnaud ex MacGarvie synanamorph (Wang and Sutton 1998), but is presently the only known species of *Diplococcium* to possess such a synanamorph. A *Dactylaria*-like anamorph was reported associated with *Synaptospora olandica* (Réblová 2002). Based on the current phylogenetic tree, anamorphs are not phylogenetically informative for predicting taxonomic relationships within this group but may be informative at the familial level. Further study on the anamorphs and synanmorphs and their connections within the Helminthosphaeriaceae is needed.

Molecular issues.—The Helminthosphaeriaceae demonstrates the difficulty of having to rely on molecular data for taxon placement. Many taxa in the family are uncommon and grow in small clusters or scattered individually over a wide surface of the substrate, making them difficult to find. When they are found, the collection usually consists of only a few ascomata (typically $<$ 15), sometimes in poor condition. Because these fungi do not germinate in culture[2] (with the exception of *R. spermoides*), extraction of DNA must be done from ascomata and, in general, 20–30 ascomata typically are required to obtain sufficient quantities of DNA for successful PCR amplification of multicopy nuclear ribosomal genes (Miller pers data). Without the ability to easily collect molecular data, a morphological-based concept of genera is expedient in this family.

One of the biggest problems with the application of molecular data to taxonomic questions at the genus level is the tendency for morphologically based genera to be recognized as polyphyletic or paraphyletic. With this comes the uncertainty in identification of novel taxa as belonging to a particular clade without the use of molecular data. In the Helminthosphaeriaceae the use of the LSU and β-tubulin gene markers provides good resolution at a level higher than the genus, in this case the family. However, with this dataset the morphologically recognizable genera fragment into taxa on single branches or small subgroups within the family clade. This has been seen before in related groups such as Boliniales, Chaetosphaeriales and Sordariales where in each case the morphological-based generic concepts fragment and what remains is a scattering of generic taxa throughout the higher-level clade.

We hoped the independent molecular dataset would result in a robust phylogenetic tree that would provide a morphological framework for predicting the generic placement of taxa in the Helminthosphaeriaceae that did not or would not sequence. This unfortunately was not the result, and thus we must be satisfied for the time being to accept paraphyletic genera. However, recognizing paraphyletic, morphologically based genera is the most efficient means for expediting the description of novel and poorly known species without creating numerous new taxa with unresolved and unsupported relationships.

[2] A culture of *E. cincinnata* reported in Bell (2010) did not come from germinating ascospores, but rather centrum material and turned out to be a contaminate (*Trichosporon* sp., Miller pers data).

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