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Molecular systematics of the Sordariales: the order and the family Lasiosphaeriaceae redefined

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Abstract: The Sordariales is a taxonomically diverse group that has contained from seven to 14 families in recent years. The largest family is the Lasiosphaeriaceae, which has contained between 33 and 53 genera, depending on the chosen classification. To determine the affinities and taxonomic placement of the Lasiosphaeriaceae and other families in the Sordariales, taxa representing every family in the Sordariales and most of the genera in the Lasiosphaeriaceae were targeted for phylogenetic analysis using partial sequences of the large-subunit (LSU) nrDNA. Based on molecular data, only genera within the families Chaetomiaceae, Lasiosphaeriaceae and Sordariaceae are retained within the redefined Sordariales. The order is a coherent group with morphologies that vary along well-defined lines, including large ascomata with large-celled membraneous or coriaceous walls and ascospores that show variation on a distinctive developmental theme, often with appendages or sheaths. The paraphyletic chaetomiaceous complex and the strongly supported Sordariaceae are nested among taxa traditionally placed in the Lasiosphaeriaceae. Analyses also indicate that 11 genera belong in the paraphyletic lasiosphaeriaceous complex. These taxa share a similar developmental pattern in their ascospore morphology that extends to the Sordariales as a whole. Based on these similarities in morphology, 13 additional genera are retained within the lasiosphaeriaceous complex and more than 35 genera have relationships in the order overall. Based on LSU data, 17 genera that have been assigned to the Lasiosphaeriaceae sensu lato are transferred to other families outside the Sordariales and 22 additional genera with differing morphologies subsequently are transferred out of the order. Two new orders, Coniochaetales and Chaetosphaeriales, are recognized for the families Coniochaetaceae and Chaetosphaeriaceae respectively. The Boliniaceae is accepted in the Boliniales, and the Nitschkiaceae is accepted in the Coronophorales. Annulatascaceae and Cephalothecaceae are placed in Sordariomycetidae inc. sed., and Batistiaceae is placed in the Euascomycetes inc. sed.

Key words: Annulatascaceae, Batistiaceae, Boliniaceae, Catabotrydaceae, Cephalothecaceae, Ceratostomataceae, Chaetomiaceae, Coniochaetaceae, Helminthosphaeriaceae, LSU nrDNA, Nitschkiaceae, Sordariaceae

INTRODUCTION

The Sordariales is one of the most taxonomically diverse groups within the Class Sordariomycetes (Phylum Ascomycota, Subphylum Pezizomycotina, fide Eriksson et al 2001). The order contains lignicolous, herbicolous and coprophilous taxa currently arranged in approximately 115 genera divided among seven families but recently has contained up to 14 families (TABLE I). These families have been placed in the Sordariales based on the putative ascomal ontogenetic characters involved in centrum development (Luttrell 1951). Two of the families (Batistiaceae, Catabotrydaceae) are monotypic, and nine others (Annulatascaceae, Boliniaceae, Cephalothecaceae, Ceratostomataceae, Chaetomiaceae, Coniochaetaceae, Helminthosphaeriaceae, Nitschkiaceae, Sordariaceae) contain fewer than 15 genera each (Eriksson et al 2001). The Lasiosphaeriaceae is by far the largest and most morphologically diverse family in the order (TABLE II). Although it contained up to 53 genera (Eriksson and Hawksworth 1998), it currently is more narrowly circumscribed with 33 genera (Kirk et al 2001).

The taxa that make up the present Sordariaceae and Lasiosphaeriaceae historically have been combined under one family (Munk 1957, Carroll and Munk 1964, Dennis 1968), separated into two families with the addition of subfamily groupings (Lundqvist 1972) or split off into a third family, Trip-

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TABLE I. Families placed in the Sordariales from 1990 to present

Family	References that place the family in the Sordariales: 1 = Barr 1990, 2 = Eriksson and Hawksworth 1993; Hawksworth et al 1995; 3 = Eriksson and Hawksworth 1998; 4 = Eriksson et al 2001, 2003; 5 = Kirk et al 2001.	**Our placement**
Annulatascaceae S. W. Wong, K. D. Hyde and E. B. G. Jones 1998	4	Sordariomycetidae inc. sed. (Kirk et al 2001)
Batistiaceae Samuels and K. F. Rodrigues 1989	1, 2, 3, 4	Pezizomycotina (Euascomycetes) inc. sed.
Boliniaceae Rick	3	Boliniales (Kirk et al 2001)
Catabotrydaceae Petrak ex M. E. Barr 1990	1, 2, 3	Sordariomycetidae inc. sed.
Cephalothecaceae Höhn. 1917	4, 5	Sordariomycetidae inc. sed.
Ceratostomataceae G. Winter 1885	1, 2, 3, 4 (removed from the order in Eriksson et al 2003)	Hypocreales or Hypocreomycetidae inc. sed.
Chaetomiaceae G. Winter 1885	1, 2, 3, 4, 5	**Sordariales, as chaetomiaceous complex**
Chaetosphaeriaceae Réblová, M. E. Barr and Samuels 1999	4, 5	Chaetosphaeriales
Coniochaetaceae Malloch and Cain 1971	1, 2, 3, 4, 5	Coniochaetales
Helminthosphaeriaceae Samuels, Candoussau and Magní 1997	4	Sordariomycetidae inc. sed.
Lasiosphaeriaceae Nannf. 1932	1, 2, 3, 4, 5	**Sordariales, as lasiosphaeriaceous complex**
Nitschkiaceae (Fitzp.) Nannf. 1932	1, 2, 3, 4, 5	Coronophorales
Sordariaceae G. Winter 1885	1, 2, 3, 4, 5	**Sordariales**
Tripterosporaceae Cain 1956	1	= Lasiosphaeriaceae

terosporaceae (Cain 1956, Barr 1990). The Sordariaceae is morphologically the best-studied family in the order. It contains primarily terricolous and coprophilous taxa, including the model organisms *Neurospora crassa* and *Sordaria fimicola* (Roberge ex Desm.) Ces. & De Not. Lundqvist (1972) provides a seminal treatment of the group with a detailed historical survey. In recent years the concept of the Lasiosphaeriaceae has become rather widely circumscribed (Barr 1990) to include many putatively unrelated members. As such, a detailed study to assess the true affinities of its members is long overdue. The various genera within the Lasiosphaeriaceae sensu lato exhibit a broad range of developmental and morphological characters in both the teleomorph and anamorph that currently are used as important indicators of phylogenetic relationships within the ascomycetes.

Selected members representing the Sordariales have been included in several molecular analyses, where they often have resolved as a monophyletic group (Spatafora and Blackwell 1994, Andersson et al 1995, Lee and Hanlin 1999, Suh and Blackwell 1999, Zhang and Blackwell 2002). In some of these analyses, taxa formerly thought to have relationships in the Sordariales were found to have their affinities elsewhere (i.e., *Ceratocystis* in Spatafora and Blackwell 1994, *Melanospora* Corda in Zhang and Blackwell 2002). In a number of these analyses, taxa under investigation were found to have close relationships to the Sordariales based on very limited taxon sampling (Fallah et al 1997, Chen et al 1999). Analyses never have been performed that have included representatives from all of the putative families in the order and a majority of genera in the Lasiosphaeriaceae. To determine the affinities and taxonomic placement of the Lasiosphaeriaceae and other families in the Sordariales, taxa representing every family in the Sordariales and a majority of the genera in the Lasiosphaeriaceae were targeted for phylogenetic analysis

TABLE II. Genera placed in the Lasiosphaeriaceae from 1972 to present.

Genus	References that place the genus in the Lasiosphaeriaceae: 1 = Lundqvist 1972 (in two subfamilies); 2 = Barr 1990; 3 = Eriksson and Hawksworth 1993; 4 = Eriksson and Hawksworth 1998; 5 = Eriksson et al 2001, 2003; 6 = Kirk et al 2001; 7 = Hyde 1995; 8 = Ramaley 1997; 9 = Hyde 1992a; 10 = Hyde 1992b; 11 = Hyde 1996	Genera of the Lasiosphaeriaceae accepted in this paper	Accepted placement of taxa outside the Lasiosphaeriaceae
Acrospermoides Miller & G.E. Thomps.	2, 3, 4, 5		Sordariomycetidae inc. sed., affinities unknown
Adomia S. Schatz	3, 4, 5		Xylariales (Kirk et al 2001)
Annulatascus K. D. Hyde	3, 4		Annulatascaceae (Hyde 1992c)
Anopodium Lundq.	1, 3, 4, 5, 6	Accepted-morphological	
Apiosordaria Arx & W. Gams	1, 3, 4, 5, 6	Accepted-molecular	
Apiospora Sacc.	2, 3		Apiosporaceae (Hyde et al 1998)
Apodospora Cain & J.H. Mirza	1, 3, 4, 5, 6	Accepted-morphological	
Aquasphaeria K. D. Hyde	7		? Annulatascaceae (Kirk et al 2001)
Arniella Jeng & J.C. Krug	3, 4, 5, 6	Accepted-morphological	
Arnium Nitschke ex G. Winter	1, 3, 4, 5, 6	Accepted-morphological	
Ascocodinaea Samuels, Cand. & Magni	4		Hypocreomycetidae inc. sed.
Ascovaginospora Fallah, Shearer & W. Chen	4, 5		Sordariomycetidae inc. sed.
Barrina A. W. Ramaley	8		Coniochaetaceae
Biconiosporella Schaum.	3, 4, 5, 6		Sordariomycetidae inc. sed., affinities unknown
Bizzozeria Sacc. & Berl.	3, 4, 5, 6		According to Höhnel (1918), *B. veneta* is *Lasiosphaeria sorbina* (Lundqvist 1972).
Bombardia (Fr.) P. Karst.	1, 2, 3, 4, 5, 6	Accepted-molecular	
Bombardioidea C. Moreau ex N. Lundq	1, 3, 4, 5, 6	Accepted-molecular	
Camptosphaeria Fuckel	2, 3, 4, 5, 6	Accepted-morphological	
Caudatispora J. Fröhlich & K.D. Hyde	4, 5, 6		Sordariomycetidae inc. sed.
Ceratocystis Ellis & Halsted	2, 3		Ceratocystidaceae (Kirk et al 2001)
Ceratosphaeria Niessl	3 (with ?), 4 (with ?), 5 (with ?)		Sordariomycetidae inc. sed.
Cercophora Fuckel	1, 2, 3, 4, 5, 6	Accepted-molecular	
Chaetosphaerella E. Müll. & C. Booth	2, 3, 4		Coronophorales
Chaetosphaeria Tul. & C. Tul.	2, 3, 4		Chaetosphaeriaceae (Réblová et al 1999)
Diffractella Guarro, P. Cannon & van der Aa	4, 5, 6	Accepted-morphological	
Echinopodospora B.M. Robison	1		Synonym of *Apiosordaria* (Kirk et al 2001)

TABLE II. Continued

Genus	References that place the genus in the Lasiosphaeriaceae: 1 = Lundqvist 1972 (in two subfamilies); 2 = Barr 1990; 3 = Eriksson and Hawksworth 1993; 4 = Eriksson and Hawksworth 1998; 5 = Eriksson et al 2001, 2003; 6 = Kirk et al 2001; 7 = Hyde 1995; 8 = Ramaley 1997; 9 = Hyde 1992a; 10 = Hyde 1992b; 11 = Hyde 1996	Genera of the Lasiosphaeriaceae accepted in this paper	Accepted placement of taxa outside the Lasiosphaeriaceae
Emblemospora Jeng & J. C. Krug	3, 4, 5, 6	Accepted-morphological	
Eosphaeria Höhn.	2 (as *Herminia* Hilber), 3, 4, 5, 6	Accepted-morphological	
Fimetariella N. Lundq.	1, 3, 4, 5, 6	Accepted-morphological	
Garethjonesia K.D. Hyde	3		Sordariomycetidae inc. sed., affinities unknown
Iodosphaeria Samuels, E. Müll. & O. Petrini	2		Amphisphaeriaceae (Kirk et al 2001); Iodosphaeriaceae (Hilber and Hilber 2002)
Jugulospora N. Lundq.	1, 3, 4, 5, 6	Accepted-molecular	
Lacunospora Caillieux	1		Synonym of *Apiosordaria* (Kirk et al 2001)
Lasiobertia Sivan.	2, 3 (with ?), 4 (with ?), 5 (with ?)		Apiosporaceae (Kirk et al 2001); Xylariales
Lasiosphaeria Ces. & De Not.	1, 2, 3, 4, 5, 6	Accepted-molecular	
Lasiosphaeriella Sivan.	2, 3, 4, 5, 6		Sordariomycetidae inc. sed.
Linocarpon Syd. & P. Syd.	9		Sordariomycetidae inc. sed.
Litschaueria Petr.	2, 3		= *Helminthosphaeria* (Samuels et al 1997a)
Melanochaeta E. Müll., Harr & Sulm.	2, 3, 4		Chaetosphaeriaceae
Melanopsammella Höhn.	2, 3, 4 (with ?)		Chaetosphaeriaceae
Merugia Rogerson & Samuels	4, 5		Sordariomycetidae inc. sed., affinities unknown (Kirk et al 2001)
Mycomedusiospora G.C. Carroll & Munk	2, 3, 4, 5, 6		Sordariomycetidae inc. sed., affinities unknown
Myelosperma Syd. & P. Syd.	4 (with ?), 5 (with ?)		Myelospermataceae (Hyde and Wong 1999); Sordariomycetidae inc. sed.
Neolinocarpon K.D. Hyde	10		Position uncertain, related to *Linocarpon* (Wang and Hyde 1999); Sordariomycetidae inc. sed.
Ophioceras Sacc.	2, 3, 4		Magnaporthaceae (Shearer et al 1999)
Palmicola K.D. Hyde	4, 5		Xylariales, affinities unknown (Kirk et al 2001)
Periamphispora J.C. Krug	3, 4, 5, 6	Accepted-morphological	
Phaeonectriella Eaton & E.B.G. Jones	3		Halosphaeriaceae (Kirk et al 2001)
Phaeotrichosphaeria Sivan.	2, 3, 4, 5		Sordariomycetidae inc. sed., affinities unknown

TABLE II. Continued

Genus	References that place the genus in the Lasiosphaeriaceae: 1 = Lundqvist 1972 (in two subfamilies); 2 = Barr 1990; 3 = Eriksson and Hawksworth 1993; 4 = Eriksson and Hawksworth 1998; 5 = Eriksson et al 2001, 2003; 6 = Kirk et al 2001; 7 = Hyde 1995; 8 = Ramaley 1997; 9 = Hyde 1992a; 10 = Hyde 1992b; 11 = Hyde 1996	Genera of the Lasiosphaeriaceae accepted in this paper	Accepted placement of taxa outside the Lasiosphaeriaceae
Phragmodiscus Hansf.	2, 3, 4, 5, 6		Sordariomycetidae inc. sed. Resembles *Ceratosphaeria* with a subiculum.
Plagiosphaera Petr.	2, 3, 4, 5		Position uncertain, possibly related to *Ophioceras*: Sordariomycetidae inc. sed.
Podospora Ces.	1, 3, 4, 5, 6	Accepted-molecular	
Porosphaerellopsis E. Müll. & Samuels	2, 3, 4		Hypocreomycetidae inc. sed.
Pseudocercophora Subram. & Sekar	3, 4, 5, 6	Accepted-morphological	
Pseudohalonectria Minoura & T. Muroi	3, 4, 5		Magnaporthaceae (Shearer et al 1999)
Pulmosphaeria J.E. Taylor, K.D. Hyde & E.B.G. Jones	5		Xylariales, affinities unknown (Kirk et al 2001)
Schizothecium Corda	1, 3, 4, 5, 6	Accepted-morphological	
Spinulosphaeria Sivan.	2, 3, 4, 5, 6		Nitschkiaceae (Subramanian and Sekar 1990); Coronophorales
Strattonia Cif.	1, 3, 4, 5, 6	Accepted-molecular	
Striatosphaeria Samuels & E. Müll.	2, 3, 4		Chaetosphaeriaceae
Submersisphaeria K.D. Hyde	11		Annulatascaceae (Wong et al 1998)
Thaxteria Sacc.	2, 3, 4, 5, 6		Coronophorales
Triangularia Boedijn	1, 3, 4, 5, 6	Accepted-molecular	
Tripterospora Cain	1		Synonym of *Zopfiella* (see Kirk et al 2001)
Tripterosporella Subram. & Lodha	1, 2, 3, 4, 5, 6	Accepted-morphological	
Zopfiella G. Winter	1, 3, 4, 5, 6	Accepted-molecular-in the Chaetomiaceae	
Zygopleurage Boedijn	1, 3, 4, 5, 6	Accepted-molecular	
Zygospermella Cain	1, 3, 4, 5, 6	Accepted-morphological	

using partial sequences of the large subunit (LSU) nrDNA. Some questions we considered were: (i) Which families belong within the Sordariales? (ii) What is the placement of families excluded from the order? (iii) Which genera belong within the Lasiosphaeriaceae? (iv) What is the placement of genera excluded from the Lasiosphaeriaceae? and (v) How is the Lasiosphaeriaceae related to other families in the Sordariales and other groups of pyrenomycetes?

MATERIALS AND METHODS

Taxon sampling.—Taxa used in this study are listed in TABLES III and IV, along with their geographical locality, collector, voucher specimen and/or isolate number, and GenBank accession number. Cultures of multispore isolates were obtained by spreading centrum material from air-dried specimens onto 1% water agar (Difco) in 60 mm diam plastic Petri plates. After 24–48 h of incubation at room temperature, germinated asci and ascospores were transferred to 60 mm diam plastic Petri plates containing 1% cornmeal agar (Difco). Cultures were maintained at 10 C on 1% potato-dextrose agar (Difco) slants in 6 dram screw-cap tubes. All voucher specimens are deposited in the Field Museum Mycology Herbarium (F).

DNA extraction, PCR amplification, sequencing and sequence alignment.—DNA was extracted from either dried ascomata or multispore isolates grown in 1.5 mL centrifuge tubes containing 1% potato-dextrose broth (Difco). A DNeasy Mini Plant extraction kit (Qiagen Inc., Valencia, California) was used to extract DNA following the manufacturer's protocols, except tissues were not ground in liquid nitrogen. Ascomata initially were rehydrated in 100 μL of AP1 buffer for 3–5 h, followed by freezing overnight at −80 C. Mycelial cultures were washed twice with ca. 500 μL of de-ionized sterile water after the broth was decanted. The quantity of total genomic DNA was observed on a 1% TBE agarose gel stained with ethidium-bromide.

PCR reaction mixtures contained: 2.5 μL of 10× reaction buffer (100 μm Tris, 500 μm KCl) with 25 mM $MgCl_2$, 2.5 μL of 8 mM d-NTPs, 2.5 μL each of 10 μM primers, 3 units of Taq DNA polymerase, 0.5–2 μL of undiluted DNA extract and double-distilled sterile water to bring the total volume to 25 μL. Occasionally 2.5 uL of 10 ng/μL BSA (bovine serum albumin) and/or 2.5 μL of 50% DMSO were added to the PCR reactions to increase efficiency. The primers LROR and LR6 or LR7 (Vilgalys and Hester 1990, Rehner and Samuels 1995; www.biology.duke.edu/fungi/mycolab/primers.htm) were used to amplify 1100 bp or 1400 bp, respectively, of the 5′ end of the LSU gene. All PCR reactions were performed on either a MJ Research PTC 200 or PTC 220 Dyad thermocycler using these thermocycling parameters: initial denaturation at 94 C for 2 min, followed by 30 or 40 cycles of 94 C for 30 s, 47 C for 15 s and 72 C for 1 min with a final extension step of 72 C for 10 min. PCR products were visualized on a 1% TBE agarose gel stained with ethidium-bromide. If these methods failed to produce any amplification product, PCR beads (Amersham Pharmacia Biotech, Piscataway, New Jersey) were used according to the manufacturer's instructions. Thermocycling parameters were as above except initial denaturation was 5 min and annealing temperature occasionally was decreased to 41 C. Further amplification failure required the gene to be amplified in two overlapping fragments using the primer pairs LROR-LR3 and LRAM1-LR6 (LRAM1 = GGAGGTAAATTYCTTCTAAAGC). In rare cases of weak amplification, a punch of the PCR product was taken from the gel, suspended in 50–150 μL double distilled sterile water, melted at 70 C, and 1 μL of this dilution was reamplified using the thermocycling parameters above, except annealing temperature was increased to 50 C. PCR products were purified with GELase Agarose Gel-Digesting Preparation (Epicentre Technologies, Madison, Wisconsin) according to manufacturers instructions, and both strands were sequenced using a combination of these primers: LROR, LRFF1, LR3, LRAM1, LR3R, LR5, LR6, LR7 (LRFF1 = CTTTTCATCTTTCGATCACTCTAC) (Vilgalys and Hester 1990, Rehner and Samuels 1995; www.biology.duke.edu/fungi/mycolab/primers.htm). Sequencing reactions were performed in a 10 μL total volume using dRhodamine Terminator or BigDye version II Terminator (ABI PRISM, Perkin-Elmer Biosystems, Foster City, California) fluorescent dyes following manufacturers protocols and precipitated with 10 μL of de-ionized sterile water, 2 μL of 3 M NaOAC and 50 μL of 95% EtOH. Sequences were generated on an Applied Biosystems 377A or 3100 automated DNA sequencer. Each sequence fragment was subjected to a BLAST search to verify its identity. Sequences were assembled and aligned with Sequencher 4.1 (Gene Codes Corp., Ann Arbor, Michigan), optimized by eye and manually corrected when necessary.

Phylogenetic analyses.—Twelve ambiguously aligned regions were delimited, and characters in these regions along with two introns and portions of the 5′ and 3′ ends were excluded from all analyses. Equally weighted (MP1) and unequally weighted (MP2, MP3) maximum-parsimony analyses were performed using PAUP* 4.0b10 (Swofford 2002) as follows: Constant characters were excluded, unambiguously aligned characters were equally weighted and unordered, gaps were treated as missing, 1000 random-addition replicates were implemented with TBR branch-swapping, MULTREES option was in effect, and zero-length branches were collapsed. All remaining unambiguously aligned characters and changes between character states were equally weighted in the MP1 analyses. In the MP2 analyses, changes among transitions, transversions and gaps were subjected to a symmetric stepmatrix generated with the program STMatrix version 2.2 (François Lutzoni and Stefan Zoller, Department of Biology, Duke University). The cost for changes among these character states was based on the negative natural logarithm of the percentages of reciprocal changes between any two character states. Five of the 12 ambiguous regions were recoded as five unequivocally coded characters using INAASE (Lutzoni et al 2000). These five characters along with the stepmatrix were used in the MP3 analyses. The remaining seven ambiguous regions were excluded from the MP3 analyses because their recoded characters contained more than 32 character states, which is not allowed in PAUP*. Branch support for all parsimony analyses was estimated by performing 1000 bootstrap replicates (Felsenstein 1985) with a heuristic search consisting of 10 random-addition replicates for each bootstrap replicate using the above settings, except the number of trees saved per random-addition replicate was limited to 100. Representatives from several additional families and orders were included to determine the phylogenetic position of polyphyletic genera currently included in the Lasiosphaeriaceae. Four loculoascomycetes, *Botryosphaeria ribis, Capnodium citri, Capronia mansonii* and *Mycopepon smithii,* were used as outgroups.

The best-fit model of evolution was determined by MODELTEST 3.06 (Posada and Crandall 1998). MODELTEST 3.06 determines the best-fit model by comparing different nested models of DNA substitution in a hierarchical hypothesis-testing framework using the likelihood ratio test. Maximum-likelihood analyses were not performed due to the extreme computational efforts required by a dataset of this size. Bayesian analyses were performed with MrBayes 3.0b3 (Huelsenbeck and Ronquist 2001; http://morphbank.ebc.uu.se/

TABLE III. Taxa sequenced in this study

Taxon	Source[a]	GenBank accession number
Albertiniella sp.	Ascomata; SMH2436, ex decayed log, Costa Rica (F)	AY346256
Annulatascus triseptatus S. W. Wong, K. D. Hyde & E. B. G. Jones	Culture; SMH2359, ex 2 cm branch, Costa Rica (F)	AY346257[b]
Apiosordaria verruculosa (C.N. Jensen) Arx & W. Gams	Culture; F-152,365 (A-12907), ex ethanol-pasteurized soil, Spain, provided by G. Bills	AY346258
Apiospora setosa Samuels, McKenzie & D.E. Buchanan	Culture; ATCC 58184, ex *Bambusa* sp., New Zealand	AY346259
Ascocodinaea stereicola Samuels, Cand. & Magni	Culture; GJS 95-184, ex *Stereum* sp., USA (holotype, BPI), provided by G. J. Samuels	AY346260
Barrina polyspora A. W. Ramaley	Culture; A. Ramaley 9560A, ex dead leaves of *Dasylirion leiophyllum,* USA (holotype, BPI), provided by A. W. Ramaley	AY346261
Batistia annulipes (Mont.) Cif.	Ascomata; G. J. Samuels 6059, ex bark, French Guiana (NY)	AY346262
Bombardia bombarda (Batsch) J. Schröt.	Culture; SMH3391, ex 6 in log, USA (F)	AY346263[b]
Bombardioidea anartia J.C. Krug & J.A. Scott	Ascomata; H.H. Burdsall s.n. (Acc#956, HHB 99-1), ex moose dung, USA (F)	AY346264
Camarops petersii Nannf.	Ascomata; J. Murphy 1655, ex log, USA (F)	AY346265
Camarops tubulina (Alb. & Schwein.) Shear	Ascomata; SMH4614, ex beech log, Denmark (F)	AF346266
Camarops ustulinoides (Henn.) Nannf.	Ascomata; SMH1988, ex log, Puerto Rico (F)	AY346267
Catabotrys deciduum (Berk. & Broome) Seaver & Waterston	Ascomata; SMH3436, ex palm petiole, Panama (F)	AY346268
Caudatispora biapiculata Huhndorf & F.A. Fernández	Culture; SMH1873, ex palm petiole, Puerto Rico (F)	AY346269
Ceratosphaeria lampadophora (Berk. & Broome) Niessl	Ascomata; SMH4822, ex branch, France (F)	AY346270
Cercophora mirabilis Fuckel	Ascomata; SMH4002, ex cow dung, Costa Rica (F)	AY346271
Chaetomium globosum Kunze	Culture; SMH4214b, ex cow dung, Jamaica (F)	AY346272
Chaetomium microascoides Guarro	Culture; F-153,395 (A-12898), ex ethanol-pasteurized soil, Spain, provided by G. Bills.	AY346273
Chaetosphaerella phaeostroma (Durieu & Mont.) E. Müll. & C. Booth	Ascomata; SMH4585, ex sycamore log, England (F)	AY346274
Coniochaeta sp.	Culture; SMH2569, ex log, USA (F)	AY346275[b]
Coniochaetidium savoryi (C. Booth) Malloch & Cain	Culture; TRTC 51980, provided by J. C. Krug	AY346276[b]
Copromyces sp.	Culture; TRTC 51747 (& CBS 386.78 given as *C. octosporus* Jeng & Krug, however this species is undescribed), provided by J. C. Krug	AY346277
Diamantinia citrina A. N. Mill., Laessøe & Huhndorf	Ascomata; Buck 26886, ex branch, Brazil (F)	AY346278
Diaporthe phaseolorum (Cooke & Ellis) Sacc.	Culture; FAU458 (SMBL, BPI), provided by A. Y. Rossman	AY346279
Eutypa sp.	Culture; SMH3580, ex branch, Panama (F)	AY346280[b]
Gelasinospora tetrasperma Dowding	Culture; ATCC 96230, Canada	AY346281
Helminthosphaeria carpathica Réblová	Ascomata; SMH3908, ex wood, USA (F)	AY346282
Helminthosphaeria clavariarum (Desm.) Fuckel	Ascomata; SMH4609, ex *Clavulina cristata,* Denmark (F)	AY346283
Helminthosphaeria hyphodermiae Samuels, Cand. & Magni	Ascomata; SMH4192, ex *Hyphoderma,* USA (F)	AY346284
Jobellisia fraterna Huhndorf, Lodge & F. A. Fernández	Ascomata; SMH2863, ex log, Puerto Rico (F)	AY346285

TABLE III. Continued

Taxon	Source[a]	GenBank accession number
Jobellisia luteola (Ellis & Everh.) M. E. Barr	Ascomata; SMH2753, ex log, USA (F)	AY346286
Jugulospora rotula (Cooke) N. Lundq.	Culture; ATCC 38359, ex ant hill soil	AY346287
Lasiobertia sp.	Ascomata; SMH2065, ex log, Puerto Rico (F)	AY346288
Lasiosphaeriella nitida Huhndorf & F. A. Fernández	Culture; SMH1664, ex log, Puerto Rico (F)	AY346289
Leptosporella gregaria Penz. & Sacc.	Ascomata; SMH4290, ex wood, Costa Rica (F)	AY346290
Linocarpon appendiculatum K.D. Hyde	Culture; ATCC 90499, ex *Nypa fruticans,* Brunei	AY346291
Melanochaeta hemipsila (Berk. & Broome) E. Müll., Harr & Sulmont	Culture; SMH2125, ex branch, Puerto Rico (F)	AY346292
Neobarya sp.	Ascomata; Buck26786 [Acc#649], ex *Bertia,* Brazil (F)	AY346293
Nitschkia grevillii (Rehm) Nannf.	Ascomata; SMH4663, ex branch, USA (F)	AY346294
Ophioceras tenuisporum Shearer, J.L. Crane & W. Chen cf.	Culture; SMH1643, ex petiole, Puerto Rico (F)	AY346295[b]
Podospora fimiseda (Ces. & De Not.) Niessl	Culture; CBS 990.96, ex horse dung, New Zealand	AY346296
Poroconiochaeta discoidea Udagawa & Furuya	Culture; SANK12878, provided by J. C. Krug.	AY346297
Porosphaerellopsis sporoschismophora (Samuels & E. Müll.) E. Müll. & Samuels	Culture; ATCC 42528, ex well-rotted decorticated wood, Brazil	AY346298
Pseudohalonectria lignicola Minoura & T. Muroi	Culture; SMH2440, ex branch, Costa Rica (F)	AY346299
Schizothecium curvisporum (Cain) N. Lundq.	Culture; ATCC 36709, ex rock hyrax dung, Kenya	AY346300
Sordaria macrospora Auersw.	Culture; Buck s.n. (Acc#957), ex caribou dung, Canada (F)	AY346301[b]
Strattonia carbonaria (W. Phillips & Plowr.) N. Lundq.	Culture; ATCC 34567, ex burned soil, Japan	AY346302
Triangularia mangenotii Arx & Hennebert	Culture; ATCC 38847, ex soil, Japan	AY346303
Valsonectria pulchella Speg.	Culture; SMH1193, ex branch, Puerto Rico (F)	AY346304[b]
Zopfiella ebriosa Guarro, P.F. Cannon & Aa	Culture; CBS 111.75, ex wine cork, Europe	AY346305[b]
Zygopleurage zygospora (Speg.) Boedijn	Culture; SMH4219, ex cow dung, USA (F)	AY346306

[a] ATCC, American Type Culture Collection; CBS, Centraalbureau voor Schimmelcultures, Netherlands; F, Field Museum of Natural History, Chicago, Illinois; NY, New York Botanical Garden, New York, New York; SMBL, BPI, Systematic Botany and Mycology Laboratory, USDA, Beltsville, Maryland; TRTC, Royal Ontario Museum, Toronto, Canada.

[b] For these taxa, although 1100 bp were used in the analyses, 1300 bp were sequenced and deposited in GenBank.

mrbayes3). Constant characters were included, the above model of evolution was implemented and 10 000 000 generations were sampled every 1000th generation resulting in 10 000 trees. The first 2000 trees, which represented the burn-in phase of the analysis, were discarded, and the remaining 8000 trees were used for calculating posterior probabilities in the consensus tree. This analysis was repeated five times starting from different random trees to ensure trees from the same tree space were being sampled during each analysis.

RESULTS

Sequence alignment.—The final alignment included 85 taxa and 1337 bp after the introduction of gaps and is deposited in TreeBase (S947). The first 61 bp of the 5′ end and the last 38 bp of the 3′ end were excluded from all analyses due to missing data in most taxa. Twelve ambiguous regions representing 337 characters also were excluded from all analyses due to uncertainty in the alignment. Two taxa (*Annulatascus triseptatus, Linocarpon appendiculatum*) possessed single introns (67 bp and 65 bp, respectively), which subsequently were excluded from all analyses. These introns were identified as spliceosomal introns because they contained the highly conserved donor, branch and acceptor sites known to occur in ascomycete spliceosomal introns (Bhattacharya et al 2000). Of the remaining 769 characters, 449 were constant and 88 were parsimony uniformative for a total of 232 parsimony-informative characters in the MP1 and MP2 analyses. Five additional parsimony-informative characters derived from the unequivocally coded ambiguous regions also were included in the MP3 analyses.

Phylogenetic analyses.—The equally weighted MP1 analysis generated 110 equally most-parsimonious

TABLE IV. Additional taxa included in the analyses

Taxon	GenBank accession number
Albertiniella polyporicola (Jacz.) Malloch & Cain	AF096185
Annulatascus velatispora K. D. Hyde	AF132320
Aporothielavia leptoderma (C. Booth) Malloch & Cain	AF096186
Ascovaginospora stellipala Fallah, Shearer & W.D. Chen	ASU85088
Botryosphaeria ribis Grossenb. & Duggar	AY004336
Capnodium citri Mont.	AY004337
Capronia mansonii (Schol-Schwarz) E. Müll., Petrini, P.J. Fisher, Samuels & Rossman	AY004338
Cephalotheca sulfurea Fuckel	AF431950
Ceratocystis virescens (R. W. Davidson) C. Moreau	CVU47824
Chaetomium globosum	AF286403
Chaetosphaeria innumera Berk. & Broome ex Tul. & C. Tul.	AY017375
Chaetosphaeria ovoidea (Fr.) Constant., K. Holm & L. Holm	AF064641
Cryptendoxyla hypophloia Malloch & Cain	AF096190
Daldinia concentrica (Bolton) Ces & De Not.	DCU47828
Diatrype disciformis (Hoffm.) Fr.	DDU47829
Farrowia longicollea (Krzemien. & Badura) D. Hawksw.	AF286408
Glomerella cingulata (Stoneman) Spauld. & H. Schrenk	GCU17403
Hypomyces luteovirens (Fr.:Fr.) Tul.	AF160237
Lasiosphaeria ovina (Pers.:Fr.) Ces. & De Not.	AF064643
Melanospora zamiae Corda	MZU17405
Microascus trigonosporus C.W. Emmons & B.O. Dodge	MTU47835
Mycopepon smithii Boise	AF279400[a]
Nectriopsis violacea (J.C. Schmidt) Maire	AF193242
Neurospora crassa Shear & B.O. Dodge	AF286411
Ophiostoma floccosum Math.-Käärik	AF234836
Ophiostoma piceae (Münch) Syd. & P. Syd.	AF234837
Petriella setifera (Alf. Schmidt) Curzi	PSU48421
Plectosphaerella cucumerina (Lindf.) W. Gams	PCU17399
Porosphaerella cordanophora E. Müll. & Samuels	AF178563
Schizoparme botrytidis Samuels, M.E. Barr & Lowen	AF408383
Striatosphaeria codinaeaphora Samuels & E. Müll.	AF466088
Thielavia cephalothecoides Malloch & Benny	AF286413
Valsa ceratosperma (Tode) Maire	AF408387
Xylaria hypoxylon (L.) Grev.	XHU47841

[a] This sequence of *Mycopepon smithii* extracted from ascomata replaces the erroneous sequence deposited in GenBank. That sequence was obtained from a culture that had become contaminated.

trees (MPT), all within a single island of trees. A strict consensus of the 110 MPT revealed only minor topological differences among genera in the Sordariales and Coniochaetales (data not shown). The inclusion of the stepmatrix in the MP2 analysis reduced the number of MPT to 12. A strict consensus of these trees revealed only minor topological differences within the Chaetomiaceae and the paraphyletic placement of *Ascovaginospora* with the Boliniales and Chaetosphaeriales (data not shown). The addition of the five recoded characters along with the stepmatrix in the MP3 analysis further reduced the number of MPT to three, which differed only in the paraphyly of *Aporothielavia leptoderma, Chaetomium globosum* and *Chaetomium sp.* One of the three MPT from this analysis is shown in FIG. 1. While minor differences in overall tree topology were found in the MPT among the three analyses, the topologies among and within the well-supported clades remained the same. As is typical in most large-scale phylogenetic analyses employing LSU sequence data, the backbone of the MPT received little bootstrap support. The effect of subjecting characters to a stepmatrix (MP2) and recovering the phylogenetic signal in five of the ambiguously aligned regions (MP3) was a reduction in the number of MPT along with a slight increase in bootstrap support for some clades.

The best-fit model determined by MODELTEST was the SYM+I+G model (Zharkikh 1994), which contained these parameters: equal base frequencies, different rates for transitions and transversions (1.2479, 5.7277, 2.2538, 0.8113, 9.6286, 1.0000), an estimated proportion of invariable sites of 0.4407 and a gamma shape parameter for the rates of variable sites of 0.5002. Therefore, Bayesian analyses were conducted with the number of rate categories set to 6, rates set to invgamma and all remaining parameters estimated from the default prior probabilities.

Order Sordariales in a broad sense was found to be highly polyphyletic in that families segregated into 10 distinct monophyletic clades dispersed throughout several orders (FIG. 1). The circumscription of Sordariales is considerably narrowed for the clade containing genera within the families Chaetomiaceae, Lasiosphaeriaceae and Sordariaceae. Because the Chaetomiaceae and Lasiosphaeriaceae are paraphyletic, they here are recognized as the ‘‘chaetomiaceous complex’’ and the ‘‘lasiosphaeriaceous complex’’ respectively. Two new orders are proposed for the clades containing the Chaetosphaeriaceae and Coniochaetaceae respectively, while the order Coronophorales is accepted for the Nitschkiaceae and Boliniales for the Boliniaceae. Four families (Annulatascaceae, Cephalothecaceae, Catabotrydaceae, Helminthosphaeriaceae) are accepted or placed in

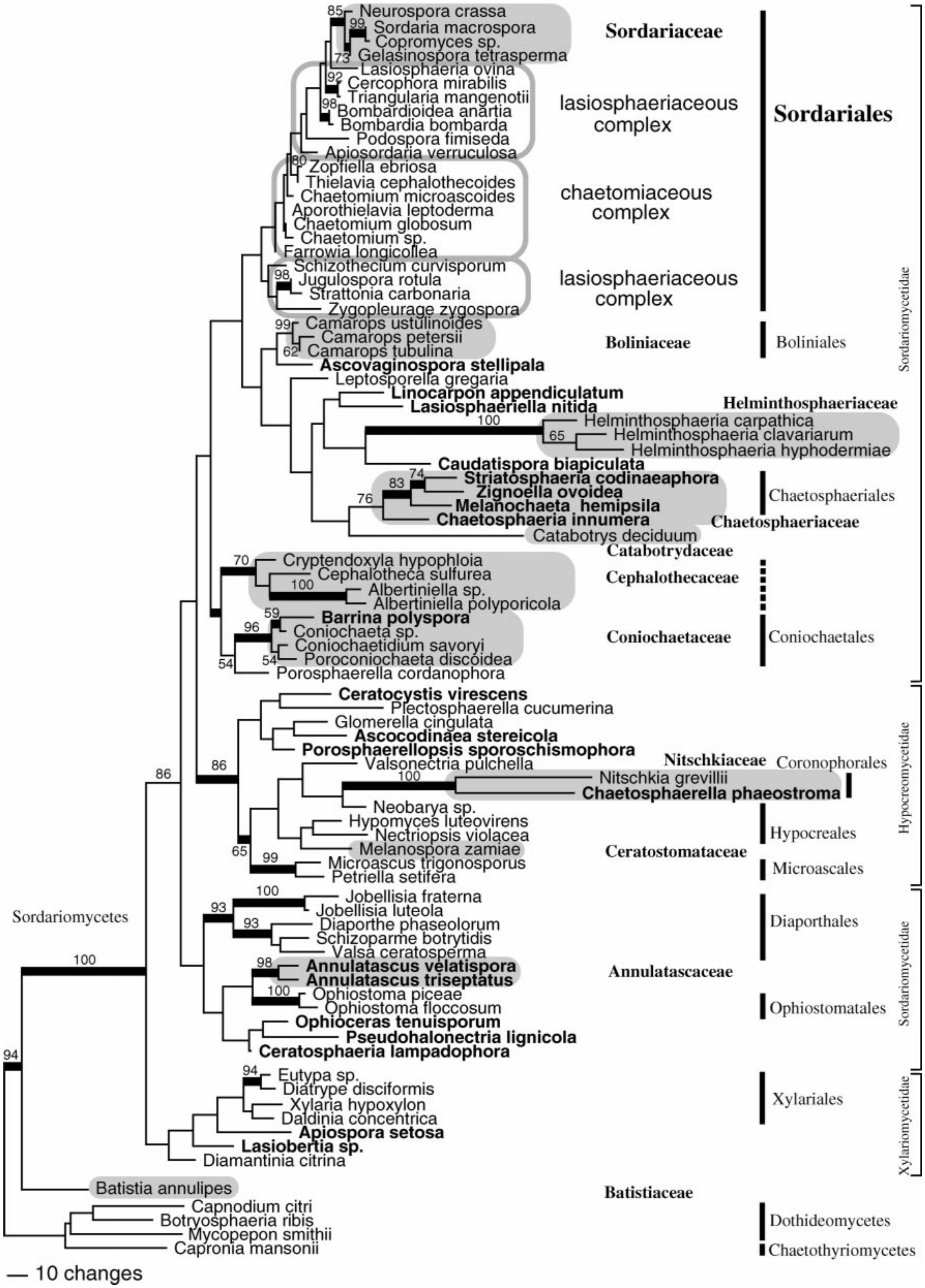

FIG. 1. Phylogram of one of the three most-parsimonous trees generated from the MP3 analysis based on 1337 bp of the 5′ end of the LSU nrDNA for 85 ascomycete sequences; length = 2629.36 steps, CI = 0.34, RI = 0.642, RC = 0.218. Bootstrap values ≥50% are shown above or below branches. Thickened branches indicate posterior probabilities ≥95%. Taxa placed in the Lasiosphaeriaceae sensu lato that occur outside the family are in bold. The 13 families recently placed in the Sordariales by at least one of the five classifications (TABLE I) are in shaded boxes or outlined.

the Sordariomycetidae inc. sed. The Batistiaceae is placed in the Euascomycetes inc. sed., and the Ceratostomataceae is accepted in the Hypocreomycetidae inc. sed.

The family Lasiosphaeriaceae in a broad sense was found to be highly polyphyletic in that genera segregated into numerous clades dispersed throughout several orders (FIG. 1). Eleven genera are retained in the redefined lasiosphaeriaceous complex with an additional 13 genera added based on morphological data, while 39 genera are excluded (TABLE II).

Taxonomic changes.—

Chaetosphaeriales Huhndorf, A.N. Mill. & F.A. Fernández, ord. nov.

Ascomata superficialia vel semi-immersa, subglobosa, globosa vel obpyriformia, ostiolata; pagina glabra, aspera vel hirsuta; subiculum praesens vel absens. Paraphyses sparsae vel copiosae, simplices, septatae. Asci clavati vel cylindracei, unitunicati, cum vel sine annulo. Ascosporae ellipsoidae vel fusiformes, septatae, hyalinae vel fuscatae, laeves. Conidiogenesis phialidicae enteroblasticae.

Ascomata superficial or semi-immersed, subglobose, globose or obpyriform, ostiolate, glabrous, roughened or setose; subiculum present or absent; paraphyses sparse or abundant, simple, septate; asci clavate or cylindrical, unitunicate, with or without apical ring; ascospores ellipsoid to fusiform, septate, hyaline or pigmented, smooth; conidiogenesis enteroblastic phialidic.

Typus: *Chaetosphaeria* Tul. & C. Tul.

Coniochaetales Huhndorf, A.N. Mill. & F.A. Fernández, ord. nov.

Ascomata superficialia vel semi-immersa, subglobosa, globosa vel obpyriformia, ostiolata vel nonostiolata; pagina glabra vel hirsuta. Paraphyses filiformes, septatae. Asci subglobosi, clavati vel cylindracei, unitunicati. Ascosporae ellipsoidae, fusiformes vel discoidae, unicellulae, hyalinae vel pigmentiferi, laeves vel foveolatae, rimaris germinationibus. Conidiogenesis phialidicae, conidia ex phialidibus discretis vel cellulis intercalaribus, phialidicis genita.

Ascomata superficial or immersed, subglobose, globose or obpyriform, ostiolate or nonostiolate, glabrous or setose; paraphyses filiform, septate; asci subglobose, clavate or cylindrical, unitunicate; ascospores ellipsoid, ellipsoid-fusoid or discoid, one-celled, hyaline or pigmented, smooth or finely pitted, with germ slit; conidiogenesis phialidic, conidia produced on discrete phialides or from phialidic intercalary cells.

Typus: *Coniochaeta* (Sacc.) Cooke

DISCUSSION

Sordariales redefined.—Based on molecular data from partial LSU nrDNA genera within the families Chaetomiaceae, Lasiosphaeriaceae and Sordariaceae are retained within the redefined Sordariales. The Tripterosporaceae is not distinguished from the Lasiosphaeriaceae at this time. The other families (sensu Eriksson et al 2001) find their placement elsewhere (see below and TABLE I).

There are several reasons for recognizing the Sordariales at this internode even though it currently lacks support. Although Bayesian inference is more likely than bootstrapping to provide support for short internodes (Alfaro et al 2002), neither method supported the Sordariales internode in these analyses. However, this internode is supported through significant Bayesian posterior probabilities in subsequent analyses using additional genes (β-tubulin, RPB2) with similar taxon sampling (Miller unpubl data). The length of this internode is quite short, suggesting a rapid radiation of this group, and, under these circumstances, it is possible that even with additional data it might always lack bootstrap support (Berbee et al 2000). The order is also a coherent group with morphologies that vary along well-defined lines. Several putative synapomorphic morphological characters help to strengthen this ordinal clade, such as: (i) relatively large ascomata (approximately 400–600 μm diam), which are erumpent to superficial and never immersed; (ii) ascomal walls that are large-celled and membraneous or coriaceous but rarely carbonized; and (iii) ascospores that show variation on a distinctive developmental theme, often with appendages or sheaths. Taxa from three families are included in this overall clade, but, except for the Sordariaceae, lineages that fit the traditional families cannot be distinguished yet.

The Lasiosphaeriaceae as circumscribed by our molecular data is paraphyletic, and its members are described in more detail below. The Chaetomiaceae is recognized here as the ‘‘chaetomiaceous complex’’ and is represented by *Chaetomium* Kunze, *Farrowia* D. Hawksw., *Thielavia* Zopf, *Aporothielavia* Malloch & Cain and here including *Zopfiella ebriosa*. This group is also paraphyletic, nested within the clade that contains all sampled members of the Lasiosphaeriaceae. There is bootstrap support for the clade containing *Z. ebriosa* and *Thielavia cephalothecoides* (FIG. 1), and consequently *Zopfiella* is accepted in the chaetomiaceous complex. *Chaetomium* and other members of the Chaetomiaceae recently have been studied using 18S and 28S nrDNA sequences (Untereiner et al 2001, Lee and Hanlin 1999). In both cases the monophyly of the Sordariales was confirmed and with the limited taxon sampling of the Lasiosphaeriaceae that was included; the Chaetomiaceae formed a sister group to the other taxa, although without bootstrap support in the 28S data (Untereiner et al 2001). Our larger sampling of the Lasiosphaeriaceae suggests that relationships among taxa in the Chaetomiaceae and the Lasiosphaeriaceae are intricate and need further work.

The Sordariaceae is represented by *Sordaria* Ces. & De Not., *Neurospora* Shear & B.O. Dodge, *Copromyces* N. Lundq. and *Gelasinospora* Dowding. The clade containing these four genera is strongly supported but never resolves as a sister group of Lasiosphaeriaceae, as expected according to traditional morphological hypotheses. The Sordariaceae always is nested among the taxa traditionally found within the Lasiosphaeriaceae. Lundqvist (1972) provides an extensive review of the history of the Sordariaceae in its various forms (sensu lato and sensu stricto) and concludes that the family can be upheld for selected dark-spored genera that have similarities in perithecial, ascal and ascospore morphologies. He discusses the phylogenetic aspects within the group and notes the close relationship between *Sordaria, Neurospora* and *Gelasinospora* that has been shown repeatedly by various authors. He believed that the family was separate from taxa in the Lasiosphaeriaceae but that its origin (ancestor) probably was close to the hyaline-spored Lasiosphaeriaceae.

Our molecular data indicate that 11 genera belong in the paraphyletic Lasiosphaeriaceae, here recognized as the ''lasiosphaeriaceous complex''. These taxa share a similar pattern of ascospore morphology that extends to the Sordariales as a whole. Based on these similarities in morphology, 13 additional genera have putative relationships within the lasiosphaeriaceous complex (TABLE II) and more than 35 genera have relationships in the order. We believe that ascospore morphology is phylogenetically informative for determining whether a taxon belongs in the Sordariales. Lundqvist (1972) provides an excellent description of the ascospore morphologies that are found in his Sordariaceae sensu lato. If the chaetomiaceous complex is included with a few exclusions, the taxa in his group are essentially the same as our circumscription of the order. In the Sordariales, ascospore morphology exists as a continuum from a hyaline, cylindrical ascospore in *Lasiosphaeria* to a one-celled, brown, ellipsoid ascospore in *Sordaria*. Intermixed between these two extremes are many genera with two-celled ascospores that possess a brown, ellipsoid cell and different degrees of a hyaline (often basal) cell. There are numerous variations on this theme (see Lundqvist 1972 for excellent illustrations).

Our molecular analyses of the LSU also indicate that 17 genera that have been assigned to the Lasiosphaeriaceae sensu lato should be transferred to other families outside the Sordariales. By extrapolation, 22 additional genera with differing morphologies also should be removed from the order; some however have uncertain placement at this time (TABLE II). None of these genera possess ascospores on the same developmental theme as those included in the Sordariales.

The removal of the disparate elements at the family and genus level makes the Sordariales a more homogeneous assemblage. Sordariales sensu lato that includes also the families Boliniaceae, Helminthosphaeriacae, Chaetosphaeriaceae and possibly Catabotrydaceae theoretically could be recognized. However, circumscribing the order along these lines would let the group remain highly heterogeneous and permit further inclusions of taxa with dubious relationships.

Families removed from the Sordariales.—The position of the Boliniaceae historically has been uncertain. Members, such as *Camarops* with large conspicuous stromata, have been allied with the Xylariaceae (Munk 1953, Dennis 1960). Nannfeldt (1972) did not believe in this close relationship and accepted the family Boliniaceae for *Camarops.* In recent years the Boliniaceae has been placed in the Xylariales (Barr 1990) or been given incertae sedis status (Eriksson 1982). Andersson et al (1995) placed the Boliniaceae in the Sordariales based on 18s nrDNA sequence data. They suggested that the stromatic Catabotrydaceae, an already accepted member of the order, was closely related to the Boliniaceae and thus the order Boliniales was erected to include both families (Kirk et al 2001).

In our analyses, the Boliniaceae is represented by three species of *Camarops* that come together in a clade with strong bootstrap support. It comes as an unsupported sister group of the taxa representing the Chaetosphaeriaceae, Helminthosphaeriaceae and Catabotrydaceae, and all four families form an unsupported sister clade of the Sordariales. We accept the placement of the Boliniaceae in the Boliniales.

Catabotrydaceae. The Catabotrydaceae was validated and placed in the Sordariales by Barr (1990). The family is monotypic based on a single species, *Catabotrys deciduum,* which forms large, dark stromata on dead tissues of large monocots. The species appears to be pantropical and rather common. Its relationships have not been understood clearly. In addition to finding a placement in the Sordariales, it has been placed in the Xylariales (Hyde et al 2000) and most recently in the Boliniales (Kirk et al 2001). While *Catabotrys* is resolved as an unsupported sister taxon to the Chaetosphaeriaceae in these analyses, it shows affinities to the Diaporthales and Hypocreales in additional analyses (data not shown). Because our analyses show its phylogenetic relationships as unresolved, we therefore place the Catabotrydaceae in the Sordariomycetes inc. sed.

Chaetosphaeriaceae and *Helminthosphaeriaceae.* The Chaetosphaeriaceae recently was established for *Chaetosphaeria* and its relatives (Réblová et al 1999). The family was placed in the Sordariales due to similarities in ascomal wall and anamorph morphologies. Samuels et al (1997a) established the Helminthosphaeriaceae for *Helminthosphaeria* and, with reservations, placed the family in the ''probably polyphyletic'' Sordariales based on the anatomical characters of the ascomata and asci. *Helminthosphaeria* species generally have porate ascospores, a feature they share with some members of the Sordariaceae, Lasiosphaeriaceae sensu lato, Ceratostomataceae and Boliniaceae. Samuels et al (1997a) did not believe however that the Helminthosphaeriaceae had a close relationship with these families. Réblová (1999) placed the family in the Trichosphaeriales and included several additional genera.

The Helminthosphaeriaceae, which is represented by three species of *Helminthosphaeria,* is well supported by 100% bootstrap support and Bayesian posterior probabilities. Our data show the Chaetosphaeriaceae, Helminthosphaeriaceae and Catabotrydaceae clustering together as an unsupported sister group of the Boliniaceae. Four additional individual taxa formerly in the Lasiosphaeriaceae (*Caudatispora biapiculata, Linocarpon appendiculatum, Lasiosphaeriella nitida* and *Ascovaginospora stellipala*) also find their placement in this overall unsupported group. With limited taxon sampling from other Sordariomycetes orders, certain members of the Chaetosphaeriaceae resolved as a monophyletic group with a high level of bootstrap support separate from the taxa representing the Sordariales (Réblová and Winka 2000). Réblová and Winka (2001) suggested that the family was a likely candidate for removal to its own order from the broadly conceived Sordariales. Their data show the Chaetosphaeriaceae separated with high bootstrap support of 98% from other families in the order. Based on these data and our own analyses we believe that the Chaetosphaeriaceae represents a broad and morphologically diverse lineage distinct from the Sordariales that warrants separation at the ordinal level. We therefore choose to establish a new order Chaetosphaeriales for the Chaetosphaeriaceae.

Although it is evident that the Chaetosphaeriaceae and the Helminthosphaeriaceae are separate from the redefined Sordariales, the relationships between the two families are not clear. A few taxa formerly in the Lasiosphaeriaceae also come into an overall unsupported clade, and a number of additional taxa not included in these analyses also appear to have their placement in this group (data not shown). This group may represent a series of evolutionary events where there was a large, rapid radiation of taxa with numerous morphological characters that provide only cryptic information about relationships.

Réblová (1999) removed the Helminthosphaeriaceae from the Sordariales and placed it in the Trichosphaeriales based on ascomal wall morphology and conidiogenesis of associated anamorphs. The placement and relationships of the Trichosphaeriaceae within the Sordariomycetes were suggested by Réblová and Winka (2001). In their analysis of several new ascomycete taxa, they included *Rhamphoria delicatula* Niessl as a single taxon that they believed represented the Trichosphaeriaceae. Based on partial LSU nrDNA data, they found that *R. delicatula* was related to several taxa in the Annulatascaceae. They concluded that some characteristics of certain taxa in the Annulatascaceae match well with the circumscription of the Trichosphaeriaceae. However, without sequence data from the type species of *Trichosphaeria* Fuckel they could not confirm whether the clade containing taxa of both families is the true Trichosphaeriaceae. If the placement of the Trichosphaeriaceae based on the *R. delicatula* sequence data is accepted, then the Helminthosphaeriaceae would not be accepted in the Trichosphaeriales. In our analyses the Helminthosphaericeae does not appear closely related to the two species of *Annulatascus* that represent the Annulatascaceae. Therefore, Helminthosphaeriaceae currently is placed in the Sordariomycetes inc. sed.

Coniochaetaceae. The Coniochaetaceae was established for two genera, *Coniochaeta* (Sacc.) Cooke and *Coniochaetidium* Malloch & Cain differing from Sordariaceae in ascospores having elongated germ slits. *Coniochaeta* has been allied variously with the Sordariaceae and the Xylariaceae, depending on the emphasis given to either the ascomal or ascospore morphologies. Most recent compilations have accepted the family in the Sordariales (TABLE I). Rogers (1994) considered it to be an isolated family whose relationship with other ascomycetes is obscure. Lee and Hanlin (1999) found the family to be strongly supported in the Sordariales with 18S nrDNA sequence data, where it came out as a well-supported sister group of the Chaetomiaceae/Sordariaceae clade. In analyses of 28S data with wider taxon sampling, Weber et al (2002) showed the strongly supported Coniochaetaceae separate from the Sordariales and clustering as a sister group to the Xylariales and Hypocreales. They declined to introduce a separate order for the family due to lack of bootstrap support.

Based on our data, we agree that the family does not belong in the Sordariales. The family represented by *Coniochaeta, Coniochaetidium, Poroconiochaeta* and herein *Barrina* (see below) has strong bootstrap and Bayesian support. Our data strongly support the Coniochaetaceae as being monophyletic and a new order, Coniochaetales, is established for the Coniochaetaceae.

Cephalothecaceae. Suh and Blackwell (1999) discuss the history of the Cephalothecaceae and the relationships of cephalothecoid and other cleistothecial taxa. In their study, *Cephalotheca* Fuckel and two members of the Pseudoeurotiaceae formed a strongly supported clade that clustered as a sister group of the Sordariaceae/Lasiosphaeriaceae/Chaetomiaceae clade. This was supported by SSU data but not LSU data.

The Cephalothecaceae is represented in our analyses by *Cephalotheca sulfurea* and *Cryptendoxyla hypophloia,* along with two representatives of *Albertiniella* Kirschst. The family was well supported with 78% bootstrap support and 100% Bayesian posterior probability. The overall clade representing the Coniochaetaceae and Cephalothecaceae lacks bootstrap support but does show significant Bayesian support. We choose to place the family in the Sordariomycetidae inc. sed. until additional data are generated, while recognizing that it could be placed in the Coniochaetales.

Nitschkiaceae. Over the years the Nitschkiaceae (= Coronophoraceae) has been variously accepted in the Coronophorales or placed in the Sordariales where it currently stands. Nannfeldt (1975) suggested the Nitschkiaceae be regarded as "a highly specialized satellite group derived from the Lasiosphaeriaceae" and be included in the Sordariales. The concept of the Lasiosphaeriaceae at that time contained taxa with characters that led to the misinterpretation of relationships between the two families. Taxa that herein are shown to be outside the Lasiosphaeriaceae were cited as having characteristics that united the Lasiosphaeriaceae with the Nitschkiaceae. Carroll and Munk (1964) suggested that the Coronophoraceae were nonostiolate relatives of the Lasiosphaeriaceae, closely related because of the putative intermediate nature of one species, *Lasiosphaeria noonaedaniae* Carroll & Munk. This is a species of *Lasiosphaeriella,* and the genus is represented here by *L. nitida* and shown to be outside the Lasiosphaeriaceae. Sivanesan (1978) suggested close affinities of the two groups when he described the genus *Lasiobertia* Sivan. (herein confirmed to be xylariaceous). Nannfeldt (1975) was quite correct in placing the Nitschkiaceae firmly in the ascohymenial and unitunicate pyrenomycetes but not correct in interpreting the closer affinities of the family.

Our data show *Nitschkia grevillii* and *Chaetosphaerella phaeostroma* (formerly a member of the Lasiosphaeriaceae) forming a strongly supported clade, which occurs as an unsupported sister group of the Hypocreales within the well-supported subclass Hypocreomycetidae. This clade is accepted as the order Coronophorales, which finds its placement in the Hypocreomycetidae.

Ceratostomataceae. The Ceratostomataceae had its placement in the Sordariales until phylogenies based on nrDNA and RPB2 sequences placed *Melanospora zamiae,* the type, and several other species in the Hypocreales (Zhang and Blackwell 2002). In our analyses, *Melanospora* maintains this placement.

Annulatascaceae. The Annulatascaceae originally was placed in the Sordariales (Wong et al 1998), but based on molecular data it was found to have affinities outside the order (Réblová and Winka 2001). Kirk et al (2001) place the Annulatascaceae in the Sordariomycetidae inc. sed. The family, which is represented here by two species of *Annulatascus, A. velatispora,* the type and *A. triseptatus,* is highly supported by bootstrap and Bayesian support. The clade that contains the Annulatascaceae also includes the Ophiostomatales and three taxa formerly in the Lasiosphaeriaceae, *Pseudohalonectria, Plagiosphaera* and *Ceratosphaeria* (see below). This overall clade occurs as an unsupported clade that is a sister group of the well-supported Diaporthales. We accept the placement of the Annulatascaceae in the Sordariomycetidae inc. sed. by Kirk et al (2001).

Batistiaceae. The Batistiaceae was established for a single species, *Batistia annulipes,* and was placed in the Sordariales based on its phialidic conidiogenesis (Samuels and Rodrigues 1989). The genus had been linked at various times to other groups, for example, to the Xylariaceae based on its stipitate ascomata, carbonaceous texture and brown ascospores (Ciferri 1958) and to the Cephalothecaceae based on its cephalothecoid peridium (Samuels and Rodrigues 1989). Kirk et al (2001) removed the Batistiaceae from the Sordariales and placed it in the Sordariomycetidae inc. sed. Our data not only support its removal from the Sordariales but also its removal from the Sordariomycetidae. Its affinities outside the perithecial ascomycetes were not expected and, thus, were not tested with this dataset. Therefore the family is placed in the Pezizomycotina inc. sed. until further studies can be conducted.

Taxa included in the lasiosphaeriaceous complex.—The Lasiosphaeriaceae as circumscribed here is paraphyletic. Based on molecular data, 11 genera are retained in the redefined lasiosphaeriaceous complex: *Apiosordaria, Bombardia, Bombardioidea, Cercophora, Jugulospora, Lasiosphaeria, Podospora, Schizothecium, Strattonia, Triangularia* and *Zygopleurage*. In addition, based on morphological data, 13 genera also belong in the group: *Anopodium, Apodospora, Arniella, Arnium, Camptosphaeria, Diffractella, Emblemospora, Eosphaeria, Fimetariella, Periamphispora, Pseudocercophora, Tripterosporella* and *Zygospermella* (TABLE II). A number of taxa in synonymy with these genera also must be re-assessed.

As discussed previously, ascospore morphology in the Sordariales exists as a continuum from hyaline and cylindrical to brown and ellipsoid. Many genera in the lasiosphaeriaceous complex possess ascospores that represent the intermediate stage in this continuum by having a brown, ellipsoid cell and different degrees of a hyaline cell. The 11 sampled genera possess ascospores that represent this continuum. *Lasiosphaeria ovina* possesses hyaline, cylindrical ascospores, while *Cercophora mirabilis* and *Bombardia bombarda* ascospores are cylindrical with a brown, ellipsoid apical cell and a wide, elongate, hyaline basal cell. In *Podospora fimiseda* the basal, hyaline cell is long and narrow and has appendages with a complex microstructure. In *Schizothecium curvisporum* the basal cell is short and narrow and the brown cell is strongly curved. *Zygopleurage zygospora* has unmistakeable elongate ascospores with swollen brown cells at each end joined by a long, hyaline, collapsing intercalary cell. In *Apiosordaria verruculosa, Jugulospora rotula* and *Strattonia carbonaria,* the variously ornamented, brown cell is ellipsoid and the basal hyaline cell is small and conical. In *Triangularia mangenotii,* the brown cell is triangular, tapered at the top, wider at the bottom and the basal hyaline cell is short, semicircular and wide. *Bombardioidea anartia* has ascospores that are one-celled, brown and ellipsoid, similar to those of *Sordaria*. The other genera that are included in the Lasiosphaeriaceae for which no molecular data is available find their placement here because of ascospore morphology. All members have ascospores that vary along the brown cell/hyaline cell continuum.

Taxa excluded from the lasiosphaeriaceous complex.—All other genera included in the Lasiosphaeriaceae by Eriksson and Hawksworth (1993, 1998), Eriksson et al (2001) or Kirk et al (2001) have their placement elsewhere (TABLE II).

Taxa with relationships within the Sordariomycetidae. *Chaetosphaeria, Melanochaeta* and *Striatosphaeria* have been transferred to the Chaetosphaeriaceae (Reblova et al 1999), and our molecular data concur with that finding. Four other taxa, *Ascovaginospora, Lasiosphaeriella, Linocarpon* and *Caudatispora,* find their placement in a larger unsupported clade containing the Helminthosphaeriaceae. Their relationships to each other and to the well-supported Chaetosphaeriaceae remain unresolved. *Lasiosphaeriella* was believed by Carroll and Munk (1964) to be intermediate between Coronophoraceae and Lasiosphaeriaceae because of its tuberculate peridium, radiating (diverging vertical) cells in the basal stroma, stalked ascus and allantoid ascospores. The germination of the ascospores by phialides suggested it belonged in the Lasiosphaeriaceae. This combination of characters made it difficult to place confidently it in any family, and it remained in the Lasiosphaeriaceae pending molecular information (Huhndorf and Fernández 1999). *Linocarpon* was placed in the Lasiosphaeriaceae by Hyde (1992a) because of ascus and ascospore morphology. It currently resides in the Hyponectriaceae (Eriksson et al 2001) with a question mark, and Kirk et al (2001) places it in the Xylariales. In our parsimony analyses, *Lasiosphaeriella nitida* occurs outside the Lasiosphaeriaceae on a branch with *Linocarpon appendiculatum* as a sister group to the Helminthosphaeriaceae. *Caudatispora* contains two species that are characterized by superficial clusters of ascomata and hyaline, ellipsoid ascospores with apiculate ends. Our data place *C. biapiculata* outside the Lasiosphaeriaceae on a lone branch as a sister taxon to the Helminthosphaeriaceae and Chaetosphaeriaceae.

Ascovaginospora was described for a single species from submerged *Carex* stems whose unicellular ascospores have a striking tetraradiate sheath (Fallah et al 1997). Using SSU nrDNA sequence data the species grouped with *Podospora anserina* and Fallah et al (1997) placed it in the Lasiosphaeriaceae. This placement was reiterated by Chen et al (1999). With our larger dataset, the genus is found to be outside the Lasiosphaeriaceae on a lone branch as a sister taxon of the Boliniales.

Barrina was not placed in the Lasiosphaeriaceae in the compiled lists of fungi (TABLE II) but based on teleomorph morphology it was thought to have a relationship with some members of the family, differing however from *Lasiosphaeria* and *Cercophora* (Ramaley 1997). The ascospores of *Barrina* are hyaline, ellipsoid, one-celled and lack a germ slit. They also are distinctive in that they readily germinate to form branched filaments that produce ascoconidia within the ascus. Ramaley (1997) suggested that the *Phialophora*-like anamorph most closely resembled anamorphs reported for some *Coniochaeta* species. The conidia may be formed on terminal or intercalary conidiogenous cells, which are reduced phialides that are not delimited from the subtending hyphal cell by a basal septum. *Coniochaeta* species with *Lecythophora* Nannf. anamorphs also form conidia on intercalary phialides (Gams 2000, Weber 2002). Our data strongly support the transfer of *Barrina* to the Coniochaetaceae.

Porosphaerella originally was described in the Trichosphaeriaceae (Müller and Samuels 1982) but later moved to the Chaetosphaeriaceae by Réblová et al (1999). In LSU analyses, Réblová and Winka (2000) found *P. cordanophora* to be outside the Chaetosphaeriaceae as a basal taxon in the Sordariales. It never was placed in the Lasiosphaeriaceae but was thought to have affinities to *Chaetosphaeria* and *Porosphaerellopsis,* putative members of the family. In our analyses it appears as an unsupported sister taxon of the Coniochaetaceae and might belong in the Coniochaetales sensu lato.

Annulatascus originally was placed in the Lasiosphaeriaceae and subsequently moved to its own family (Hyde 1992c, Wong et al 1998). The Annulatascaceae since has been shown to have affinities outside the Sordariales (Réblová and Winka 2001) with our data indicating possible affinities to the Ophiostomatales and the Diaporthales.

Pseudohalonectria and *Ophioceras* also had a place in the Lasiosphaeriaceae at one time but were found to have affinities to *Gaeumannomyces* (Chen et al 1999), and both were moved to the Magnaporthaceae (Shearer et al 1999). Our representatives grouped together, however, without support. We included a sequence of *P. lignicola* and a taxon we called *O. tenuisporum* because of its long, very thin ascospores (75–85 × 1.0–1.5 μm) and its tropical distribution. This collection differs from other collections of the species in having pale-colored ascomata occurring on a soft-textured petiole. Pale-colored ascomata are found mostly in *Pseudohalonectria* species, whereas most *Ophioceras* have darker ascomata. These characteristics also are reminiscent of the genus *Plagiosphaera* occurring on herbaceous stalks (Barr 1978). Most of the known species of *Pseudohalonectria* and *Ophioceras* occur on wood, and the relationships of those taxa with morphologically similar herbicolous ones have not been explored fully. Sequences for additional taxa would be helpful in understanding the delimitation of character states in these genera.

Our data suggest that *Ceratosphaeria lampadophora* also has affinities to this unsupported group. *Ceratosphaeria lampadophora* was shown to have a distinctive ascomal wall with a middle hyaline layer between two darker layers (Hyde et al 1997). Hyde et al (1999) recently described *Pseudohalonectria eubenangeensis* K.D. Hyde, Joanne E. Taylor & J. Fröhl. as a new species on palm with an ascomal wall structure very similar to *C. lampadophora*. *Pseudohalonectria eubenangeensis* spores are long, filiform and fasciculate, resembling some species of *Ophioceras*. *Ceratosphaeria lampadophora* spores are shorter, slightly curved at the ends and resemble some species of *Pseudohalonectria.* It also should be noted that the ascus apical rings in a number of these taxa are very similar (viz. refractive and thimble-shaped). However, ascal rings were found to be phylogenetically uniformative in the putative members of the Annulatascaceae (Ranghoo et al 1999, Réblová and Winka 2001).

Ordinal placement of these taxa is not clear with this dataset. They again come close to the Ophiostomatales clade, as was shown previously by Chen et al (1999). Overall the clade containing the Annulatascaceae, Ophiostomatales and Magnaporthaceae comes closest to the Diaporthales, although with no support. Relationships to the Diaporthales have been speculated for *Ophioceras* and *Pseudohalonectria* based on the morphological characteristics of long-beaked ascomata and deciduous asci (Shearer et al 1999).

Taxa with relationships within the Hypocreomycetidae. *Ceratocystis* long since has been removed from the Lasiosphaeriaceae and is thought to have its relationships in the Microascales (Spatafora and Blackwell 1994, Eriksson et al 2001). Our analyses show *C. virescens* clustering with *Plectosphaerella* as a sister group to a clade containing *Glomerella* (placed in Phyllachorales and Glomerellaceae respectively by Kirk et al 2001; both Sordariomycetes inc. sed. fide Eriksson et al 2001). This concurs with 18S data (Zhang and Blackwell 2002) showing *C. fimbriata* and *C. virescens* grouping with *Plectosphaerella* and *Glomerella.* Rehner and Samuels (1995) likewise show similar relationships using 28S data. Our molecular data suggest that *Porosphaerellopsis* and *Ascocodinaea* have affinities to *Glomerella* and possibly *Ceratocystis* and *Plectosphaerella* but without support. This assemblage forms a sister group of a larger clade containing Hypocreales, Microascales and Coronophorales, which is highly supported with 86% bootstrap and 95% Bayesian support.

The affinities of *Porosphaerellopsis* have never been clear, with *P. sporoschismophora* having characteristics such as net-like paraphyses that are uncommon in the Sordariomycetes. The anamorph is suggestive of that of *Melanochaeta* in the Chaetosphaeriaceae, but it cannot be unequivocally referred to *Sporoschisma* Berk. & Broome because of the terminal pores in the conidia (Samuels and Müller 1978). The fusiform, septate ascospores also resemble those in *Melanochaeta* but again differing in having germ pores. Our data show that *P. sporoschismophora* is not related to *M. hemipsila.* The affinities of *Ascocodinaea* were thought to be clearer. Its small, dark, setose, pseudoparenchymatic ascomata and dematiaceous phialidic anamorphs placed it firmly in the Lasiosphaeriaceae (Samuels et al 1997b). Its simple teleomorph morphology is very similar to *Chaetosphaeria* and is distinguished by its stout tapering setae and versicolorous ascospores. Its *Codinaea* anamorph is similar to those found in a number of *Chaetosphaeria* species. Our data indicate that *A. stereicola* is not related to *Chaetosphaeria* or taxa in the Lasiosphaeriaceae. Both *Porosphaerellopsis* and *Ascocodinaea* have similar net-like paraphyses, but these are not seen in the other taxa in this clade. Additional molecular analyses with other taxa are necessary to refine the placement of *P. sporoschismophora* and *Ascocodinaea,* but at present they both are placed in the Hypocreomycetidae inc. sed.

Based on molecular data, *Chaetosphaerella* finds its placement in the Coronophorales. *Chaetosphaerella phaeostroma* clusters with *Nitschkia grevillii* with strong support. *Chaetosphaerella* shares the characteristics of munk pores in the ascomal wall cells, sterile ascomal base and inflated paraphyses with some members of the Nitschkiaceae. Based on morphology, two additional genera formerly in the Lasiosphaeriaceae also belong in the Coronophorales. *Spinulosphaeria* is very similar to *Chaetosphaerella* in having obpyriform to clavate ascomata with a stout sterile base, seated on a dense hyphal subiculum. These taxa also share other characteristics, such as broadly cellular, inflated paraphyses and asci without any distinct apical apparatus. *Spinulosphaeria* differs from *Chaetosphaerella* in its tooth-like spines on the ascomata, long-stipitate asci and ellipsoid, one-septate, brown ascospores. All attempts to sequence DNA from *Spinulosphaeria* failed. The morphology of *Thaxteria* has been used in the past to infer relationships to the Lasiosphaeriaceae or the Nitschkiaceae. Direct sequencing from PCR products of *Thaxteria* was problematic, so attempts were made to sequence from cloned copies. However, three different LSU copies were found from seven cloned sequences. Analyses including these copies placed *Thaxteria* in either the Lasiosphaeriaceae or the Nitschkiaceae (data not shown). *Thaxteria* has the Nitschkiaceae characteristics of munk pores in the ascomal wall cells, long stipitate asci and collapsing ascomata. Subramanian and Sekar (1990) accepted both *Spinulosphaeria* and *Thaxteria* in the Coronophorales, a disposition we also accept.

Taxa with relationships within the Xylariomycetidae. Based on molecular data, two taxa, *Apiospora* and *Lasiobertia,* find their placement in the Xylariales. *Apiospora* was included in the Lasiosphaeriaceae in Eriksson and Hawksworth (1993) but since had been moved to its own family, Apiosporaceae (Hyde et al 1998). *Lasiobertia* was described by Sivanesan as differing from the Coronophorales and Lasiosphaeriaceae only in the presence of an amyloid ring. Hyde (1993) emphasized the amyloid nature of the ascus ring and the morphology of the ascospores and paraphyses, which he thought suggested a relationship to *Oxydothis* Penz. & Sacc. Wang and Hyde (1999) suggested the placement of *Lasiobertia* in the Clypeosphaeriaceae, while Kirk et al (2001) place the genus in the Apiosporaceae. Our representative is a new species that will be described shortly. *Iodosphaeria* was not sampled, but the presence of the amyloid ring suggests its affinities are also in the Xylariales and we accept its placement in the Amphisphaeriaceae (Eriksson et al 2001) although it recently was placed in its own family Iodosphaeriaceae (Hilber and Hilber 2002).

Taxa not sampled or with uncertain relationships. For many genera currently included in the Lasiosphaeriaceae no molecular data are available. Characteristics of some of these genera suggest relationships to other families in the order or even to other orders, however their placement is uncertain. Taxa with long, narrow ascospores, such as *Acrospermoides, Neolinocarpon, Palmicola, Plagiosphaera* and *Pulmosphaeria,* may show affinities to *Linocarpon, Ophioceras* or the Diaporthales. *Mycomedusiospora,* with light-colored ascomata, may show a relationship with the Hypocreales. *Myelosperma* was placed in its own family but the affinities of it were not certain (Hyde and Wong 1999, Kang et al 1998). *Merugia,* with its filiform ascospores, has a *Chalara*-like anamorph associated with it, suggesting it might be allied with the Chaetosphaeriaceae. *Phragmodiscus* has fusiform multiseptate ascospores and an ascus apical ring that is suggestive of *Ceratosphaeria.* It differs in its ascomata immersed in a large, soft, spongy subiculum. With the Lasiosphaeriaceae redefined to include only those taxa with a characteristic morphology, these other taxa must be removed and for now are placed in the Sordariomycetidae inc. sed. (TABLE II).

CONCLUSION

In this work we have modified the circumscription of the Sordariales to better reflect phylogenetic relationships of the true members of the order. Dissimilar elements at the family and genus level have been transferred to groups that reflect their relationships. In doing so, we considered it necessary to make the nomenclatural changes for some taxa removed from the order. Two clades, Chaetosphaeriales and Coniochaetales, were natural candidates for elevation to ordinal rank. These clades received strong support, have distinctive teleomorph and anamorph morphologies and are considered places in the tree where large radiations of taxa occurred. The use of the family complex designation in place of the family name for the Lasiosphaeriaceae and Chaetomiaceae emphasizes the paraphyletic nature of these groups and thus serves to distinguish them from the monophyletic groups constituting families in the tree.

In this paper, traditional morphological-based hypotheses of relationships were tested using molecular data. In many cases these hypotheses conflicted with molecular-based hypotheses and new morphological-based hypotheses have been suggested that correspond to the molecular framework. The morphological data from numerous previous workers in various groups provided a good framework from which to test old hypotheses and form new ones. The use of a combination of molecular and morphological data herein have provided a more natural classification of the Sordariales and the lasiosphaeriaceous complex that leads to clear directions for additional work in these groups.

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