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Article *in* Mycologia · January 2010

DOI: 10.3852/09-043 · Source: PubMed

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In Press at Mycologia, published on July 17, 2009 as doi:10.3852/09-043

Short title: Coronophorales phylogeny

Multigene phylogeny of the Coronophorales: morphology and new species in the order

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Abstract: The phylogenetic relationships within Coronophorales have been debated because of uncertainty over the taxonomic usefulness of characterisitics such as quellkörper, number of ascospores per ascus, presence of ascospore appendages, presence of subiculum and ascomatal vestiture. The phylogenetic relationships are examined with DNA sequence data from three nuclear genes targeting 69 taxa and 130 new sequences representing collections from Africa and the Americas. Analyses recovered monophyletic Bertiaceae, Chaetosphaerellaceae and Scortechiniaceae and a paraphyletic Nitschkiaceae. A single collection of *Coronophora gregaria* is included and Coronophoraceae is accepted. Bertiaceae is expanded to include *Gaillardiella*, and *Thaxteria* is synonymized with *Bertia* with a new combination, *B. didyma*. Three new species of *Bertia* are described: *B. ngongensis* from Kenya, *B. orbis* from Kenya and Costa Rica and *B. triseptata* from Ecuador and Puerto Rico. *Bertia gigantospora* is transferred from *Nitschkia*. Scortechiniaceae is confirmed for the quellkörper-bearing taxa including monotypic *Biciliospora, Coronophorella*, *Neofracchiaea*, *Scortechiniella* and *Scortechiniellopsis*. *Tympanopsis* is reinstated for *T. confertula* and *T. uniseriate*, while *Scortechinia* is more narrowly circumscribed to include *S. acanthostroma* and the new species, *S. diminuspora* from Ecuador. *Cryptosphaerella* is accepted in Scortechiniaceae including six new species from Kenya and Costa Rica, *C. celata*, *C. costaricensis*, *C. cylindriformis*, *C. elliptica*, *C. globosa* and *C. malindensis*. *Spinulosphaeria* is accepted in Coronophorales with uncertain family placement. The number of ascospores in the ascus is not phylogenetically useful in distinguishing genera within the order. The quellkörper continues to be an important character in defining the Scortechiniaceae, while taxa within the group show a mixture of morphological characteristics of varying phylogenetic importance. The presence of smooth versus spinulose subiculum aids in separating *Tympanopsis* and *Scortechinia*, and erumpent ascomata distinguish *Cryptosphaerella* species. Taxa within the Bertiaceae vary along the lines of robust, tuberculate, collapsing ascomata and large, hyaline to pigmented, septate ascospores.

Key words: Ascomycota, Coronophorales, LSU rDNA, phylogeny, quellkörper, *rpb2*, *tef1*

INTRODUCTION

Members of the Coronophorales are common wood-inhabiting Ascomycete fungi with a worldwide distribution. Coronophorales is characterized by taxa with mostly superficial ascomata, sometimes with an extensive hyphal subiculum or well developed basal stroma that often becomes cupulate or collapsed, and in some cases an ostiolar opening is either indistinct or lacking. In many taxa a quellkörper is present in the centrum, and this structure is unique to this group of ascomycetes. The quellkörper is a subcylindrical to inverted-conical structure attached to the roof of the centrum, composed of thick-walled, concentrically arranged, hyaline cells that functions by enlarging and forcibly breaking open the ascoma and allowing ascospore release. Other important characteristics of the group include Munk pores that are found in the ascomatal wall cells, thin-walled asci with a long stipe and in most cases without an apical ring and ascospore numbers often greater than eight.

Coronophorales are found on woody substrates in many parts of the world. Collections from temperate European localities form the majority of the early names in the group with some additional collections made from North America (von Höhnel 1907; Fitzpatrick 1923; Nannfeldt 1975a, b). Over the years new species and collections have been added from tropical locations such as French Guiana, India, Singapore and western Africa (Sivanesan 1974, Nannfeldt 1975b). Until now Coronophorales have not been seriously studied in eastern Africa, although a few species were described from Congo and Kenya (von Arx and Müller 1954, Nannfeldt 1975b).

Members of the Coronophorales have been treated in their own order (Nannfeldt 1932, Müller and von Arx 1973, Subramanian and Sekar 1990) or in order Sordariales (Nannfeldt 1975a, b; Barr 1990; Hawksworth et al 1995) under either one or two families, Coronophoraceae and Nitschkiaceae (Nannfeldt 1932; Nannfeldt 1975a, b) (TABLE I). Huhndorf et al (2004) used molecular data to show that the group is not related to Sordariales and to demonstrate the monophyly of the Coronophorales in subclass Hypocreomycetidae. They suggested the separation of the taxa into four families (family Coronophoraceae was not sampled). However their molecular study was based on limited taxon sampling and therefore did not adequately address various conflicting taxonomic treatments previously proposed for taxa within the group by different taxonomists.

Narrow generic circumscriptions for taxa in the Coronophorales were adopted by Müller and von Arx (1973) (TABLE I). Nannfeldt (1975a, b) and Subramanian and Sekar (1990) presented detailed historical perspectives of the Coronophorales and its components. The phylogenetic relationships within group have long been debated because of uncertainty over the taxonomic usefulness of distinguishing characterisitics, such as quellkörper, number of ascospores per ascus, presence of ascospore appendages, presence of subiculum and ascomatal vestiture. Nannfeldt (1975b) accepted five genera in the Nitschkiaceae and also published detailed morphology, taxonomy and nomenclature of the many taxa. He considered most of the morphological characters of value in the delimitation of the taxa at specific levels only and therefore adopted broad generic concepts, which resulted in drastic reduction in the number of genera recognized (TABLE I). Von Arx (1981) followed the generic circumscriptions of Müller and von Arx (1973) (TABLE I), adding a few more taxa including *Lasiobertia*, which since has been shown to belong outside the group (Huhndorf et al 2004). Subramanian and Sekar (1990) also adopted narrow generic circumscriptions, differing from Nannfeldt (1975b) and chose to recognize two families for the taxa (TABLE I).

Huhndorf et al (2004) in molecular studies of Coronophorales used large subunit ribosomal nuclear DNA sequence data that resulted in their segregation of four families in the group, including two new families, Chaetosphaerellaceae for *Chaetosphaerella phaeostroma* (Durieu & Mont.) E. Müll. & C. Booth and *Crassochaeta nigrita* (Berk. & Broome) Réblová and Scortechiniaceae for *Scortechinia conferta* (Schwein.) Subram. & Sekar, *Neofracchiaea callista* (Berk. & M.A. Curtis) Teng and *Euacanthe foveolata* (Berk. & M.A. Curtis ex Berk.) Subram. & Sekar. In their analyses Bertiaceae was represented by *Bertia tropicalis* Huhndorf, A.N. Mill. & F.A. Fern. and *B. moriformis* (Tode) de Not. and a paraphyletic Nitschkiaceae by *Nitschkia meniscoidea* Huhndorf, A.N. Mill. & F.A. Fern., *N. grevillei* (Rehm) Nannf., *Acanthonitschkea argentinensis* Speg. and *Fracchiaea broomeiana* (Berk.) Petch.

Due to the limited number of taxa used by Huhndorf et al (2004), taxonomic relationships and circumscriptions of some groups in the order remained uncertain. As a result in this followup study we not only target broad taxon sampling but also take into account the great morphological variability that is observed within currently recognized groups. Consequently taxa in 19 morphologically recognized genera were targeted for phylogenetic analyses with DNA partial sequence data of large subunit ribosomal nuclear DNA (LSU rDNA), ribosomal polymerase II subunit 2 (*rpb2*) and translation elongation factor 1 alpha (*tef1*). The questions we considered in this study include (i) what are the generic and familial circumscriptions within the order, (ii) what are the taxonomic placements of previously unsequenced taxa and (iii) which are the robust morphological characters that can be used in delineating taxa within Coronophorales?

MATERIALS AND METHODS

Taxon sampling and morphological analyses.—The taxa used in this study are listed (TABLE II) together with their geographical locality, associated information and GenBank accession numbers. Ascomata were mounted in water and replaced with lactophenol containing azure A. A minimum of 30 asci, ascospores were measured with Scion Image (www.scioncorp.com) and measurements were made and images were captured of material in both mounting fluids. Ascomata were sectioned at 5 µm for light microscopy following Huhndorf (1991) or were freehand sectioned. Images were captured with photomacrography, bright field (BF), phase contrast (PH) and differential interference microscopy (DIC), and photographic plates were produced following Huhndorf and Fernández (1998). Representative species covering five families and 19 genera within the Coronophorales were included in the analyses to determine the phylogenetic position of taxa currently accepted in the order. A total of 78 taxa were included in the analyses; 69 were newly sequenced for this study (TABLE II). The full datasets contained respectively 72, 35 and 44 taxa for the LSU rDNA, *rpb2*, and *tef1* genes, while a reduced dataset of 40 taxa from which at least two genes were available was used in the combined analyses allowing for some missing data. All voucher specimens are deposited in F and the Kenyan specimens also are deposited in EA.

DNA extraction, PCR amplification, sequencing and sequnce alignment.—Total DNA was extracted with the Dneasy Plant Mini Kit (QIAGEN, Hilden, Germany) following the instructions of the manufacturer. Phylogenetic analyses were conducted with partial sequences of three genes: translation elongation factor 1 alpha (*tef1*), nuclear ribosomal large subunit (LSU rDNA) and RNA polymerase II subunit (*rpb2*). Nuclear LSU was amplified with primers LROR, LR6 and LR3 (Vilgalys and Hester 1990); *tef1* was amplified with primers EF1-526F, EF1-983F, EF1-1567R, Ef-df and EF-gr obtained from the Assembling the Fungal Tree of Life Website (http://ocid.nacse.org/research/aftol/primers.php), while *rpb2* was amplified with fRPB2-5F and fRPB2-7cR (Liu et al 1999).

Polymerase chain reaction (PCR) was carried out with this protocol: Final volume of the PCR reaction was 25 µL and contained 2.5 µL buffer, 2.5 µL dNTP mix, 1 µL each primer (10 µm), 5 µL BSA, 1.5 µL taq, 2 µL genomic DNA extract and 9.5 µL deionized water. The reaction was allowed to run for 34 cycles. The annealing temperature was set at 50 C for LSU rDNA and at 58 C for both *tef1* and *rpb2* reducing by 1 C each cycle for total of eight cycles and then set at 50 C for the remaining cycles. The fragments were sequenced with the Big Dye Terminator reaction kit (ABI PRISM, Applied Biosystems, Foster City, California). Sequencing was performed with the same set of primers as PCR. The other sequences were obtained from GenBank. Sequences were aligned with multiple sequence alignment program, MUSCLE® (Edger 2004) and further edited manually. Ambiguously aligned regions were removed from the data matrices. Sequence data were deposited in GenBank and alignments in TreeBASE (XXXXX).

Phylogenetic analyses.—Phylogenetic analyses were carried out with maximum parsimony (MP), maximum likelihood (ML) and Bayesian analyses for single-gene data matrices and on combined gene dataset. Maximum parsimony (MP) analyses were carried out with PAUP* 4.0b10 (Swofford 2002). Heuristic searches were performed with random addition and TBR branch swapping procedures, characters unordered and MULTREES option in effect. Bootstraping (Felsenstein 1985) was performed with 1000 replicates to estimate branch support.

Modeltest 3.7 (Posada and Crandall 1998) was used to determine the best-fit model of evolution for Bayesian and maximum likelihood analyses. Bayesian analyses employing Markov chain Monte Carlo (MCMC) were carried out with MrBayes 3.1 (Huelsenbeck and Ronquist 2001). Four MCMC chains were run simultaneously for 1–5 million generations for the single gene and combined datasets with trees sampled every 100th generation. Maximum likelihood (ML) analyses were carried out for each of the four datasets employing the best-fit model of evolution obtained from Modeltest 3.7 (Posada and Crandall 1998) with Garli 0.951 (Zwickl 2006).

RESULTS

Sequence alignment and phylogenetic analyses.—Sequence alignment resulted in LSU rDNA with 1139 characters. A total of 34 were ambiguously aligned and hence excluded from analyses, 586 were constant, 91 parsimony uninformative ,while 428 were parsimony informative. *Tef1* had 824 characters. Three ambiguously aligned were excluded, 391 were constant, 134 were parsimony uninformative and 296 were parsimony informative. In the case of *rpb2* 1041 characters, 443 were constant, 72 were parsimony uninformative while 526 were parsimony informative. The combined dataset had a total of 2954 characters, of which 1580 were constant, 274 were parsimony uninformative, while 1100 were parsimony informative. The best-fit model of evolution for LSU rDNA and combined datasets was GTR + I + G (Rodriguez et al 1990), while TRN + I + G (Tamura and Nei 1993) was the preferred model of evolution for *tef1* and *rpb2* datasets. Maximum parsimony analyses of LSU rDNA and combined datasets generated respectively 12 and five most parsimonious trees, while *tef1* and *rpb2* generated two trees each. Because there were no conflicts in the phylogenies produced by different analyses (MP, ML and Bayesian), we present only maximum likelihood trees for LSU, *tef1*, *rpb2* and combined data analyses (FIGS. 1–4).

Taxon relationships.—The multiple gene genealogies all contain monophyletic clades representing Bertiaceae, Chaetosphaerellaceae, Nitschkiaceae and Scortechiniaceae. Coronophoraceae is represented in all trees except in the LSU rDNA by *Coronophora gregaria* (Lib.) Fuckel. There were some differences among generic placements within individual families resulting from different analyses, but most of these relationships were not supported. Bertiaceae included species of *Bertia*, *Thaxteria* and *Gaillardiella* and formed a strongly supported monophyletic group with high bootstrap (BS) and Bayesian posterior probabilities (PP) (FIGS. 1, 2). In our analyses *Thaxteria didyma* (Speg.) Sacc. is nested within *Bertia* (FIG. 1). Chaetosphaerellaceae, composed of *Chaetosphaerella* and *Crassochaeta,* forms a strongly supported clade (FIGS. 1–4). Genus *Coronophora,* represented by the type species *C. gregaria*, does not group within Bertiaceae, Chaetosphaerellaceae, Nitschkiaceae or Scortechiniaceae (FIGS. 2, 4). *Spinulosphaeria* whose placement in the Coronophorales has been debated is also nested within the order but of unclear position (FIG. 1). Taxa in *Nitschkia* group together with *Acanthonitschkea* in all analyses, but this relationship is weakly supported in *tef1* and *rpb2* gene analyses (FIGS. 1–4). Genus *Fracchiaea* as currently circumscribed is polyphyletic (FIG. 2). Scortechiniaceae form a strongly supported monophyletic group comprising *Scortechinia*, *Scortechiniella*, *Scortechiniellopsis*, *Biciliospora*, *Neofracchiaea*, *Euacanthe*, *Neotrotteria*, *Cryptosphaerella*, *Tympanopsis* and an unnamed Coronophorales (FIGS. 1–4). *Scortechinia* is recognized for two species as is *Tympanopsis* (FIGS. 1–4). *Cryptosphaerella* species form a monophyletic group within Scortechiniaceae in the *tef1* and combined datasets with significant PP (FIGS. 2, 4) but are polyphyletic in the LSU rDNA and *rpb2* datasets (FIGS. 1, 3). *Coronophorella*, *Scortechiniella* and *Biciliospora* form a supported clade with high PP in the combined data analysis (FIG. 4).

Taxonomy.—Currently recognized families in the Coronophorales, Bertiaceae, Scortechiniaceae and Chaetosphaerellaceae were found to be monophyletic. The concept of Bertiaceae is expanded to include *Gaillardiella* (FIGS. 1, 2, 4), and *Thaxteria* is found to be nested within *Bertia*. Scortechiniaceae contains the quellkörper-bearing taxa including six new species of *Cryptosphaerella* (FIGS. 1–4). Family Coronophoraceae is recognized for taxa in *Coronophora* (FIGS. 2–4). Nitschkiaceae is composed of *Nitschkia, Fracchiaea* and *Acanthonitschkea,* taxa that group together in supported clade (FIGS. 1, 4). However we were not able to obtain type of *Nitschkia* and therefore the circumscription of the genus and family remains equivocal until it is included in analyses.

Bertia didyma (Speg.) Mugambi & Huhndorf, comb. nov. FIG. 5a–e

MycoBank MB 513306

≡ *Bizzozeria didyma* Speg., Boletín de la Academia Nacional de Ciencias de Córdoba 11(4):519. 1889. Basionym.

≡ *Thaxteria didyma* (Speg.) Sacc., Sylloge fung. 9:687. 1891.

Specimens examined: COSTA RICA. Guanacaste: Cantón Cañas, Sector Hacienda Montezuma, 715 m, 7 Mar 2000, on 10 cm diam branch, *F.A. Fernández, G.M.Mueller, B. Strack, J.P. Schmit, L. Umaña, SMH4256* (F); Puntarenas: Los Alturas Forest Biosphere Research Park, adjacent to Parque International la Amistad, 8°96′16″N; 82°82′00″7W, 21 Jan 2007, on decayed wood, *J.L. Crane et al*, *CR-206* (ILLS). ECUADOR. Orellana Province: Yasuni Biosphere Reserve, Tiputini Biological Station, Danta trail, 26 Mar 2002, on 25 cm log, *F.A. Fernández, A.N. Miller, SMH4719* (F).

Descriptions of this species are given by Fitzpatrick (1923) and Subramanian and Sekar (1990). Both of these authors based their information on the type specimen, but they differ somewhat in their interpretation of ascomatal and ascospore morphology. Fitzpatrick (1923) describes the ascomata as not prominently tuberculate and the surface as brownish and fibrilose with age, and Subramanian and Sekar (1990) describe ascomata as having a warty surface. Our collections best match the description given by Fitzpatrick and also match the drawing given by Müller and Booth (1972), which they also base on the type specimen.

Bertia gigantospora (Nannf.) Mugambi & Huhndorf, comb. nov. FIG. 5f–i

MycoBank MB 513307

≡ *Nitschkia gigantospora* Nannf., Svensk bot. Tidskr. 69(3):313. 1975. Basionym.

≡ *Calyculosphaeria macrospora* Fitzp., Mycologia 15:53. 1923. [non *Nitschkia macrospora* Teng, 1934; non *Bertia macrospora* Sacc., 1878]

Specimens examined: KENYA. Rift Valley Province: Kajiando District, Ngong Hills Forest, near aviation equipment, 1°24.682S, 36°38.182E, elev 2391 m, 16 Jun 2005, on branch on the ground, *GKM1136* (EA).

Bertia gigantospora is represented in our trees by a single collection from Kenya that yielded only *rpb2* and *tef1* sequences (FIGS. 2, 3). The collection matches the description of

Calyculosphaeria macrospora, which was transferred to *Nitchkia* by Nannfeldt (1972) and given a new name because the *macrospora* epithet was already occupied in the genus. The same is true within *Bertia* so the transfer must be made with the name given by Nannfeldt.

Bertia ngongensis Mugambi & Huhndorf, sp. nov. FIG. 5j–m

MYCOBANK MB 513308

Ascomata erumpentia, separata ad denso aggregata, tuberculata, turbinatascens in statu humectato, collabens in statu sicco, 850–900 µm alta, 730–900 µm diam. Paries ascomatis cellulis pseudoparenchymatis. Munk pori preasens. Asci clavati, curvi, octospori, 115–150 × 16–18 µm, partibus sporiferis 60–85 µm longitudine, stipitibus 45–75 µm longitudine. Ascosporae cylindricae, geniculatae, hyalinae, 1-septatae, 26–33 × 7–8 µm.

Etymology: Refers to the collection locality.

Ascomata erumpent through cracks in the bark, solitary or in small to large groups, turbinate when fresh, collabent when dry, tuberculate, with large sterile base, 730–900 µm wide, 850–900 µm high including the sterile base. Ascomatal wall composed of outer layer of brown thick-walled pseudoparenchymatous cells and inner layer of flattened hyaline cells. Munk pores present in ascomal wall cells, few per cell. Quellkörper absent, paraphyses few inflated, branched and septate. Asci clavate, long stipitate, 115–150 × 16–18 µm, spore-bearing part 60–85 µm, pedicel 45–75 µm, curved, thin-walled, no apical ring, 8-spored, biseriately arranged. Ascospores cylindrical, hyaline, geniculate, 1-septate, without mucilagenous sheath or appendages, 26–33 × 7–8 µm.

Habitat: On partialy decorticated woody branch on the ground in forested area.

Anamorph: Unknown.

Distribution: Presently known only from one tropical highland forest in Kenya.

Specimen examined: KENYA. Rift Valley Province: Kajiando District, Ngong Hills Forest near communication towers, 1°23.934S, 36°38.287E, elev 2367 m, 7 Dec 2006, on woody branch, *GKM1239* (EA HOLOTYPE, F ISOTYPE).

Bertia orbis Mugambi & Huhndorf, sp. nov. FIG. 5n–r

MycoBank MB 513310

Ascomata superficialia, separata vel dense aggregata, tuberculata, turbinatascens in statu humectato, collabens in statu sicco, 515–665 µm alta, 495–560 µm diam. Paries ascomatis cellulis pseudoparenchymatis, Munk pori preasens. Sine quellkörper, paraphysoides ramosus, hyalinae, crassi. Asci cylindrici-clavati, annulus apicalis, octospori, longe stipititae, 112–130 × 7–9 µm, partibus sporiferis 45–70 µm longitudine, stipitibus 45–65 µm longitudine. Ascosporae cylindricae ad fusoidae, hyalinae, 1-septatae, saepe curvus, 17–20 × 3–4 µm.

Etymology: *Orbis* (*lat.*) = world, denotes the wide geographical occurrence of the species.

Ascomata superficial, solitary or in large groups, turbinate when fresh, collabent when dry, with thick sterile base, tuberculate, 495–560 µm wide 515–665 µm high including the sterile base. Ascomal wall composed of outer layers of brown isodiametric pseudoparenchymatous cells and inner layer flattened hyaline cells, Munk pores present in ascomal wall cells. Quellkörper absent, paraphyses few, inflated, branched and hyaline. Asci cylindrical-clavate, long stipitate, 112–130 × 7–9 µm, spore-bearing part 45–70 µm, pedicel 45–65 µm, ascus apex with ring, eight spores partially biseriate. Ascospores cylindrical to broadly fusoid, hyaline, often slightly curved, 1-septate, median, without mucilagenous sheath or appendages, four guttulate, two per cell, 17–20 × 3–4 µm.

Habitat: Found growing on decorticated woody substrates in tropical forests above 1500 m.

Anamorph: Unknown.

Distribution: Known from tropical forests in Kenya and Costa Rica.

Specimen examined: COSTA RICA. Alajuela: Parque Nacional Volcan Arenal, La Fortuna de San Carlos, Pilón Trail, [10.4419, −84.7167], 15-VII-2001, on woody branch 1 cm diam, *S.M. Huhndorf, F.A. Fernández, A.N. Miller, M.P. DaRin, SMH4557* (USJ HOLOTYPE, F ISOTYPE); Punta Arenas: La Amistad Pacifico, Las Tablas, 8°56.47N 82°46.38W, elev 1680 m, 16-I-1999, on wood fragment, *F. A. Fernández, E. Fletes SMH4035* (F). KENYA. Western Province: Kakamega forest near south gate, 0°13N 34°51E, elev 1585 m, 17 Jan 2007, on woody branch, *GKM1271* (F, EA); Western Province: Kakamega Forest near north gate, 0°21N 34°51E, elev 1500 m, 17 Jan 2007, on woody branch, *GKM1259* (F, EA).

Bertia triseptata Mugambi & Huhndorf, sp. nov. FIG. 6a–e

MycoBank MB 513311

Ascomata superficialia, dispersa vel dense aggregata, atrobrunnea, turbinatascens in statu humectato, collabens in stactu sicco, basim grandis, tuberculata, 590–650 µm alta, 685–785 µm diam., paries ascomatis cellulis pseudoparenchymatis. Munk pori preasens, sine quellkörper, paraphysoides crassi, septati. Asci clavati, longe stipititae, octospori, 170–200 × 19–22 µm, partibus sporiferis 110–130 µm longitudine, stipitibus 75–100 µm longitudine. Ascosporae cylindricae, hyalinae, geniculatae et 3-septatae, 29–43 × 6–9 µm.

Etymology: Refers to the septation of ascospores.

Ascomata superficial, dark brown, usually aggregated in small or large clusters, turbinate when fresh, becoming collabent when dry, with large sterile base making the ascomata look as if stalked, tuberculate, 685–785 µm wide and 590–650 µm high including the sterile base. Ascomal wall ca. 95–136 µm wide, composed of outer layers of brown thick-walled pseudoparenchymatous cells and inner layers of flattened hyaline cells. Munk pores present in ascomatal wall cells. Quellkörper absent, paraphyses few, inflated, branched, hyaline and septate. Asci clavate, long stipitate, 170–200 × 19–22 µm, spore-bearing part 110–130 µm, pedicel 75–100 µm, thin-walled, no apical ring, eight spores partially biseriate to triseriate. Ascospores cylindrical, hyaline, geniculate, 3-septate, without mucilagenous sheath or appendages, 29–43 × 6–9 µm.

Habitat: On decorticated woody substrates in forested areas.

Anamorph: Unknown.

Distribution: Known from tropical forests in Ecuador and Puerto Rico, USA.

Specimen examined: USA. Puerto Rico: Luquillo Mountains, El Verde research area, 16 ha Grid 07.04.14, 18°19′28″N 65°48′59″W, elev 382 m, 18-VI-1995, on log 50 cm, 1 m above ground, *S.M. Huhndorf SMH1525*

(HOLOTYPE, F). ECUADOR. Orellana Province: Yasuni National Park, Bariso trail, 7-III-2001, on 10 cm log, *F.A. Fernández, A.N. Miller, R.Briones, SMH4379* (F).

Cryptosphaerella celata Mugambi & Huhndorf, sp. nov. FIG. 6f–j

MycoBank MB 513312

Ascomata immersa vel erumpentia, atrobrunnea, separata vel gregaria, in subiculo denso hyphis brunneis, turbinatascens in statu humectato, collabens in stactu sicco, paries ascomatis cellulis pseudoparanchymatis, Munk pori preasens, quellkörper conocus, 395 µm longitudine, basim 245 µm diam. Paraphyses absens. Asci clavati, longe stipititae, multispori, 100–127 × 9–11 µm, partibus sporiferis 38–70 µm longitudine, stipitibus 45–75 µm longitudine. Ascosporae oblongae ad cylindricae, curvae, hyalinae, aseptatae, 8–14 × 2–3 µm.

Etymology: *Celatus* (*lat.*) = hidden, describing the habit of the ascomata that are usually concealed under thick subiculum.

Ascomata immersed becoming erumpent, dark brown, solitary or aggregated in small groups, with thick, brown tomentum around ascomata and often completely covering them, turbinate when fresh, collabent when dry. Ascomal wall ca. 80–115 µm thick, composed of outer layer of brown thick-walled pseudoparenchymatous cells with the cells becoming hyaline and flattened toward the locule, Munk pores present in ascomal wall cells. Quellkörper present, large, conical, 395 µm long and 245 µm wide at the base, paraphyses absent. Asci clavate, long stipitate, 100–127 × 9–11 µm, spore-bearing part 38–70 µm, pedicel 45–75 µm, thin-walled, no apical ring, multispored, spores irregularly arranged. Ascospores oblong to cylindrical, curved, hyaline, 1-celled, without mucilagenous sheath or appendages, two guttulate one at each end of the spore, 8–14 × 2–3 µm.

Habitat: Found growing on partially decorticated woody branch on the ground in a disturbed forest patch.

Anamorph: Unknown.

Distribution: Currently known only from a tropical highland forest in Kenya.

Specimen examined: KENYA. Rift Valley Province: Nanyuki District, behind Bantu Lodge, 0°6′91″S, 37°2′70″E, 1 Dec 2006, on woody branch, *GKM1231* (HOLOTYPE EA).

Cryptosphaerella costaricensis Mugambi & Huhndorf, sp. nov. FIG. 6k–o

MycoBank MB 513313

Ascomata erumpentia, separata vel gregaria, turbinatascens in statu humectato, collabens in stactu sicco, brunnea setosus, 490–555 µm alta, 785–825 µm diam, paries ascomatis cellulis pseudoparenchymatis. Munk pori preasens, quellkörper conicus, 200 µm longitudine, basim 165 µm diam. Asci clavati, brevi stipititae, 95–115 × 11–12 µm, apice rotundatus, multisporae. Ascosporae cylindricae, hyalinae, aseptatae, 7–10 × 2–3 µm.

Etymology: Refers to the country in which the species was collected, Costa Rica.

Ascomata erumpent appearing superficial when the surrounding tissue wears off, solitary or in small groups, turbinate when fresh, collabent when dry, covered with short thick walled brown, septate tomentum, 490–555 µm high and 785–825 µm wide. Ascomal wall composed of outer layer of brown pseudoparenchymatous cells with the cells becoming hyaline and flattened toward the locule, Munk pores present in ascomal wall cells. Quellkörper present, conical, 200 µm long and 165 µm wide at the base. Asci clavate, short stipitate, 95–115 × 11–12 µm, thin-walled, rounded apex, no apical ring, multispored, spores irregularly arranged. Ascospores cylindrical, slightly curved, hyaline, 1-celled, with two large guttules, without mucilagenous sheath or appendages, 7–10 × 2–3 µm.

Habitat: Found growing on log in a forested area.

Anamorph: Unknown.

Distribution: Presently known only from one forest in Costa Rica.

Specimen examined: COSTA RICA. Guanacaste, Bagaces, Tempisque Conservation Area, Parque Nacional Palo Verde, 10:21:26.5245N −85:19:10.0313W, 13 Nov 2001, on log, *M. Oses MO2111* (HOLOTYPE F).

Cryptosphaerella cylindriformis Mugambi & Huhndorf, sp. nov. FIG. 6p–t

MycoBank MB 513314

Ascomata erumpentia, atrobrunnea, separata vel gregaria, in subiculo sparsi hyphis brunneis, turbinatascens in statu humectato, collabens in stactu sicco, 380–485 µm alta, 735–835 µm diam, setae sparsi. Ostiolum nullum, spinalis brevibus dentiformibus saepe ornata, paries ascomatis cellulis pseudoparenchymatis. Munk pori preasens, quellkörper conicus, 285 µm longitudine, basim 255 µm diam, paraphyses absens. Asci cylindricae-clavati, longae stipitatae, 90–220 × 9–12 µm, partibus sporiferis 38–55 µm longitudine, stipitibus 25–60 µm longitudine, apice rotundatus, multispori. Ascosporae cylindrici vel oblonge, hyalinae, curvus, aseptatae, 5–7 × 1–2 µm.

Etymology: Refers to the cylindrical ascospores.

Ascomata erumpent through the bark sometimes appearing superficial when the surrounding plant tissue weathers off, dark brown, sparse setae often on the surface, solitary or in small groups, turbinate when fresh, collabent when dry, nonostiolate, 380–485 µm high and 735–835 µm wide, sparse brown subiculum at the bases of ascomata. Ascomal wall of thick brown-walled pseudoparenchymatous cells, becoming flattened and hyaline in the inner cells, outer cells toothed, Munk pores present in the cells. Quellkörper present, conical, 285 µm long and 255 µm wide at the base, paraphyses absent. Asci cylindrical-clavate, long stipitate, 90–220 × 9–12 µm, spore-bearing part 38–55 µm, pedicel 25–60 µm, thin-walled, apex rounded, no apical ring, multispored, spores irregularly arranged. Ascospores cylindric to oblong, hyaline, curved, 1-celled, without mucilaginous sheath or appendages, often with two guttules, 5–7 × 1–2 µm.

Habitat: Found growing on partially decorticated woody substrates on the ground in forested areas.

Anamorph: Unknown.

Distribution: Known from highland forests in Kenya.

Specimen examined: KENYA. Coast Province: Taita Taveta District, Taita Hills, Ngangao forest, 3°22′30″S 38°20′45″E, 14 Nov 2006, on woody branch 5 cm diam, *GKM434N* (HOLOTYPE EA, ISOTYPE F); 10 Nov 2006, on woody branch, *GKM1187* (EA); 16 Apr 2005, on woody branch, *GKM1042* (EA); Nairobi Province: Nairobi Arboretum, 1°16′S, 36°48′E, 7 Jun 2005, on wood, *GKM1075* (EA).

Cryptosphaerella elliptica Mugambi & Huhndorf, sp. nov. FIG. 7a–e

MycoBank MB 513315

Ascomata erumpentia, gregaria, turbinatascens in statu humectato, collabens in stactu sicco, 635–665 µm alta, 935–1035 µm diam., spinalis brevibus dentiformibus saepe ornata, paries ascomatis cellulis pseudoparenchymatis. Munk pori preasens, quellkörper conicus, 245–320 µm longitudine, basim 165–220 µm diam., paraphyses absens. Asci clavati, longe stipiti, 295–325 × 25–30 µm, partibus sporiferis 140–155 µm longitudines, stipitibus 150–180 µm, apice rotundatus, miltisporae. Ascosporae ellipsoidae, aseptatae, 5–8 × 3–4 µm.

Etymology: Refers to the elliptical ascospores.

Ascomata erumpent often appearing superficial when surrounding tissues fall off, in large clusters, turbinate when fresh, collabent when dry, 935–1035 µm wide and 635–665 µm high. Ascomal wall ca. 65–80 µm in thick, composed of external wall of brown pseudoparenchymatous cells becoming flattened and hyaline in cells lining the locule, ascomal wall outer layer with tooth-like projections, Munk pores present in the cells. Quellkörper present, conical, 245–320 µm long and 165–220 µm wide at the base, paraphyses absent. Asci clavate, long stipitate, 295–325 × 25–30 µm, spore-bearing part 140–155 µm, pedicel 150–180 µm, thin-walled, apex rounded, multispored, spores irregularly arranged. Ascospores ellipsoid, hyaline, single celled, without mucilagenous sheath or appendages, 1–2 large guttules present in the cell, 5–8 × 3–4 µm.

Habitat: On decorticated woody branch on the ground.

Anamorph: Unknown.

Distribution: Presently known only from a single forested locality in Ecuador.

Specimen examined: ECUADOR. Orellana Province: Yasuni Biosphere Reserve, Tiputini Biological Station, Guacamayo Trail, beyond 500 m marker, [−.6361, −76.1528], 26-III-2002, on woody branch 4 cm diam, *F.A. Fernández, A.N. Miller SMH4722* (HOLOTYPE F).

Cryptosphaerella globosa Mugambi & Huhndorf, sp. nov. FIG. 7f–j

MycoBank MB 513316

Ascomata immersa vel erumpentia, separata vel gregaria, atrobrunnea, subiculum sparsum, lateralis collapsa in statu sicco, paries ascomatis cellulis pseudoparenchymatis, Munk spori preasens, quellkörper subcylindricae, 450 µm longitudine, basim 185 µm diam. Paraphyses absens. Asci clavati, partibus sporiferis rotundatus, 60–68 × 19-23 µm, partibus sporiferis 28–35 µm longitudine, stipitibus 25–37 µm longitudine, multispori. Ascosporae cylindricae, curvae, hyalinae, aseptatae, 8–12 × 2–3 µm.

Etymology: Refers to the globose asci.

Ascomata mostly immersed rarely becoming erumpent, dark brown, sparse brown subiculum around the ascomata, solitary or aggregated in small groups, occasionally laterally collabent. Ascomal wall ca. 65 µm thick, composed of brown pseudoparenchymatous cells, becoming hyaline and flattened toward the locule, surface cells of ascomatal wall more darkly pigmented and ridged. Munk pores present in ascomatal wall cells. Quellkörper present, subcylindrical, large, 450 µm long and 185 µm wide at the base. Paraphyes absent. Asci clavate, stipitate, 60–68 × 19–23 µm, spore-bearing part 28–35 µm, pedicel 25–37 µm, thin-walled, apex rounded, no apical ring, multispored, spores irregularly arranged. Ascospores cylindrical, allantoid, hyaline, aseptate, without mucilaginous sheath or appendages, wall often collapsing in parts, 8–12 × 2–3 µm.

Habitat: Found growing on partially decorticated woody branches in forest at 1800 m.

Anamorph: Unknown.

Distribution: Known only from single highland forest in Kenya.

Specimen examined: KENYA. Coast Province: Taita Taveta District, Taita Hills, Ngangao Forest, 3°22′30″S 38°20′45″E, elev 1800 m, 14 Nov 2006, on woody branch, *GKM471N* (EA HOLOTYPE); on woody branch, *GKM396N*, *GKM414N* (EA).

Cryptosphaerella malindensis Mugambi & Huhndorf, sp. nov. FIG. 7k–q

MycoBank MB 513317

Ascomata superficialia, atrobrunnea, in subiculo denso hyphis brunneis et ramosis, dispersa vel gregaria, turbinatascens in statu humectato, collabens in stactu sicco, spinalis brevibus dentiformibus saepe furcatis ornata, 455–515 µm alta, 630–650 µm diam, paries ascomatis cellulis pseudoparenchymatis. Ostiolum nullum. Quellkörper conicus, 385 µm longitudine, basim 153 µm diam, Munk pori preasens. Asci clavati, longe pedicellati, octospori, 75–130 × 7–11 µm, partibus sporiferis 25–45 µm longitudine, stipitibus 45–85 µm longitudine. Ascosporae fusoidae ad ellipsoidae, hyalinae, aseptatae, 10–14 × 3–5 µm.

Etymology: Refers to locality where the collection was made in Kenya, Malindi.

Ascomata dark brown, superficial, embedded in thick brown, smooth, septate subiculum, nonostiolate, turbinate when fresh, collabent when dry, 455–515 µm high, 630–650 µm wide. Ascomal wall ca. 54–60 µm thick, composed of two layers, a fibrous outer layer composed of loosely packed brown septate hyphae and an inner layer made of brown thick walled pseudoparenchymatic cells with outer layers of darkly pigmented cells with short spines and an inner layer hyaline flattened cells, Munk pores present, few per cell. Quellkörper present, large, conical, 385 µm long and 185 µm wide at the base, paraphyses absent. Asci clavate, long stipitate, 75–130 × 7–11 µm, spore-bearing part 25–45 µm, pedicel 45–85 µm, thin-walled, no apical ring, 8-spored, partially biseriate,. Ascospores broadly fusoid to ellipsoid, hyaline, aseptate, without mucilagenous sheath or appendages, containing 1–2 large guttules 10–14 × 3–5 µm.

Habitat: On decorticated woody branch under forested area.

Anamorph: Unknown.

Distribution: Known only from a coastal lowland forest in Kenya.

Specimen examined: KENYA. Coast Province: Malindi District, Arabuko-Sokoke National Park, 3°19′30″S 39°57′10″E, elev 6 m, 30 Oct 2006, on wood fragment, *GKM1150* (HOLOTYPE EA).

Scortechinia diminuspora Mugambi & Huhndorf, sp. nov. FIG. 7r–v

MycoBank MB 513318

Ascomata superficialia, in subiculo denso hyphis brunneis, spinalis et ramosis, ostiolum nullum, turbinatascens in statu humectato, collabens in stactu sicco, coriacea, 210–245 µm alta, 215–235 µm diam, paries ascomatis cellulis pseudoparenchymatis. Munk pori preasens, quellkörper subcylindrici, 175 µm longitudine, basim 75 µm diam, paraphyses absens. Asci clavati, longe stipitatae, 25–27 × 6–7 µm, partibus sporiferis 15–18 µm longitudine, stipitibus 7–11 µm longitudine, octospori. Ascosporae ellipsoidae, hyalinae, aseptatae, 5–6 × 2–3 µm.

Etymology: *diminutus* (*lat.*) = made small, refers to the size of the ascospores.

Ascomata superficial, embedded in thick subiculum whose hyphal terminations are characteristically spiny, subglobose, dark brown, nonostiolate, collabent when dry, coriaceous, 210–245 µm high and 215–235 µm wide. Ascomal wall membranous, thin, composed of brown pseudoparenchymatous cells, Munk pores present in ascomal wall cells. Quellkörper present, subcylindrical, 175 µm long and 75 µm wide at the base, paraphyses absent. Asci clavate, long stipitate, 25–27 × 6–7 µm, spore-bearing part 15–18 µm, pedicel 7–11 µm, apex rounded, no apical ring, eight spores irregularly arranged. Ascospores ellipsoid, hyaline, single celled, without mucilagenous sheath or appendages, 5–6 × 2–3 µm.

Habitat: On decorticated woody substrate on the ground.

Anamorph: Unknown.

Distribution: Known only from one forested locality in Ecuador.

Specimen examined: ECUADOR. Orellana Province: Yasuni Biosphere Reserve, Tiputini Biological Station, Puma Trail, [−.6361, −76.1528], 29-III-2002, on log, *F.A. Fernández, A.N. Miller SMH4763* (HOLOTYPE F).

Spinulosphaeria nuda Mugambi & Huhndorf, sp. nov. FIG. 8a–h

MycoBank MB 513319

Ascomata ovoidea, superficialia, dispersa, nigra, metallice nitentia, tuberculata, 455–530 µm alta, 475–525 µm diam. Paries ascomatis cellulis pseudoparanchymatis, Munk pori preasens, quellkörper absens, paraphysiodes hyalino, crassi et septata. Asci clavati, longe stipitatae, octospori, 125–145 × 14–19 µm, partibus sporiferis 48–60 µm longitudine, stipitibus 70–85 µm. Ascosporae ellipsoidea ad oblongae, brunnea, 1-septata, habens mucosae vaginae, 12–15 × 4–6 µm.

Etymology: Refers to ascomatal surface devoid of spines.

Ascomata ovoid, superficial, scattered, black with metallic irridescence, glabrous, noncollabent, tuberculate, 455–530 µm high and 475–525 µm wide. Subiculum is absent, ascomatal wall is composed of brown pseudoparenchymatous cells, munk pores present in the cell, few per cell. Quellkörper absent, paraphyses are broad, longer than asci, septate and constricted at the septa. Asci clavate, long stipitate, 125–145 × 14–19 µm, spore-bearing part 48–60 µm, pedicel 70–845 µm, thin-walled, lacking apical ring, eight spores partially biseriate, obliquely arranged,. Ascospores are ellipsoid to oblong, hyaline when young becoming brown at maturity, verruculose, 1-septate, with large persistent mucilaginous sheath, 12–15 × 4–6 µm.

Habitat: On decorticated woody substrate on the ground.

Anamorph: Unknown.

Distribution: Known only from a tropical rain forest in Puerto Rico, USA.

Specimen examined: USA: Puerto Rico: Luquillo Mountains, El Verde Research Area, 16 ha Grid, 18°19′26″N, 65°48′58″W, elev 395 m, 18-I-1996, on log 20 cm diam, *S.M. Huhndorf SMH1952* (HOLOTYPE F).

KEY TO THE FAMILIES

1. Ascomata with quellkörper …………….. Scortechiniaceae
1. Ascomata without quellkörper …………….. 2
2. Ascomata mostly tuberculate (if smooth ascospores uniformly brown), ascospores longer than 15 µm …………….. Bertiaceae
2. Ascomata smooth or with short spines …………….. 3
3. Ascomata erumpent, laterally collapsing …………….. Coronophoraceae
3. Ascomata superficial …………….. 4
4. Asci 8-spored, ascospores versicolorous …………….. Chaetosphaerellaceae
4. Asci 4- to multispored, ascospores concolorous …………….. Nitschkiaceae

KEY TO THE GENERA INCLUDED IN THE PHYLOGENETIC ANALYSES

1. Ascomata with quellkörper …………….. 2

1. Ascomata without quellkörper …………….. 11

2. Ascomata immersed, becoming erumpent (occasionally appearing superficial through wearing away of the substrate) …………….. *Cryptosphaerella*

2. Ascomata superficial …………….. 3

3. Ascospores with appendage-like extensions on both ends …………….. 4

3. Ascospores without extensions …………….. 5

4. Asci 8-spored …………….. *Biciliospora*

4. Asci multispored …………….. *Scortechiniella*

5. Ascomata with spiny setae on the surface …………….. 6

5. Ascomata lacking spiny setae …………….. 7

6. Asci 8-spored …………….. *Euacanthe*

6. Asci multispored …………….. *Neotrotteria*

7. Ascomata with brown, flexuous tomentum …………….. *Neofracchiaea*

7. Ascomata without tomentum …………….. 8

8. Asci 8-spored …………….. 9

8. Asci multispored, ascospores reniform …………….. *Scortechiniellopsis*

9. Ascospores allantoid …………….. *Coronophorella*

9. Ascospores ellipsoid to globose …………….. 10

10. Ascomata on thick subiculum with hyphal terminations characteristically spiny …………….. *Scortechinia*

10. Ascomata on smooth subiculum …………….. *Tympanopsis*

11. Ascomata mostly tuberculate (if smooth, then ascospores becoming uniformly brown), collabent or collapsing laterally, sometimes not collapsing …………….. *Bertia*

11. Ascomata not tuberculate …………….. 12

12. Ascomata immersed becoming erumpent, collapsing laterally …………….. *Coronophora*

12. Ascomata superficial, collapsing collabent or not …………….. 13

13. Ascomata spinulose …………….. 14

13. Ascomata not spinulose …………….. 17

14. Asci multispored …………….. *Fracchiaea*

14. Asci 8-spored …………….. 15

15. Ascospores versicolorous …………….. 16

15. Ascospores hyaline …………….. *Acanthonitschkea*

16. Ascomata collabent or not, spines restricted toward the base of fruit body …………….. *Chaetosphaerella*

16. Ascomata not collabent, with spiny setae on the surface and on the subiculum …………….. *Crassochaeta*

17. Ascospores hyaline, smaller than 15 µm long …………….. *Nitschkia*

17. Ascospores brown …………….. 18

18. Ascomata collabent, ascospores without mucilagenous sheath …………….. *Gaillardiella*

18. Ascomata not collabent ascospores with mucilagenous sheath …………….. *Spinulosphaeria nuda* (the type species, *S. thaxteri* has spinulose ascomata and lacks ascospore sheath)

KEY TO THE *BERTIA* SPECIES INCLUDED IN THE PHYLOGENETIC ANALYSES

1. Ascospores hyaline, not turning brown …………….. 3

1. Ascospores becoming brown …………….. 2

2. Ascospores cylindrical to broadly allantoid, curved, three septate …………….. *B. didyma*

2. Ascospores fusiform, straight or slightly curved, 3- or more septate …………….. *B. multiseptata*

3. Ascospores 1-septate …………….. 4

3. Ascospores 3-septate …………….. *B. triseptata*

4. Ascospores fusiform, straight or slightly curved …………….. 5

4. Ascospores cylindrical curved or oblong straight …………….. 7

5. Ascospores greater than 20 µm long …………….. 6

5. Ascospores less than 20 µm long …………….. *B. orbis*

6. Ascospores 25–30 × 6.5–8 µm, slightly curved geniculate …………….. *B. sinensis*

6. Ascospores 35–50 × 4–6.5 µm, straight …………….. *B. moriformis*

7. Ascospores cylindrical, strongly curved geniculate …………….. 8

7. Ascospores wide oblong, straight …………….. *B. gigantospora*

8. Ascomata erumpent through cracks in bark, known only from Kenya …………….. *B. ngongensis*

8. Ascomata occurring widely on substrate, known mainly from the Caribbean and Central America

…………….. *B. tropicalis*

KEY TO THE *CRYPTOSPHAERELLA* SPECIES INCLUDED IN THE PHYLOGENETIC ANALYSES

1. Asci multispored …………….. 2

1. Asci 8-spored …………….. *C. malindensis*

    2. Ascomata with outer surface vestiture …………….. 3

    2. Ascomata without vestiture …………….. 5

3. Ascomal wall with tooth-like projections …………….. *C. elliptica*

3. Ascomal wall with tomentose covering …………….. 4

    4. Ascomata with thick, brown tomentum …………….. *C. celata*

    4. Ascomata with short tomentum …………….. *C. costaricensis*

5. Ascomata mostly remaining immersed in the substrate, ascospores 8–12 × 2–3 µm …………….. *C. globosa*

5. Ascomata erumpent to superficial, ascospores 5–7 × 1–2 µm …………….. *C. cylindriformis*

DISCUSSION

Based on LSU rDNA data, Huhndorf et al (2004) accepted a monophyletic Coronophorales composed of four families, Chaetosphaerellaceae, Bertiaceae, Scortechiniaceae and a paraphyletic Nitschkiaceae. Based on the larger taxon sampling and three nuclear DNA markers, the analyses presented here corroborate these findings. However the circumscriptions of Bertiaceae and Scortechiniaceae are expanded and we accept Coronophoraceae as distinct from Nitschkiaceae (FIGS. 1–4). Subramanian and Sekar (1990) took a broad concept of the Coronophoraceae and placed all Coronophorales genera except *Bertia* and *Spinulosphaeria* in the family. Here we limit Coronophoraceae to the species of *Coronophora* and possibly some taxa that currently are placed in *Fracchiaea* (FIG. 2). At the same time we propose some changes in the generic circumscriptions within the order.

Bertia generally has been treated as an isolated genus within the Coronophorales and more recently was placed in its own family, Bertiaceae (Subramanian and Sekar 1990, Huhndorf et al

2004). In our analyses Bertiaceae forms a strongly supported clade including taxa in *Thaxteria* and *Gaillardiella*. Three collections of *T. didyma* (= *B. didyma*) group together in a clade that is nested within *Bertia* (FIG. 1). Based on these results we propose that *Thaxteria* should be synonymized with *Bertia*. The position of *Thaxteria* has been debated for long time with the genus recieving varied taxonomic placement over the years. Nannfeldt (1975) was of the view that *Thaxteria* showed affinities to taxa in Lasiosphaeriaceae (Sordariales) and therefore placed it in that family. Subramanian and Sekar (1990) transferred the genus back into Coronophorales but synonymized it with *Nitschkia*. The inclusion of the genus in Bertiaceae had been suggested based on its morphology (e.g. by Huhndorf et al 2004), however our analyses do not support its separation from *Bertia*. Its combination of morphological characters agrees with those observed in species of *Bertia*. The three collections of *B. didyma* match the descriptions given by Fitzpatrick (1923) who examined the type collection. *Bertia didyma* has vertically elongate, smooth ascomata that collapse laterally, long stipitate asci and cylindrical curved to widely allantoid ascospores that remain hyaline and 1-septate for prolonged time but the ascospores later become 3-septate and turn brown. This ascospore character was used by Fitzpatrick (1923) to distinguish it from species of *Nitschkia*. *Bertia multiseptata* (Sivan.) Huhndorf, A.N. Mill. & F.A. Fern. also has ascospores that become brown and septate, but these are long and narrow instead of short and wide as in *B. didyma*. Along with the ascospores *B. didyma* differs primarily from the other species of *Bertia* by its smooth laterally collapsing ascomata.

Our two collections of *Gaillardiella pezizoides* Pat. forms a basal clade in strongly supported sister relationship with the taxa in *Bertia* (FIGS. 1–4). Its close relationship to *Bertia* had been suggested based on its morphology (Huhndorf et al 2004), and in this study we corroborate these findings and support its inclusion in the Bertiaceae. The species in the genus resembles those of *Bertia* in their collabent ascomata but differs by having a circular thickening around the edge, forming a cup-like structure.

Bertia occurs in both tropical and temperate regions, and in this study the genus is represented by 21 specimens comprising eight species (including *B. didyma*) from a wide geographic range. Three new species are described in the genus. *Bertia orbis* is represented by four geographically diverse collections that group together in a well supported clade (FIG. 1). *Bertia orbis* shows some morphological similarity to *B. moriformis* (Tode) de Not. in the shape of asci and ascospores but differs in the size of both. The ascomata of *Bertia orbis* are collabent and much smaller than those of *B. moriformis*. The two species also differ in molecular sequence data (FIG. 1). *Bertia turbinata* Petch was not included in our analyses but was described as having superficial, clustered, collabent ascomata with hyaline, 1-septate, straight or slightly curved ascospores (Petch 1922). *Bertia orbis* differs from this species in the smaller sizes of asci and ascospores.

Bertia triseptata differs from the other species of *Bertia* by possessing 3-septate, geniculate ascospores, a combination of characters not previously reported in the genus. Geniculate ascospores also occur in *B. tropicalis*, *B. convolutispora* K.D. Hyde, *B. ngongensis* and to some extent *B. sinensis* J.C. Krug & Corlett, but in all these cases the ascospores are 1-septate. In the LSU rDNA analyses *B. triseptata* forms a supported sister relationship with *B. multiseptata* (FIG. 1). *Bertia multiseptata* was first described by Sivanesan (1978) as a variety of *B moriformis* and raised to species level by Huhndorf et al (2004). It produces ascospores that are multiseptate (3–7), mostly straight or slightly curved as opposed to smaller, 3-septate geniculate ones found in *B. triseptata*. The single collection of *Bertia ngongensis* does not group with any species included in the analyses and also differs from the rest of the taxa by having ascomata that are erumpent through cracks in the bark and mature asci that are distinctly curved with geniculate ascospores. *Bertia latispora* (Corlett & J.C. Krug) Lar. N. Vassiljeva was not included in our analyses but is reported to occasionally have erumpent ascomata, but our collection differs from this species by having much smaller ascospores and asci appearing curved. *Bertia ngongensis* shares geniculate 1-septate ascospore characters with *B. sinensis* and *B tropicalis* but differs from these species in its erumpent ascomata, shape and size of the asci and in its phylogenetic placement (FIG. 1). *Bertia convolutispora*, the other species with similar ascospore characters, differs from our collection in its size of ascospores, superficial ascomata and habit. *Bertia convolutispora* was described from wood submerged in water, with superficial ascomata that are solitary and rarely clustered (Hyde 1995).

Subramanian and Sekar (1990) in their taxonomic revision of Coronophorales adopted a broad concept of Coronophoraceae. They placed all the genera of Coronophorales except *Bertia* and *Spinulosphaeria* within the family. In our analyses *Coronophora* is represented by a single collection obtained from the USA whose morphology matches that of the type species *Coronophora gregaria* (Lib.) Fuckel. The species shows no close affinities to the currently recognized families, and therefore Coronophoraceae is retained for the taxa in the genus (FIGS. 2–4). However in the *tef1* analyses *C. gregaria* groups in moderately supported clade with a collection obtained from Kenya bearing morphology similar to that of *Fracchiaea* (FIG. 2). The outcome was unexpected, but this grouping probably suggests that some of the taxa currently accepted in *Fracchiaea* might belong in Coronophoraceae. More species of *Coronophora* need to be included in analyses to better understand the generic and familial circumscriptions.

Huhndorf et al (2004) accepted Chaetosphaerellaceae for *Chaetosphaerella* and *Crassochaeta*. *Chaetosphaerella* was described by Müller and Booth (1972) for versicolorous species in *Chaetosphaeria* Tul. & C. Tul. Réblová (1999a, b) accepted two species, *C. phaeostroma* (Durieu & Mont.) E. Müll. & C. Booth and *C. fusca* (Fuckel) E. Müll. & C. Booth, in the genus. In our analyses *C. fusca* groups together with *C. phaeostroma* in a strongly supported clade further suggesting close relationship of the two species (FIGS. 1–4). Collections of *Crassochaeta nigrita* form a strongly supported sister relationship with species of *Chaetosphaerella* further corroborating the finding of Huhndorf et al (2004) (FIG. 1).

We accept Nitschkiaceae for the taxa in *Nitschkia*, *Fracchiaea* and *Acanthonitschkea*. The three genera group together with high PP in LSU rDNA and combined analyses (FIGS. 1, 4). This relationship however is not supported for *tef1* and *rpb2* analyses (FIGS. 2, 3). In both cases *Fracchiaea* groups separately but *Nitschkia* and *Acanthonitschkea* group together in all gene trees (FIGS. 1–4). Despite this outcome we are inclined to retain *Fracchiaea* in Nitschkiaceae until more taxa, especially in *Nitschkia* and *Fracchiaea*, are available for analyses to confirm the relationship in the family. We were not able to obtain a collection of *Nitschkia parasitans* (Schwein.) Nannf., the type species of *Nitschkia*, for the analyses, hence the circumscription of the family remains unclear.

Fiztpatrick (1924) synonymized all the species that had been described in *Fracchiaea* with *F. broomeiana*. Phylogenetic analyses presented here indicate that *Fracchiaea* might be polyphyletic, with one collection of an unnamed species grouping with that of *Coronophora* (FIG. 2). A collection identified as *F. lunata* Patw. & G.T. Joshi is represented by a single *rpb2* sequence and it groups together with *F. broomeiana*. Another unnamed Coronophorales also shares the ascomatal morphology of *Fracchiaea* but instead groups together with *Neotrotteria pulchella* Sacc. (FIG. 1). More work is clearly needed in this group before the generic and the species concepts become clear. In our analyses three collections of *Nitschkia tetraspora* group together in a well supported clade with another collection of *Nitschkia* that consistently forms eight ascospores per asci (FIG. 1). The morphology of this collection is in every way similar to that of *N. tetraspora* except for the number of ascospores per ascus. In *N. tetraspora* four ascospores abort leaving only four to attain maturity. Based on the close relationship of these collections in the analyses and similarity in their morphology, we are inclined to think that they represent a single species despite the differences in ascospores numbers. At this moment we treat the ascospore number as a variable character within the species until more collections of both kinds are included in analyses to acertain the validity of the character in the taxonomy.

Based on three collections Huhndorf et al (2004) established Scortechiniaceae for the taxa that possess a quellkörper in the centrum. In our analyses composed of expanded taxon sampling, the quellkörper-bearing taxa group together in a strongly supported clade (FIGS. 1–4), corroborating Huhndorf et al (2004). Nannfeldt (1975a, b) did not consider presence or absence of a quellkörper of taxonomic importance at the genus level and therefore grouped together taxa with or without the character. He accorded prominence to other ascomal characters, such as smooth versus tuberculate walls, and presence or absence of spines. In doing so he synonymized quellkörper-bearing genera with *Nitschkia* and *Acanthonitschkea*. Subramanian and Sekar (1990) reinstated the genera Nannfeldt (1975b) had placed in synonymy, and our molecular analyses support the separation of these genera from *Nitschkia* and *Acanthonitschkea*. Phylogenetic analyses presented here support the conclusion of Huhndorf et al (2004b) that presence or absence of a quellkörper is a family-level taxonomic character. The analyses also demonstrate that some of the currently used generic characters, such as presence or absence of subiculum, presence or absence of spines on ascomata and the number of ascospores per ascus, are probably homoplasious. Several monotypic genera have been erected historically based on single character state changes (TABLE III), including *Biciliospora velutina* Petr., *Scortechiniella similis* (Bres.) Arx & E. Müll. and *Scortechiniellopsis leonensis* Sivan. *Biciliospora velutina* and *S. similis* both have a smooth subiculum and ascospores that bear elongate appendage-like wall extensions but differ in their ascospore number, while *S. leonensis* has a spinulose subiculum and multispored asci with ascospores that lack wall extensions. In our analyses these species group together in fairly well supported clades (FIGS. 2–4) indicating the characters currently used in generic delimitation in the family might include homoplasies and further evaluation of their usefulness is needed.

Six new species of *Cryptosphaerella* Sacc. are proposed for morphologically distinct collections that group within Scortechiniaceae (FIGS. 1–4). The collections were obtained from Africa, Central and South America. The species do not group together in the LSU rDNA tree (FIG. 1) but form a supported monophyletic clade in the *tef1* and combined gene trees (FIGS. 2, 4). *Cryptosphaerella* was established for Coronophoralean taxa that are immersed becoming erumpent, solitary or in small groups, cupulate, nonostiolate and bearing a quellkörper. Members of the group have asci that are multispored, with ascospores irregularly arranged. Of the 13 names known in the genus Petrak (1962) accepted four species with the remainder belonging elsewhere. However the genus is collected infrequently and aside from *C. malabarica* Subram. & Sekar no modern illustrations are available. To the best of our knowledge none of the currently described species match our new collections. Most of the species accepted by Petrak (1962) have temperate distributions and differ from our collections by having smaller and/or allantoid ascospores. Only *C. marylandica* Petr. is described as having oblong, subfusoid ascospores, a shape similar to that found in several of our species. But again this species differs in smaller spores and temperate distribution. *Cryptosphaerella shearii* Petr. has a tropical Hawaiian distribution but has small allantoid ascospores. The tropical *C. malabarica* differs from all other species in its 1-septate ascospores and its 16-spored asci. *Cryptosphaerella cylindriformis* differs from *C. elliptica* by having smaller asci, and smaller, cylindrical, slightly curved ascospores. *Cryptosphaerella costaricensis* differs primarily from the other species by having ascomata that possess brown, thick-walled, septate tomentum and cylindrical ascospores that are much larger than those observed in *C. cylindriformis*. *Cryptosphaerella globosa* differs from all the species by possessing ascomata that are mostly immersed, rarely erumpent and collapse laterally as well as having asci that are rounded, with a globose appearing spore-bearing part and a thin pedicel. Ascospores in this species have walls that are collapsed in some places and therefore appear uneven. *Cryptosphaerella celata* is unique in having ascomata that are erumpent but become covered by thick, brown septate subiculum. The ascomata are cupulate and asci are clavate and multispored. However the most unique species we recognize in this genus is *C. malindensis*, collected from Kenya. This species consistently groups in a well supported clade with *C. cylindriformis*, *C. elliptica* and *C. costaricensis* (FIGS. 1–4). The ascomata in this species are superficial, seated on a thick subiculum, the asci are 8-spored and the ascospores are hyaline and ellipsoid. However, apart from superficial ascomata and possession of eight ascospores per ascus, other morphological characters are consistent with those of *Cryptosphaerella*, and therefore based on morphological and molecular data we place it in the genus.

Scortechinia was described by Saccardo (Saccardo and Berlese 1885), and later Fitzpatrick (1923) treated *Scortechinia* species under genus *Tympanopsis* Fitzp. *Scortechinia* was recognized by Huhndorf et al (2004) based on *S. conferta* (Schwein.) Subram. & Sekar, a name used by Subramanian and Sekar (1990). Fries' (1823) use of the name “*Sphaeria conferta* Fr.” for another entity takes page precedence over *Sphaeria conferta* Schwein:Fr., and therefore the combination into *Scortechinia* made by Subramanian and Sekar (1990) should have had the "*confertula*" epithet (see Nannfeldt 1975a:59 for discussion). However we here propose that genus *Scortechinia* should be limited to the clade with *S. acanthostroma*, the type species (Figs 1–4). This includes taxa with superficial collabent ascomata that are embedded in thick spinulose subiculum, with thin ascomal walls as observed in *S. acanthostroma*. Members also have a long subcylindrical quellkörper, while ascospores are fusoid, hyaline or brown and smooth or striate. We reinstate genus *Tympanopsis* for the clade with *T. confertula* and *T. uniseriata*. They are characterised by superficial ascomata, with firm ascomal walls, sparse to thick subiculum that is smooth. However, although these two taxa constantly grouped together except in the LSU rDNA tree, the relationship was mostly not supported and only in combined data analyses did they recieve significant Bayesian support (FIGS. 1–4).

The taxonomic position of *Spinulosphaeria* has been debated since its description by Sivanesan in 1974. The monotypic genus was described for *S. thaxteri* (Pat.) Sivan. and placed in Coronophorales. However Nannfeldt (1975b) accepted it in Lasiosphaeriaceae (Sordariales) and Subramanian and Sekar (1990) in Bertiaceae (Coronophorales). A specimen in our collection fits the description as an additional species in the genus, and in our analyses it nested within the Coronophorales (FIG. 1). The taxonomic placement is further supported by its possession of morphological characters that are consistent with taxa in the order. We therefore accept *Spinulosphaeria* in the Coronophorales, corroborating the placement of the genus in the order (Sivanesan 1974, Subramanian and Sekar 1990, Huhndorf 2004). However the taxonomic position of the genus remains unclear to us and based on the analyses it might represent a new lineage within the order. We were not able to obtain DNA from *S. thaxteri*, and therefore the true position of the genus will be clear only when this is included in analyses. *Spinulosphaeria nuda* differs from *S. thaxteri* by having ascomata that lack spines, lacking a subiculum and possessing paraphyses that are broad, septate and constricted at septa. The asci are much larger than those reported for *S. thaxteri* and the ascospores possess a persistent mucilaginous sheath.

This study includes a mixture of specimens that represent temperate and tropical collecting sites. By including different climatic types some biogeographic data can be inferred. Certain species seem to be restricted to temperate areas (e.g. *B. moriformis*) or tropical regions (e.g. *B. tropicalis*). In certain widespread taxa such as *T. confertula* there are few genetic differences between collections from Kenya, USA or France. *Fracchiaea broomeiana* is another widespread species that shows little genetic difference among the collections from Kenya, Venezuela and USA. *Scortechinia acanthostroma,* a species thought to be restricted to a subtropical/tropical distribution, was found to occur in central Illinois, albeit with some genetic differences from the tropical collections. Specimens used in this study were collected in South and Central America over a number of years and in Kenya in 2005 and 2006. Some species that were described from or are known to occur in Africa were recollected in this study, including *C. chaetomioides*, *E. foveolata*, *F. broomeiana*, *N. pulchella*, *N. calyculus*, *N. tetraspora*, *S. acanthostroma* and *S. leonensis*. Other named species, such as *B. gigantospora*, *B. velutina*, *C. fusca*, *G. pezizoides*, *F. lunata*, *T. confertula*, and *T. uniseriate*, previously were not found in eastern Africa. Seven of the new species described are from Africa. Quellkörper-bearing taxa tended to predominate among the collections from Africa, making up 12 out of the 22 species of Coronophorales collected. In general quellkörper-bearing taxa show a tendency to be more diverse in tropical regions than temperate areas but more studies are needed to confirm this hypothesis.

CONCLUSION

The Coronophorales is confirmed for species in the monophyletic families Bertiaceae, Chaetosphaerellaceae, Scortechiniaceae and a paraphyletic Nitschkiaceae. A single collection of *Coronophora gregaria* occurs separate from taxa in the other families so the Coronophoraceae is applied for this genus. The Bertiaceae is expanded to include *Gaillardiella* and *B. didyma*, taxa with ascospores that become brown. In *G. pezizoides* the ascomata are cup-shape with a circular thickening at the top edge, and in *B. didyma* the ascomata are smooth and collapse laterally. With these additions taxa within the family continue to vary along the morphological lines of large, robust ascomata that mostly have warted or tuberculate walls and collapse either collabent or laterally and ascospores that are commonly hyaline, can vary in septation and most often are larger than in other taxa in the Coronophorales. The quellkörper continues to be an important character in defining the Scortechiniaceae, but within the family the characters that define relationships among taxa remain ambiguous. *Cryptosphaerella* species with mostly erumpent ascomata separate from taxa with superficial ascomata, but one species of *Cryptosphaerella* is superficial. *Tympanopsis* and *Scortechinia* are recognized as separate genera and differ in their smooth versus spinulose subiculum. However other taxa with these character states also occur in different places in the clade. Taxa with multispored asci also are dispersed within the clade. The monotypic genera, *Biciliospora, Scortechiniella* and *Scortechiniellopsis*, show strong relatedness indicating the generic-level morphological character-state changes that separate them probably are untenable. Nitschkiaceae remains paraphyletic with *Fracchiaea* not consistently grouping together or with *Nitschkia* and *Acanthonitschkea*. The correct placement of the generic type *N. parasitans* remains elusive. *Spinulosphaeria* is expanded to include a species lacking spines and subiculum, and the genus is included as a member within the order however with uncertain family placement.

ACKNOWLEDGMENTS

This work was supported in part by NSF PEET Grant (Partnerships for Enhancing Expertise in Taxonomy) DEB–

0118695. The authors are grateful for the help of F.A. Fernández who provided access to specimens and of A.N. Miller, INBio and D. J. Lodge for fieldwork assistance. The National Museums of Kenya provided logistical support for the fieldwork carried out in Kenya. Sequences were generated in the Pritzker Laboratory for Molecular Systematics and Evolution at the Field Museum of Natural History.

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LEGENDS

FIG. 1. Phylogram of the maximum likelihood analyses generated from nuclear LSU rDNA partial sequences. Bootstrap values ≥ 70% are shown above or below branches. Thickened branches indicate Bayesian posterior probabilities ≥ 95%. The Coronophorales families accepted in this study also are indicated. Roman numerals refer to collections (TABLE II).

FIG. 2. Phylogram of the maximum likelihood analyses generated from translation elongation factor 1 alpha (*tef1*) partial sequences. Bootstrap values ≥ 50% are shown above or below branches. Thickened branches indicate Bayesian posterior probabilities ≥ 95%. The Coronophorales families accepted in this study also are indicated. Roman numerals refer to collections (TABLE II).

FIG. 3. Phylogram of the maximum likelihood analyses generated from partial sequences of the ribosomal polymerase II subunit 2 (*rpb2*). Bootstrap values ≥ 70% are shown above or below branches. Thickened branches indicate Bayesian posterior probabilities ≥ 95%. The Coronophorales families accepted in this study also are indicated. Roman numerals refer to collections (TABLE II).

FIG. 4. Phylogram of the maximum likelihood analyses generated from the combined genes (partial sequences of ribosomal polymerase II subunit 2, Translation elongation factor 1 alpha and nuclear LSU rDNA). Bootstrap values ≥ 70% are shown above or below branches. Thickened branches indicate Bayesian posterior probabilities ≥9 5%. The Coronophorales families accepted in this study also are indicated. Roman numerals refer to collections (TABLE II).

FIG. 5a–e. *Bertia didyma*. a. Ascomata on substrate; b. Ascus; c. Inflated paraphyses; d. Mature hyaline and brown ascospores; e. Asci showing thickened apical ring (arrow). f–i. *Bertia gigantospora*. f. Ascomata on substrate; g. Munk pores on ascomatal wall; h. Ascospores and inflated paraphyses (arrow); i. Ascus. j–m. *Bertia ngongensis*. j. Ascomata on substrate; k. Munk pores on ascomatal wall; l. Ascospores; m. Ascus and ascospores. n–r. *Bertia orbis*. n. Ascomata on substrate; o. Ascus; p. Asci showing thickened apical ring (arrow); q. Inflated paraphyses; r. Ascospores. Bars: a = 1 mm; f, j = 500 µm; n = 250 µm; b, c, i, o, q = 20 µm; d, e, g–i, k–m, p, r = 10 µm. a, f, j, n by photomacrography; d, e, g–i, k–m, o–r by DIC; b, c by PH. a from SMH4719; b–e from SMH4256; f–i from GKM1136; j–m from GKM1239; n from GKM1259; o–r from GKM1271.

FIG. 6a–e. *Bertia triseptata*. a. Ascomata on substrate; b. Longitudinal section through ascoma; c. Section through ascomatal wall; d. Ascus; e. Ascospores. f–j. *Cryptosphaerella celata*. f. Ascomata on substrate; g. Ascomatal wall section with tomentum on outer surface (arrow); h. Ascus; i. Ascospores; j. Quellkörper. k–o. *Cryptosphaerella costaricensis*. k. Ascomata on substrate; l. Longitudinal section through ascoma showing quellkörper in place (arrow); m. Ascus; n. Ascospores; o. Quellkörper. p–t. *Cryptosphaerella cylindriformis*. p. Ascomata on substrate; q. Section through ascomatal wall; r. Ascus; s. Ascospores; t. Quellkörper. Bars: a, f, k, p = 500 µm; b = 200 µm; j, l, o, t = 100 µm; g, h, m, q, r = 20 µm; c–e, i, n, s = 10 µm. a, f, k, p by photomacrography; g by BF; b–e, h–j, l–o, q–t by DIC. a–e from SMH1525; f–j from GKM1231; k–o from MO2111; p–t from GKM434N.

FIG. 7a–e. *Cryptosphaerella elliptica*. a. Ascomata on substrate; b. Section through ascomatal wall showing outer toothed cells (arrow); c. Quellkörper; d Ascus; e. Ascospores. f–j. *Cryptosphaerella globosa*. f. Ascoma on substrate; g. Ascus; h. Section through ascomatal wall; i. Ascospores; j. Quellkörper. k–q. *Cryptosphaerella malindensis*. k. Ascomata on substrate embedded in thick subiculum; l. Section through ascomatal wall; m. Ascus. n. Ascospores; o. Smooth subicular hyphae; p. Munk pores (arrow) few and scattered; q. Quellkörper. r–v. *Scortechinia diminuspora*. r. Ascomata on substrate embedded in thick subiculum; s. Spinulose subicular hyphae;

t. Quellkörper; u. Asci; v. Ascospores. Bars: a, f, k, r = 500 µm; c, j, q = 100 µm; t = 50 µm; d, h, o = 20 µm; b, e, g, i, l–n, p, s, u, v = 10 µm. a, f, k, r by photomacrography; b–e, g–j, l–q, s–v by DIC. a–e from SMH4722; f–j from GKM414N; k–q from GKM1150; r–v from SMH4763.

FIG. 8a–h. *Spinulosphaeria nuda*. a. Ascomata on substrate; b. Section through ascomatal wall; c. Asci; d. Inflated paraphyses (arrow); e. Mature hyaline ascospores; f. Mature brown ascospores; g. Ascospores showing surface roughening; h. Ascospores with mucilagenous sheath (arrow). Bars: a = 500 µm; b–d = 20 µm; e–h = 10 µm. a by photomacrography; b–h by DIC; a–h from SMH1952.

FOOTNOTES

Submitted 18 Mar 2009; accepted for publication 22 Jun 2009.

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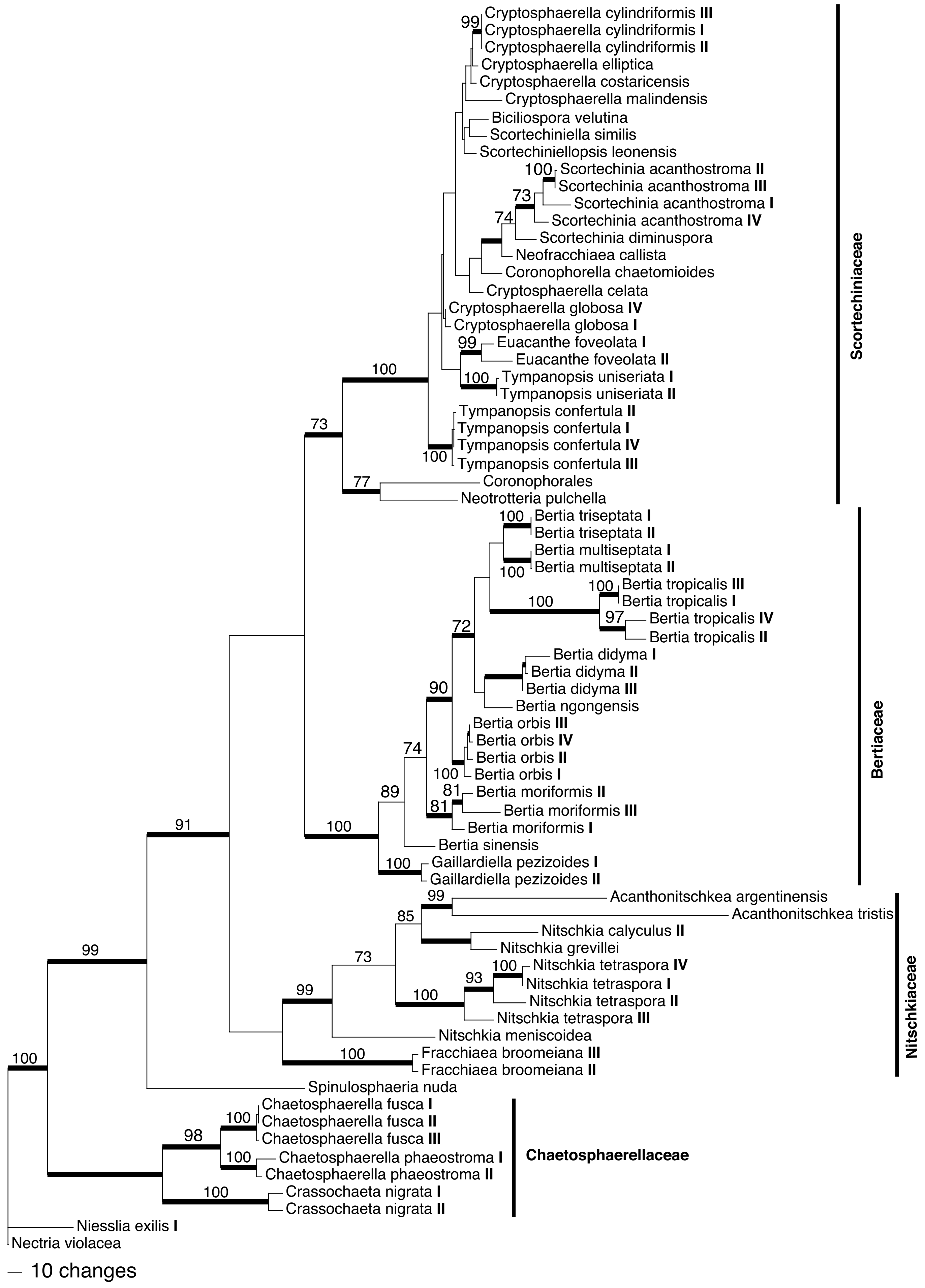
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Cryptosphaerella cylindriformis **III**
Cryptosphaerella cylindriformis **I**
Cryptosphaerella cylindriformis **II**
Cryptosphaerella elliptica
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Cryptosphaerella malindensis
Biciliospora velutina
Scortechiniella similis
Scortechiniellopsis leonensis
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Scortechinia acanthostroma **II**
Scortechinia acanthostroma **III**
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Scortechinia acanthostroma **I**
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Scortechinia acanthostroma **IV**
Scortechinia diminuspora
Neofracchiaea callista
Coronophorella chaetomioides
Cryptosphaerella celata
Cryptosphaerella globosa **IV**
Cryptosphaerella globosa **I**
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Euacanthe foveolata **I**
Euacanthe foveolata **II**
100
100
Tympanopsis uniseriata **I**
Tympanopsis uniseriata **II**
Tympanopsis confertula **II**
73
Tympanopsis confertula **I**
Tympanopsis confertula **IV**
100
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Coronophorales
Neotrotteria pulchella
Scortechiniaceae
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Bertia triseptata **II**
Bertia multiseptata **I**
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Bertia multiseptata **II**
100
Bertia tropicalis **III**
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Bertia tropicalis **I**
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Bertia tropicalis **IV**
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Bertia tropicalis **II**
Bertia didyma **I**
Bertia didyma **II**
Bertia didyma **III**
90
Bertia ngongensis
Bertia orbis **III**
Bertia orbis **IV**
74
Bertia orbis **II**
100
Bertia orbis **I**
89
81
Bertia moriformis **II**
81
Bertia moriformis **III**
91
100
Bertia moriformis **I**
Bertia sinensis
100
Gaillardiella pezizoides **I**
Gaillardiella pezizoides **II**
Bertiaceae
99
Acanthonitschkea argentinensis
85
Acanthonitschkea tristis
Nitschkia calyculus **II**
99
Nitschkia grevillei
73
100
Nitschkia tetraspora **IV**
93
Nitschkia tetraspora **I**
99
100
Nitschkia tetraspora **II**
Nitschkia tetraspora **III**
Nitschkia meniscoidea
100
100
Fracchiaea broomeiana **III**
Fracchiaea broomeiana **II**
Nitschkiaceae
Spinulosphaeria nuda
100
Chaetosphaerella fusca **I**
Chaetosphaerella fusca **II**
98
Chaetosphaerella fusca **III**
100
Chaetosphaerella phaeostroma **I**
Chaetosphaerella phaeostroma **II**
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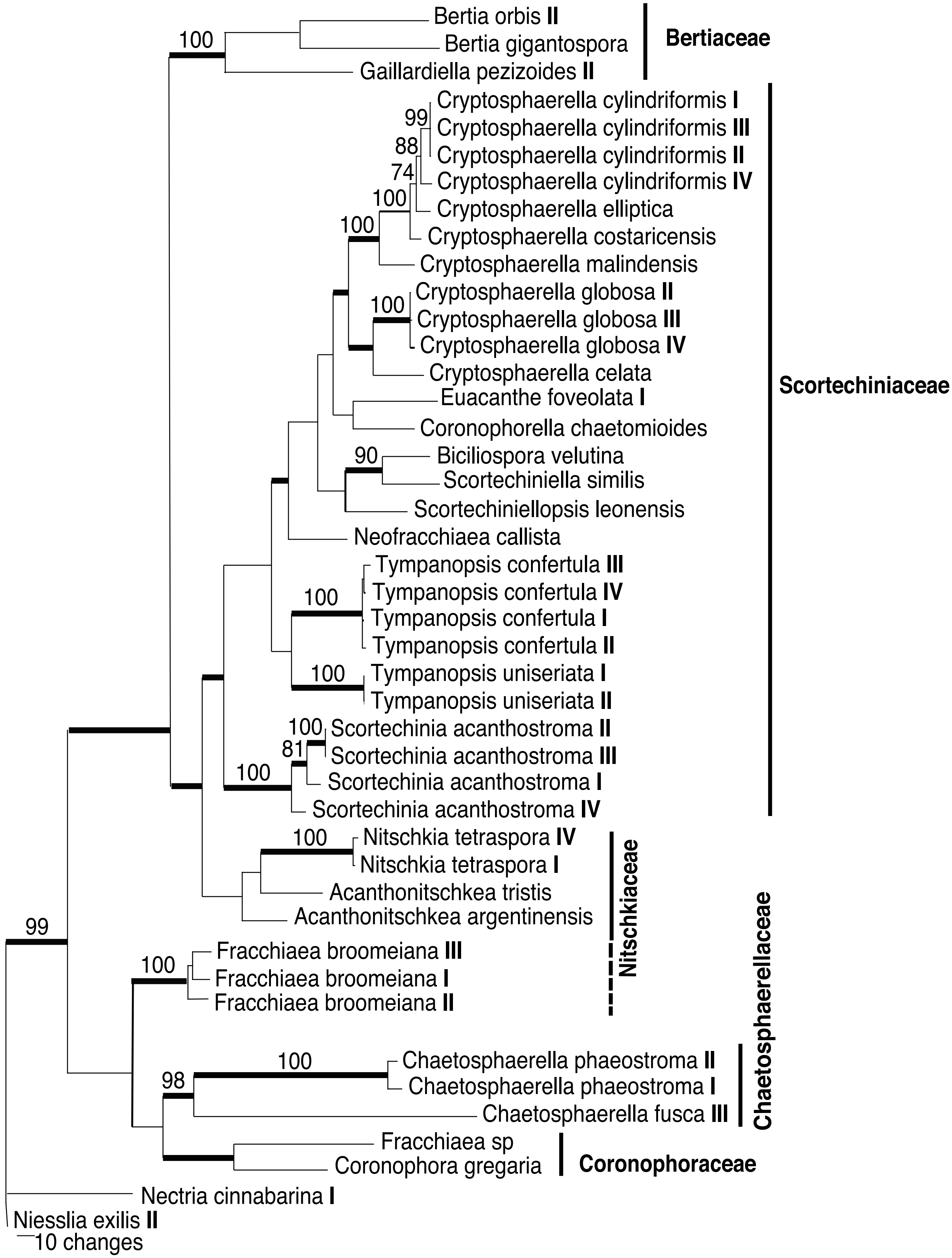
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Bertiaceae
100
Cryptosphaerella cylindriformis I
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Cryptosphaerella cylindriformis IV
Cryptosphaerella elliptica
Cryptosphaerella costaricensis
Cryptosphaerella malindensis
99
88
74
100
100
Cryptosphaerella globosa II
Cryptosphaerella globosa III
Cryptosphaerella globosa IV
Cryptosphaerella celata
100
Euacanthe foveolata I
Coronophorella chaetomioides
Biciliospora velutina
Scortechiniella similis
Scortechiniellopsis leonensis
90
Neofracchiaea callista
Tympanopsis confertula III
Tympanopsis confertula IV
Tympanopsis confertula I
Tympanopsis confertula II
100
Tympanopsis uniseriata I
Tympanopsis uniseriata II
100
Scortechinia acanthostroma II
Scortechinia acanthostroma III
Scortechinia acanthostroma I
Scortechinia acanthostroma IV
100
81
100
Scortechiniaceae
Nitschkia tetraspora IV
Nitschkia tetraspora I
100
Acanthonitschkea tristis
Acanthonitschkea argentinensis
Fracchiaea broomeiana III
Fracchiaea broomeiana I
Fracchiaea broomeiana II
100
Nitschkiaceae
99
Chaetosphaerella phaeostroma II
Chaetosphaerella phaeostroma I
Chaetosphaerella fusca III
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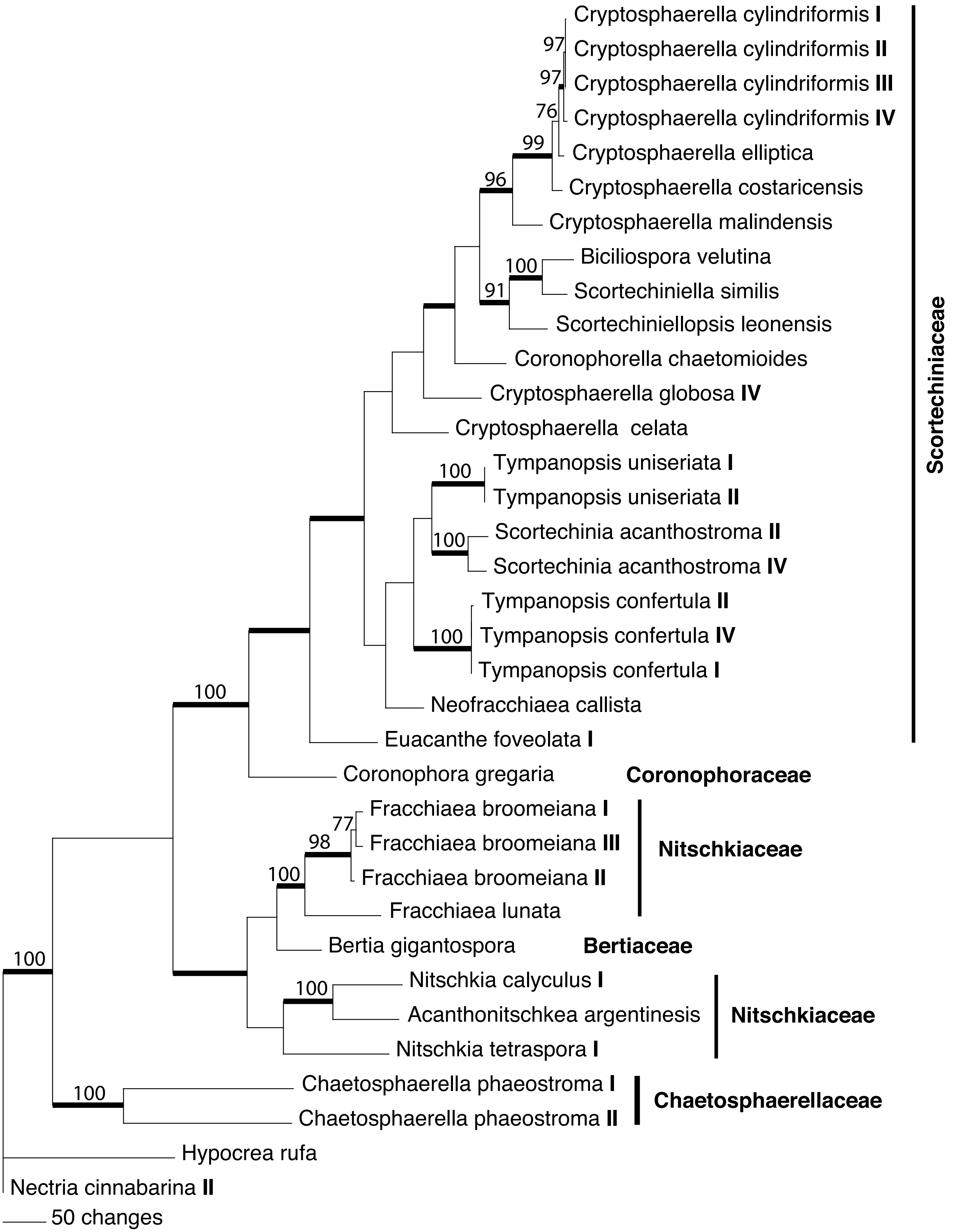
Chaetosphaerellaceae
Fracchiaea sp
Coronophora gregaria
Coronophoraceae
Nectria cinnabarina I
Niesslia exilis II
10 changes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Cryptosphaerella elliptica
96
Cryptosphaerella costaricensis
Cryptosphaerella malindensis
100
Biciliospora velutina
91
Scortechiniella similis
Scortechiniellopsis leonensis
Coronophorella chaetomioides
Cryptosphaerella globosa IV
Cryptosphaerella celata
100
Tympanopsis uniseriata I
Tympanopsis uniseriata II
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Scortechinia acanthostroma II
Scortechinia acanthostroma IV
Tympanopsis confertula II
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Tympanopsis confertula IV
Tympanopsis confertula I
100
Neofracchiaea callista
Euacanthe foveolata I
Scortechiniaceae
Coronophora gregaria
Coronophoraceae
Fracchiaea broomeiana I
77
98
Fracchiaea broomeiana III
Nitschkiaceae
100
Fracchiaea broomeiana II
Fracchiaea lunata
Bertia gigantospora
Bertiaceae
100
100
Nitschkia calyculus I
Acanthonitschkea argentinesis
Nitschkiaceae
Nitschkia tetraspora I
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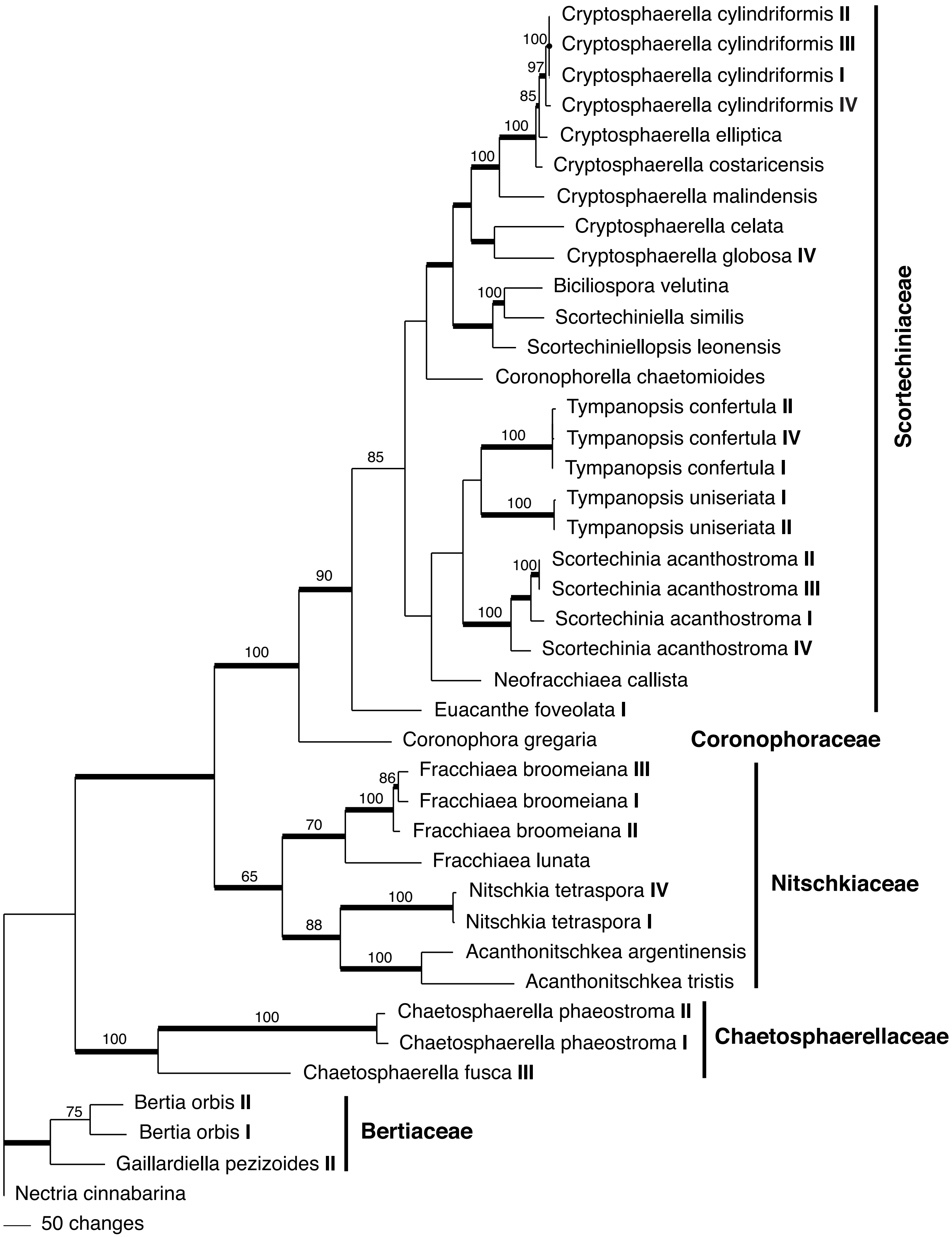
Chaetosphaerellaceae
Chaetosphaerella phaeostroma II
Hypocrea rufa
Nectria cinnabarina II
50 changes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Cryptosphaerella costaricensis
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Cryptosphaerella celata
Cryptosphaerella globosa IV
100
Biciliospora velutina
Scortechiniella similis
Scortechiniellopsis leonensis
Coronophorella chaetomioides
85
Tympanopsis confertula II
100
Tympanopsis confertula IV
Tympanopsis confertula I
100
Tympanopsis uniseriata I
Tympanopsis uniseriata II
100
Scortechinia acanthostroma II
Scortechinia acanthostroma III
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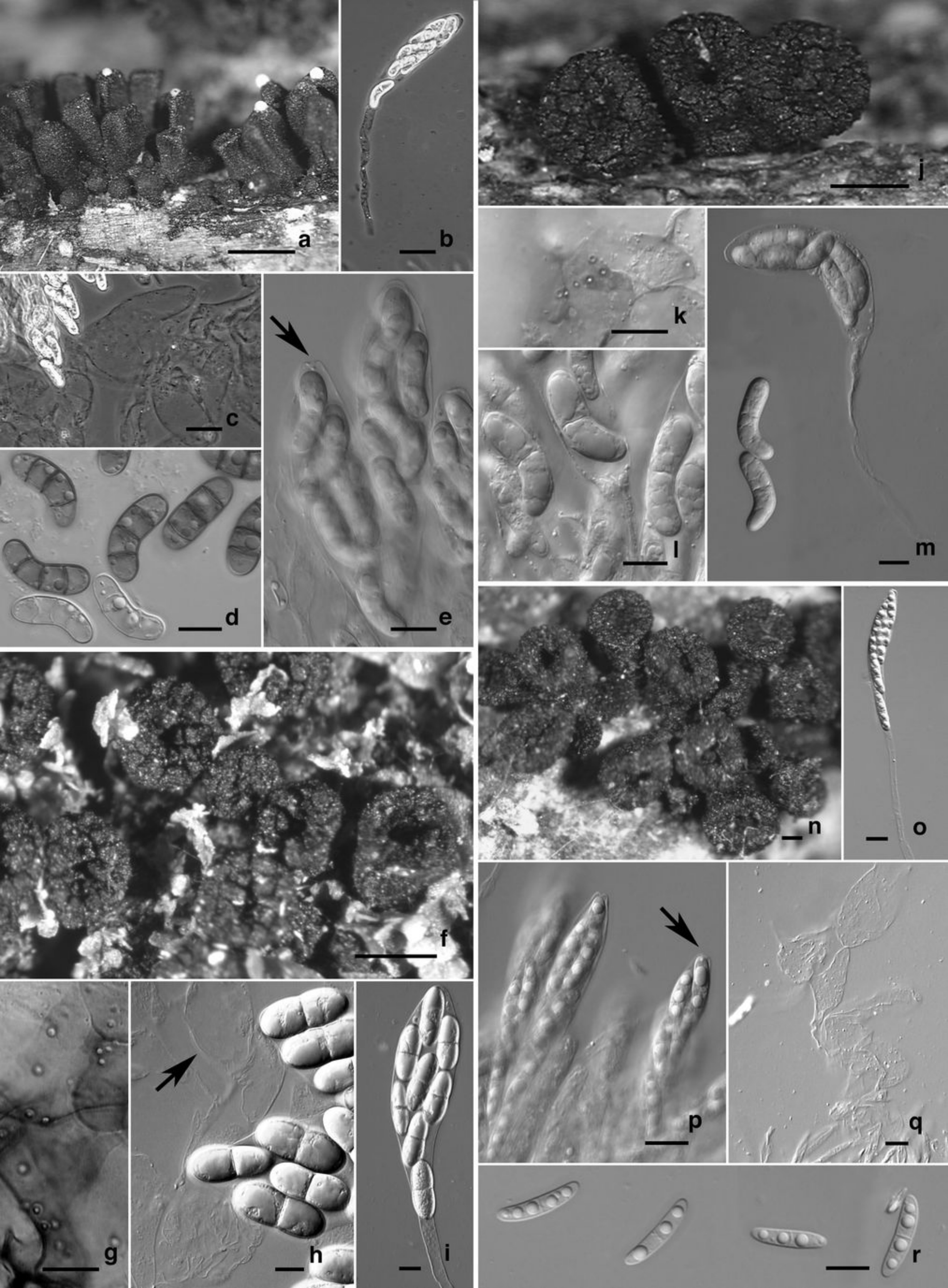
Scortechinia acanthostroma I
Scortechinia acanthostroma IV
90
Neofracchiaea callista
100
Euacanthe foveolata I
Coronophora gregaria
Scortechiniaceae
Coronophoraceae
86
Fracchiaea broomeiana III
100
Fracchiaea broomeiana I
70
Fracchiaea broomeiana II
Fracchiaea lunata
65
100
Nitschkia tetraspora IV
Nitschkia tetraspora I
88
100
Acanthonitschkea argentinensis
Acanthonitschkea tristis
Nitschkiaceae
100
Chaetosphaerella phaeostroma II
100
Chaetosphaerella phaeostroma I
Chaetosphaerella fusca III
Chaetosphaerellaceae
75
Bertia orbis II
Bertia orbis I
Gaillardiella pezizoides II
Bertiaceae
Nectria cinnabarina
50 changes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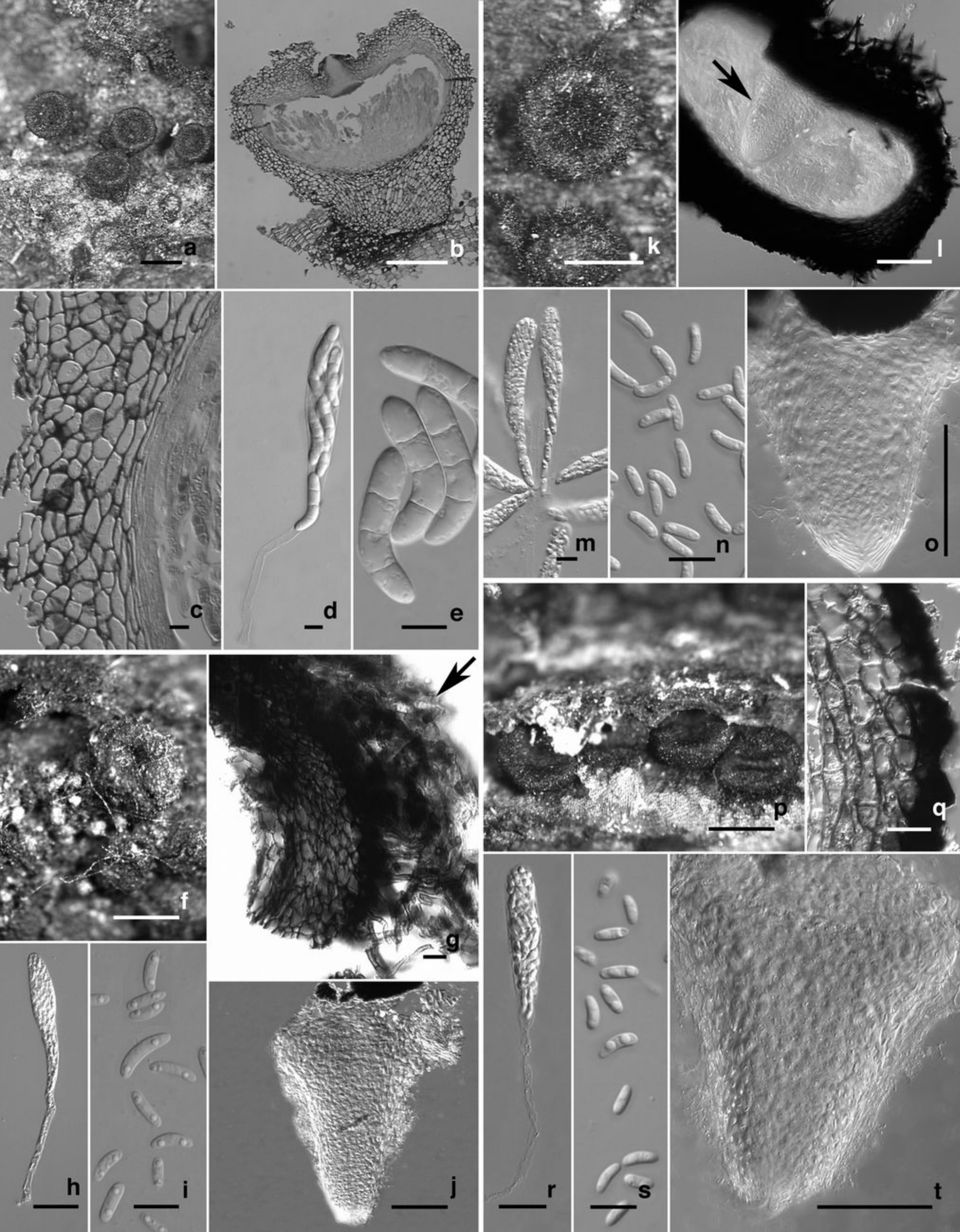
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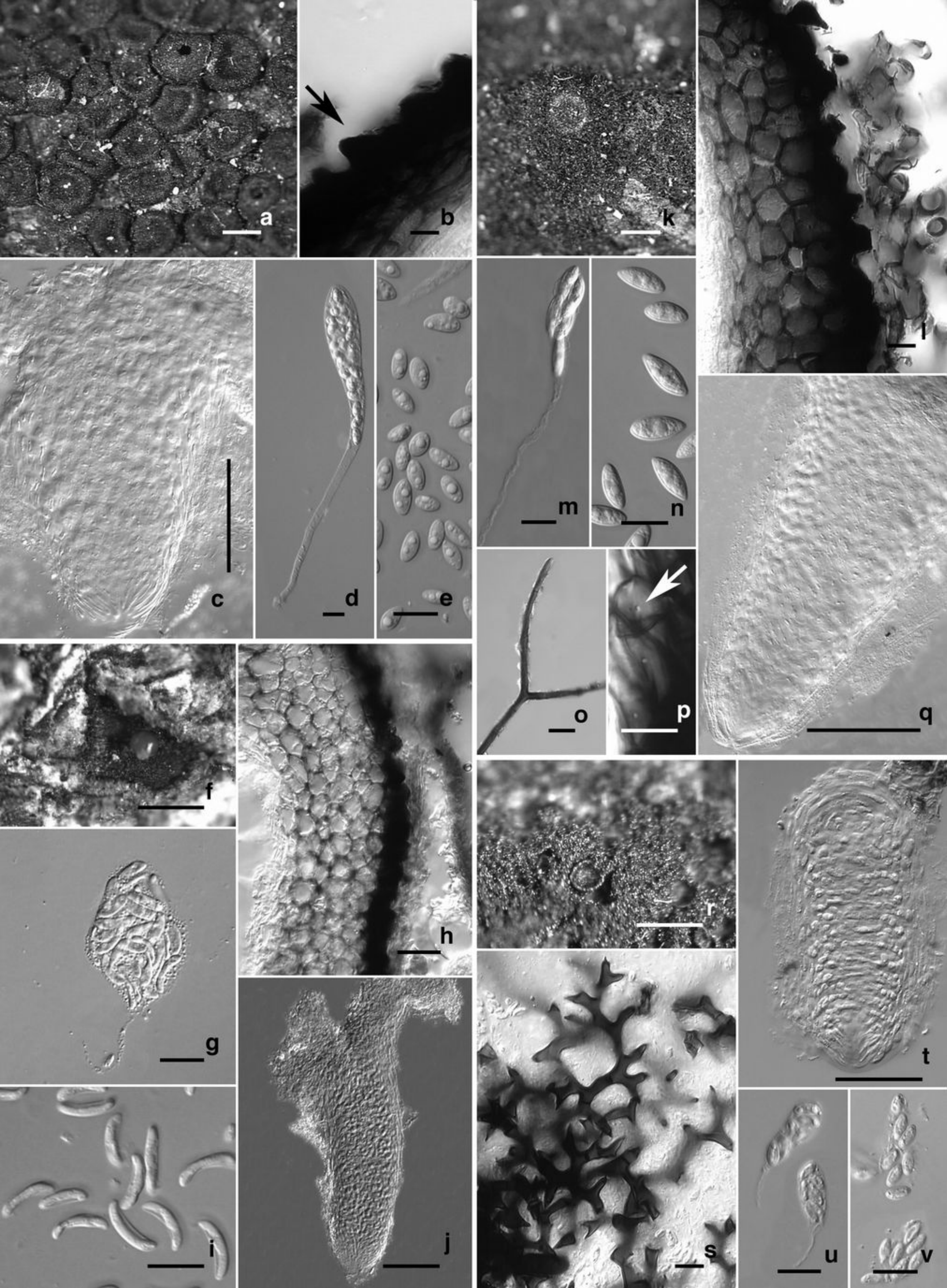
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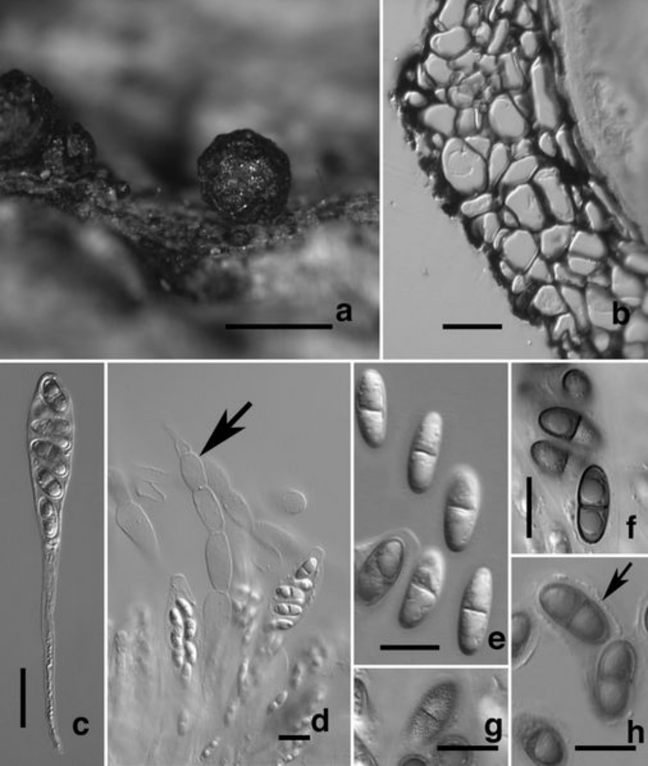
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TABLE I. Coronophoralean genera accepted in selected works since 1973

Müller and von Arx 1973, one family	Nannfeldt 1975a, b, one family	von Arx 1981, one family	Subramanian and Sekar 1990, two families
Coronophoraceae, Coronophorales	Nitschkiaceae, Sordariales	Coronophoraceae, Coronophorales	Coronophoraceae, Coronophorales
Acanthonitschkea Speg. *Bertia* de Not. *Biciliospora* Petr. *Calyculosphaeria* *Coronophora* Fuckel *Fracchiaea* Sacc. *Gaillardiella* Pat. *Nitschkia* G. H. Otth *Scortechiniella* Arx & E. Müll. *Thaxteria* Sacc. *Tympanopsis* Starbäck	*Acanthonitschkea* (syn. *Euacanthe* Theiss., *Neotrotteria* Sacc.) *Bertia* *Coronophora* (syn. *Cryptosphaerella* Sacc.) *Gaillardiella* *Nitschkia* (syn. *Biciliospora, Coronophorella* Höhn., *Fracchiaea, Neofracchiaea* Teng, *Scortechinia* Sacc., *Scortechiniella, Scortechiniellopsis* Sivan., *Tympanopsis*	*Acanthonitschke*a *Bertia* *Biciliospora* *Coronophora* *Fracchiaea* *Gaillardiella* *Lasiobertia* Sivan. *Nitschkia* *Spinulosphaeria* Sivan. *Sydowinula* Petr. *Tympanopsis*	*Acanthonitschkea* *Biciliospora* *Biciliosporina* Subram. & Sekar *Cryptosphaerella* *Euacanthe* *Fracchiaea* *Gaillardiella* *Janannfeldtia* Subram. & Sekar *Neotrotteria* *Nitschkia* (syn. *Thaxteria)* *Schizocapnodium* Fairman *Scortechinia*
			Bertiaceae, Coronophorales
			Bertia *Spinulosphaeria*

TABLE II. Taxa used in this study (new sequences in boldface)

Taxon	**Source**	**Origin**	**GenBank accession number**		
			LSU rDNA	***tef1***	***rpb2***
Acanthonitschkea argentinensis	S. Huhndorf 1395	Puerto Rico, Luquillo Mts.	AY695259	**FJ969042**	**FJ968943**
Acanthonitschkea tristis	S. Huhndorf 4723	Ecuador, Orellana Prov.	**FJ968949**	**FJ969043**	—
Bertia didyma I	L. Crane CR-206	Costa Rica, Puntarenas	**FJ968996**	—	—
Bertia didyma II	S. Huhndorf 4256	Costa Rica, Guanacaste	**FJ968950**	—	—
Bertia didyma III	S. Huhndorf 4719	Ecuador, Orellana Prov.	**FJ968958**	—	—
Bertia gigantispora	G. Mugambi 1136	Kenya, Ngong hills	—	**FJ969008**	**FJ968937**
Bertia moriformis I	S. Huhndorf 5169	USA, WI, Columbia Co.	**FJ968951**	—	—
Bertia moriformis II	S. Huhndorf 3344	USA, MI, Marquette Co.	AY695261		
Bertia moriformis III	S. Huhndorf 4320	USA, MI, Berrien Co.	AY695260		
Bertia multiseptata I	S. Huhndorf 1153	Puerto Rico, Luquillo Mts.	**FJ968953**	—	—
Bertia multiseptata II	S. Huhndorf 3127	Puerto Rico, Luquillo Mts.	**FJ968952**	—	—
Bertia ngongensis	G. Mugambi 1239	Kenya, Ngong hills	**FJ968954**	—	—

Bertia orbis I	G. Mugambi 1259	Kenya, Kakamega forest	**FJ968959**	—	—
Bertia orbis II	G. Mugambi 1271	Kenya, Kakamega forest	**FJ968955**	**FJ969009**	—
Bertia orbis III	S. Huhndorf 4035	Costa Rica, Puntarenas	**FJ968960**	—	—
Bertia orbis IV	S. Huhndorf 4557	Costa Rica, Alajuela	**GQ184146**		
Bertia sinensis	S. Huhndorf 4034	Costa Rica, Puntarenas	**FJ968961**	—	—
Bertia triseptata I	S. Huhndorf 1525	Puerto Rico, Luquillo Mts.	**FJ968957**	—	—
Bertia triseptata II	S. Huhndorf 4379	Ecuador, Orellana Prov.	**FJ968956**	—	—
Bertia tropicalis I	S. Huhndorf 3132	Puerto Rico. Luquillo Mts.	**FJ968962**	—	—
Bertia tropicalis II	S. Huhndorf 4046	Jamaica, Manchester Parish	**FJ968963**	—	—
Bertia tropicalis III	S. Huhndorf 1707	Puerto Rico. Luquillo Mts.	AY695262		
Bertia tropicalis IV	S. Huhndorf 3513	Panama, Barro Colorado Island	AY695263		
Biciliospora velutina	G. Mugambi 1268	Kenya, Kakamega forest	**FJ968964**	**FJ969018**	**FJ968932**

Chaetosphaerella fusca I	A. Miller 605	USA, NC, Blount Co.	**FJ968965**	—	—
Chaetosphaerella fusca II	A. Miller 852	USA, TN, Sevier Co.	**FJ968966**	—	—
Chaetosphaerella fusca III	G. Mugambi L124N	Kenya, Taita	**FJ968967**	**FJ969002**	—
Chaetosphaerella phaeostroma I	S. Huhndorf 4257	Costa Rica, Guanacaste	AY695264	**FJ969004**	**FJ968940**
Chaetosphaerella phaeostroma II	S. Huhndorf 4585	UK, Northumberland	AY346274	**FJ969003**	—
Coronophora gregaria	A. Miller 1555	USA, TN, Sevier Co.	—	**FJ969007**	**FJ968938**
Coronophorales	F. Fernández 1073	Costa Rica, San José	**FJ968968**	—	—
Coronophorella chaetomioides	G. Mugambi 1099	Kenya, Ololua forest, Nairobi	**FJ968969**	**FJ969034**	**FJ968922**
Crassochaeta nigrita I	S. Huhndorf 1667	Puerto Rico. Luquillo Mts.	AY695265		
Crassochaeta nigrita II	S. Huhndorf 2931	Puerto Rico. Luquillo Mts.	AY695266		
Cryptosphaerella celata	G. Mugambi 1231	Kenya, Mt. Kenya	**FJ968975**	**FJ969035**	**FJ968929**
Cryptosphaerella cylindriformis I	G. Mugambi 434N	Kenya, Taita	**FJ968972**	**FJ969031**	**FJ968934**
Cryptosphaerella cylindriformis II	G. Mugambi 1042	Kenya, Taita	**FJ968973**	**FJ969032**	**FJ968918**
Cryptosphaerella	G. Mugambi 1187	Kenya, Taita	**GQ217531**	**FJ969033**	**FJ968925**

cylindriformis III					
Cryptosphaerella cylindriformis IV	G. Mugambi 1075	Kenya, Taita	—	**FJ969030**	**FJ968920**
Cryptosphaerella costaricensis	M. Oses MO2111	Costa Rica, Guanacaste	**FJ968971**	**FJ969028**	—
Cryptosphaerella elliptica	S. Huhndorf 4722	Ecuador, Orellana Prov.	**FJ968974**	**FJ969029**	**FJ968944**
Cryptosphaerella globosa I	G. Mugambi 396N	Kenya, Taita	**FJ968976**	—	—
Cryptosphaerella globosa II	G. Mugambi 414N	Kenya, Taita	–	**FJ969037**	—
Cryptosphaerella globosa III	G. Mugambi 437N	Kenya, Taita	–	**FJ969038**	—
Cryptosphaerella globosa IV	G. Mugambi 471N	Kenya, Taita	**FJ968977**	**FJ969036**	**FJ968935**
Cryptosphaerella malindensis	G. Mugambi 1150	Kenya, Taita	**FJ968970**	**FJ969027**	**FJ968923**
Euacanthe foveolata I	G. Mugambi 1221	Kenya, Taita	**FJ968978**	**FJ969026**	**FJ968927**
Euacanthe foveolata II	S. Huhndorf 4408	Ecuador, Orellana Prov.	AY695267	—	—
Fracchiaea broomeiana I	G. Mugambi 1071	Kenya, Nairobi arboretum	—	**FJ969040**	**FJ968919**
Fracchiaea broomeiana II	S. Huhndorf 347	Venezuela, Guanare	**FJ968979**	**FJ969041**	**FJ968947**
Fracchiaea broomeiana III	S. Huhndorf 2809	USA, IN, Lake Co.	AY695268 (as 'broomeana')	**FJ969039**	**FJ968942**

Fracchiaea lunata	G. Mugambi 1089	Kenya, Nairobi arboretum	—	—	**FJ968921**
Fracchiaea sp	G. Mugambi 1250	Kenya, Ololua forest, Nairobi	—	**FJ969005**	—
Gaillardiella pezizoides I	G. Mugambi 1144	Kenya, Ololua forest, Nairobi	**FJ968980**	—	—
Gaillardiella pezizoides II	G. Mugambi 1245	Kenya, Ololua forest, Nairobi	**FJ968981**	**FJ969006**	—
Hypocrea rufa	GJS 90-97				EU341808
Nectria cinnabarina I	GJS 89-107			AF543785	
Nectria cinnabarina II	GJS 91-111				AF545567
Nectria violacea	MUCL40056		AF193242		
Neofracchiaea callista	S. Huhndorf 2689	USA, IL, Ogle Co.	AY695269	**FJ969020**	**FJ968941**
Neotrotteria pulchella	G. Mugambi 1255	Kenya, Ololua forest, Nairobi	**FJ968982**	—	—
Niesslia exilis I	CBS357.70		AY489718		
Niesslia exilis II	CBS560.74			AY489614	
Nitschkia calyculus I	G. Mugambi 1243	Kenya, Ololua forest, Nairobi	—	—	**FJ968931**
Nitschkia calyculus II	S. Huhndorf 918	French Guiana, Saül	**FJ968983**	—	—
Nitschkia grevillei	S. Huhndorf 4663	USA, IL, La Salle Co.	AY346294		
Nitschkia meniscoidea	S. Huhndorf 1523	Puerto Rico. Luquillo Mts.	AY695270		

Nitschkia tetraspora I	G. Mugambi L148N	Kenya, Taita	FJ968987	FJ969011	FJ968936
Nitschkia tetraspora II	G. Mugambi L213N	Kenya, Taita	FJ968985	—	—
Nitschkia tetraspora III	S. Huhndorf 4692	Ecuador, Orellana Prov.	FJ968986	—	—
Nitschkia tetraspora IV	S. Huhndorf 4787	Ecuador, Orellana Prov.	FJ968984	FJ969010	—
Scortechinia acanthostroma I	SMH5313	USA, IL, De Witt Co.	FJ968990	FJ969013	—
Scortechinia acanthostroma II	G. Mugambi 1164	Kenya, Arabuko-Sokoke	FJ968989	FJ969014	FJ968924
Scortechinia acanthostroma III	G. Mugambi L163N	Kenya, Taita	FJ968991	FJ969015	—
Scortechinia acanthostroma IV	S. Huhndorf 1143	Puerto Rico, Luquillo Mts.	FJ968988	FJ969012	FJ968948
Scortechinia diminuspora	S. Huhndorf 4763	Ecuador, Orellana Prov.	FJ968992	—	—
Scortechiniella similis	S. Huhndorf 2006	Puerto Rico, Luquillo Mts.	FJ968994	FJ969019	FJ968945
Scortechiniellopsis leonensis	G. Mugambi 1269	Kenya, Kakamega forest	FJ968993	FJ969021	FJ968933
Spinulosphaeria nuda	S. Huhndorf 1952	Puerto Rico, Luquillo Mts.	FJ968995	—	—
Tympanopsis confertula I	A. Miller 1567	USA, TN, Sevier Co.	FJ969001	FJ969025	FJ968939

Tympanopsis confertula II	G. Mugambi 1242	Kenya, Ololua forest, Nairobi	**FJ968997**	**FJ969023**	**FJ968930**
Tympanopsis confertula III	S. Huhndorf 2648	USA, IL, Cook Co.	AY695272 (as ‘Scortechinia conferta’)	**FJ969022**	—
Tympanopsis confertula IV	S. Huhndorf 4841	France, Midi-Pyrénées	**FJ968998**	**FJ969024**	**FJ968946**
Tympanopsis uniseriata I	G. Mugambi 1203	Kenya, Mt. Kenya	**FJ968999**	**FJ969016**	**FJ968926**
Tympanopsis uniseriata II	G. Mugambi 1228	Kenya, Mt. Kenya	**FJ969000**	**FJ969017**	**FJ968928**

TABLE III. Morphological characteristics of included Coronophorales genera

Taxon (* indicates monotypic)	**Ascomatal position on substrate**	**Ascomatal surface**	**Ascomata collapsing when dry**	**Subiculum**	**Paraphyses**	**Quellkörper**	**Ascospores per ascus**	**Ascospore appendage-like wall extensions**
Acanthonitschkea	Superficial	Setose	Collabent	Sparse to dense, spinulose	Absent	Absent	8	No
Bertia	Superficial	Glabrous	Collabent, lateral or not collapsing	Inconspicuous	Wide, inflated	Absent	8	No
*Biciliospora**	Superficial	Glabrous	Collabent	Sparse to dense, smooth	Absent	Present	8	Yes
Chaetosphaerella	Superficial	Setose around base	Collabent or not collapsing	Dense, spinulose	Wide, inflated	Absent	8	No
Coronophora	Immersed/erumpent	Glabrous	Lateral	Inconspicuous	Absent	Absent	Many	No
*Coronophorella**	Superficial	Glabrous	Collabent	Dense, smooth	Absent	Present	8	No
Crassochaeta	Superficial	Setose	Not collapsing	Dense, spinulose	Wide, inflated	Absent	8	No

Cryptosphaerella	Immersed/erumpent	Glabrous or hyphal	Collabent or lateral	Inconspicuous to sparse	Absent	Present	Many	No
Euacanthe	Superficial	Setose	Collabent	Dense, spinulose	Absent	Present	8	No
Fracchiaea	Immersed/erumpent/superficial	Setose, barbed	Not collapsing	Inconspicuous	Absent	Absent	Many	No
Gaillardiella	Superficial	Glabrous	Collabent	Inconspicuous	Absent	Absent	8	No
*Neofracchiaea**	Superficial	Setose	Collabent	Sparse, smooth	Absent	Present	Many	No
Neotrotteria	Superficial	Setose	Collabent	Dense, spinulose	Absent	Present	Many	No
Nitschkia	Superficial	Glabrous	Collabent	Sparse to dense, smooth	Absent	Absent	8 or 4	No
Scortechinia	Superficial	Glabrous	Collabent	Dense, spinulose	Absent	Present	8	No
*Scortechiniella**	Superficial	Glabrous to hyphal	Collabent	Dense, smooth	Absent	Present	Many	Yes
*Scortechiniellopsis**	Superficial	Glabrous	Collabent	Dense, spinulose	Absent	Present	Many	No

Spinulosphaeria	Superficial	Broad tooth-like spines or glabrous	Not collapsing	Dense, spinulose	Wide, inflated	Absent	8	No
Tympanopsis	Superficial	Glabrous to hyphal	Collabent	Sparse to dense, smooth	Absent	Present	8	No