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A molecular, morphological and ecological re-appraisal of *Venturiales*—a new order of *Dothideomycetes*

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Abstract

The *Venturiaceae* was traditionally assigned to *Pleosporales* although its diagnostic characters readily distinguish it from other pleosporalean families. These include a parasitic or saprobic lifestyle, occurring on leaves or stems of dicotyledons; small to medium-sized ascomata, often with setae; deliquescing pseudoparaphyses; 8-spored, broadly cylindrical to obclavate asci; 1-septate, yellowish, greenish or pale brown to brown ascospores; and hyphomycetous anamorphs. Phylogenetically, core genera of *Venturiaceae* form a monophyletic clade within *Dothideomycetes*, and represent a separate sister lineage from current orders, thus a new order—*Venturiales* is introduced. A new family, *Sympoventuriaceae*, is introduced to accommodate taxa of a well-supported subclade within *Venturiales*, which contains *Sympoventuria*, *Veronaeopsis simplex* and *Fusicladium*-like species. Based on morphology and DNA sequence analysis, eight genera are included in *Venturiaceae*, *viz. Acantharia*, *Apiosporina* (including *Dibotryon*),

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Caproventuria, *Coleroa*, *Pseudoparodiella*, *Metacoleroa*, *Tyrannosorus* and *Venturia*. Molecular phylogenetic information is lacking for seven genera previously included in *Venturiales*, namely *Arkoola*, *Atopospora*, *Botryostroma*, *Lasiobotrys*, *Trichodothella*, *Trichodothis* and *Rhizogenee* and these are discussed, but their inclusion in *Venturiaceae* is doubtful. *Crotone*, *Gibbera*, *Lineostroma*, *Phaeocryptopus*, *Phragmogibbera*, *Platychora*, *Polyrhizon*, *Rosenscheldiella*, *Uleodothis* and *Xenomeris* are excluded from *Venturiales*, and their ordinal placement needs further investigation. *Zeuctomorpha* is treated as a synonym of *Acantharia*.

Keywords

Fusicladium; Generic type; *Sympoventuriaceae*; Taxonomy; *Venturiaceae*

Introduction

The name *Venturiaceae* was first introduced by Müller and von Arx (1950), and a systematic generic key given by von Arx (1952) includes 12 genera, i.e. *Atopospora*, *Coleroa*, *Gibbera*, *Lasiobotrys*, *Neogibbera*, *Parodiella*, *Phaeocryptopus*, *Pseudoparodia*, *Stigmatea*, *Trichodothella*, *Trichodothis* and *Venturia*. Further detailed studies and additions to the family have been made (von Arx 1954; Menon 1956; Müller 1958; Müller and Menon 1955; Müller and von Arx 1962; Nüesch 1960; Petrak 1950, 1953, 1954; Shoemaker 1963). The first valid description of *Venturiaceae* was provided by Barr (1979) who considered setose ascomata and hyaline, olive to greenish brown, obovate to oblong, generally 1-septate ascospores as the most important diagnostic characters. Based on these morphological characters, 12 genera were included, i.e. *Acantharia*, *Apiosporina*, *Coleroa*, *Gibbera*, *Metacoleroa*, *Phaeocryptopus*, *Platychora*, *Protoventuria*, *Pyrenobotrys*, *Trichodothis*, *Venturia* and *Xenomeris*. Species of *Venturiaceae sensu* Barr (1968) have a parasitic or saprobic habit, and they usually grow in living or dead leaves, stalks, or twigs of various higher plants, rarely on *Sphagnum* or dung. Many species of *Venturiaceae* parasitize perennial plants, and some of them are notable cosmopolitan plant pathogens, causing diseases such as apple scab (*Venturia inaequalis*), pear scab (*V. pyrina*), poplar shoot blight (*V. populina*), soybean black leaf blight (*Arkoola nigra*), and the widespread black knot disease of cherry (*Dibotryon morbosum*) (von Arx and Müller 1975; Talbot 1971). Currently, 27 genera are included in *Venturiaceae* (Lumbsch and Huhndorf 2010).

Venturiaceae was assigned to *Pleosporales* based on its "*Pleospora* type of centrum and bitunicate asci" (Barr 1968, 1979). However, this placement is not supported by recent phylogenic studies (Kodsueb et al. 2006; Kruys et al. 2006; Winton et al. 2007). Results obtained by Kruys et al. (2006) based on combined *nu*SSU, *nu*LSU and *mt*SSU DNA sequences indicated that *Venturiaceae* forms a clade outside *Pleosporales*, a well-supported monophyletic group with members of *Phaeotrichaceae*. Kodsueb et al. (2006) noted a close relationship with *Tubeufiaceae* based on 28S *nu*rDNA sequences, but their affinity with *Pleosporales* lacked clear statistical support. The polyphyletic nature of *Venturiaceae* was indicated by Winton et al. (2007) based on the analysis of combined *nu*SSU and *nu*LSU rDNA sequences. Although core members of *Venturiaceae* form a monophyletic group, their ordinal placement remains unsettled in all these papers.

It is now possible to gain a better understanding of *Venturiaceae* by combining recently obtained DNA sequences from a brader sampling of taxa. The aim of present investigation is therefore to re-examine the taxonomic status of *Venturiaceae* based on morphological, ecological, molecular phylogenetic data and anamorphic states and to evaluate its ordinal placement and relationships within *Dothideomycetes*.

Materials and methods

Morphological studies

The type specimens of 15 representative genera as well as collections of an additional four genera of *Venturiaceae* (*sensu* Lumbsch and Huhndorf 2010) were loaned from NY, K, L, PH and S. Some type specimens or collections are in poor condition, while others could not be located during the course of this study and therefore, only 12 generic type species are described here. Measurements and descriptions of sections of the ascomata, hamathecium, asci and ascospores were carried out by immersing ascomata in water or in 10% lactic acid. Microphotography was taken with material mounted in water or 10–100% lactic acid. Slides were rendered semi-permanent by the addition of 90% lactic acid. Photographs were taken on an Olympus BX50 microscope using an Olympus CA 35 AD-4 camera. The generic descriptions are based on the type species of each genus. In this study, the terms "ascoma" (pl. ascomata) refers to a unilocular fruiting body, and "ascostroma" (pl. ascostromata) to a multilocular fruiting body. Other morphological criteria follow to Zhang et al. (2009, 2012).

DNA amplification and sequencing

Cultures used in this study were obtained from the Centraalbureau voor Schimmelcultures in the Netherlands (CBS). Fungal isolates and DNA extraction isolates were on PDA and MEA, and total genomic DNA extracted from mycelia following the protocols as outlined by Shenoy et al. (2007, 2010). DNA amplification and sequencing were performed following the protocol of Zhang et al. (2009).

Sequence alignment and phylogenetic analyses

The phylogeny was performed with four markers: partial sequence from the small and large subunits of the nuclear ribosomal RNA genes (*nu*SSU, *nu*LSU) and three protein coding genes, translation elongation factor-1 alpha (*TEF*1) and the largest and second largest subunits of RNA polymerase (*RPB*1*, RPB*2) and. Sequences were downloaded from GenBank according to Table 1. Each of the individual ribosomal genes was aligned in SATé under default settings with at least 20 iterations (Liu et al. 2009). The protein coding genes were aligned in BioEdit (Hall 2004) and completed with manual adjustment. Introns and variable columns were removed and all genes were concatenated in a single nucleotide alignment with 54.77% missing and gap characters out of a total set of 5,496. The final data matrix had 94 taxa including outgroups (Table 1). Previous results indicated no clear conflict amongst the majority of the data used (Schoch et al. 2009) and a phylogenetic analysis of the concatenated alignment was performed at the CIPRES webportal (Miller et al. 2010) using RAxML v. 7.2.8 as part of the "RAxML-HPC2 on TG" tool (Stamatakis 2006; Stamatakis et al. 2008) applying unique model parameters for each gene and codon (11 partitions). A general time reversible model (GTR) was applied with a discrete gamma distribution and four rate classes. One hundred thorough maximum likelihood (ML) tree searches were done in RAxML v. 7.2.7 under the same model, each one starting from a separate randomised tree and the best scoring tree selected with a final ln value of –62920.113547. Two isolates of *Arthoniomycetes* (*Schismatomma decolorans* and *Opegrapha dolomitica*), the sister class to *Dothideomycetes*, were used as outgroup. One thousand non parametric bootstrap iterations were run with the GTR model and a discrete gamma distribution. The resulting replicates were plotted on to the best scoring tree obtained previously. The phylogram with bootstrap values above the branches is presented in Fig. 1 by using graphical options available in TreeDyn v. 198.3 (Chevenet et al. 2006).

We also analyzed the same data set mentioned previously using the Bayesian method of Huelsenbeck et al. (2001) by implementing Markov Chain Monte Carlo (MCMC) sampling using the software MrBayes v.3.1.2 (Huelsenbeck and Ronquist 2001) at the CIPRES

webportal. Data was partitioned as in the RAxML run and the same likelihood models were applied with four discrete gamma categories. The Bayesian prior distributions treated all trees as equally likely. Two parallel runs were performed with four chains each and this was continued for 2000 000 generations. Every 100th tree was saved and the two runs were examined for convergence. The first 50% of each run was discarded as burn in and the remaining two sets of 10 000 trees combined. The best scoring RAxML tree was used as a template and the percentage presence of all nodes within the combined set of 20 000 trees plotted on its nodes as Bayesian posterior probabilities. These are indicated as values below nodes in Fig. 1.

In order to see if missing data had any influence on our previous phylogeny we trimmed all taxa which did not have LSU present and removed all other genes, resulting in a matrix with 1,200 characters and 90 taxa. This data set had only 20.42% missing characters. *Schismatomma decolorans* was used as a outgroup. Using the CIPRES webportal as before, we ran a combined ML tree search with bootstrap resampling and a bootstopping criterion in effect (Pattengale et al. 2010). Likelihood of the final tree was estimated using the same model parameters as for the previous RAxML run but the rapid bootstrap option was used in this case. The run was stopped after 450 bootstraps and combined with an optimized tree with a final likelihood value of –10697.749925. The tree was plotted as described but all ordinal level clades were collapsed in MEGA 5 (Tamura et al. 2011). This is shown in Fig. 2.

Taxonomy

Venturiales Yin. Zhang, C.L. Schoch & K.D. Hyde, **ord. nov.** MycoBank: MB 513386

Ascomata immersa, erumpentia vel superficialia, vel in stroma vel infra adusta clypei, aliquando coalitus subiculum, globosi vel subglobosi vel conicus, integer vel apices setosi, ostiolati. Pseudoparaphyses vulgo dissolvis, asci bitunicati, fissitunicati; ascosporae hyalinae viridae olivaceae vel brunneae, obovoidae, oblongae, uniseptatae, symmetricae vel asymmetricae.

Familia typica: *Venturiaceae*.

Habitat saprobic or parasitic on leave or stems of dicotyledons, rarely on monocotyledons. *Ascomata* immersed, erumpent to superficial, scattered or gregarious, or as locules in a stroma or below a blackened clypeus, globose, subglobose, or dome-shaped or flat-conical, with or without seta around papilla or covering whole ascomata, ostiolate, sometimes ascomata sitting on a well-developed subiculum. *Hamathecium* of narrowly cellular pseudoparaphyses, mostly evanescent and rarely persistent. *Asci* 8-spored, bitunicate, fissitunicate, broadly or usually obclavate, usually lacking a pedicel. *Ascospores* hyaline, light greenish olivaceous to brown, 1-septate, symmetrical, asymmetrical or apiosporous.

Anamorphs: *Fusicladium sensu stricto, Pollaccia, Spilocaea, Sympodiella*-like, *Pseudocladosporium,* ?*Didymochora, Veronaeopsis* and *Zeloasperisporium.*

Type family: *Venturiaceae*.

Note: The phylogenetic comparison of selected species from *Dothideomycetes* is shown in Figs. 1 and 2. This includes representatives of all major orders in the class, and unambiguously supports *Venturiales* as a separate entity. In spite of our complete sampling the placement of a sister lineage to *Venturiales* remains uncertain. We also find weak to moderate support for a relationship to *Microthyriales* (based on relationship to a single isolate) and *Phaeotrichaceae*. Within *Venturiales* two lineages can be defined, i.e. the main

group containing *Venturia* and allies (*Venturiaceae*) and a separate lineage containing *Veronaeopsis, Sympoventuria* and several *Fusicladium*-like or *Sympodiella*-like anamorph species. Herein a new family, *Sympoventuriaceae*, is introduced to accommodate the second lineage.

Sympoventuriaceae Yin. Zhang, C.L. Schoch & K.D. Hyde, **fam. nov.** MycoBank: MB 563117

Ascomata immersi, subglobosi, papillati, ostiolati. Pseudoparaphyses hyalinis, septatis. Asci bitunicati, fissitunicati. Ascosporae hyalinae, obovoidae, oblongae, uniseptatae.

Habitat saprobic. *Ascomata* subglobose, immersed, black, papillate, ostiolate. *Pseudoparaphyses* hyaline, septate, constricted at septa, anastomosing, extending above the asci. *Asci* 8-spored, bitunicate, fissitunicate, subcylindrical, pedicellate. *Ascospores* hyaline, fusoid-ellipsoidal, constricted at median septum.

Anamorphs: *Sympodiella*-like, *Fusicladium*-like, *Veronaeopsis.*

Type genus: *Sympoventuria* Crous & Seifert.

Genus included in *Sympoventuriaceae*

Multigene phylogenetic analysis in this study indicated that species of *Venturiales* are subdivided into two groups which represent two familial clades, i.e. *Sympoventuriaceae* and *Venturiaceae. Sympoventuriaceae* is represented by *Sympoventuria*, and can be distinguished from species of *Venturiales* by its saprobic life style, presence of pseudoparaphyses, and hyaline, symmetrical ascospores.

Sympoventuria Crous & Seifert, Fungal Divers 25: 31 (2007).

Generic description:

Habitat saprobic on leaf litter. *Ascomata* subglobose, immersed, black, inconspicuous, papillate, ostiolate. *Pseudoparaphyses* hyaline, septate, constricted at septa, anastomosing, extending above the asci. *Asci* hyaline, subcylindrical, stipitate, 8-spored. *Ascospores* hyaline, fusoid-ellipsoidal, constricted at median septum (from Crous et al. 2007b).

Anamorph reported for genus: *Sympodiella*-like.

Type species:

Sympoventuria capensis Crous & Seifert, Fungal Divers 25: 32 (2007).

Anamorph: *Sympodiella*-like.

Note: The small-sized immersed ascomata agree with *Venturia sensu stricto*, but the persistent pseudoparaphyses, saprobic life style, hyaline, 1-septate, symmetric ascospores and subcylindrical asci of *Sympoventuria capensis* differ from those of *Venturia sensu stricto* (Crous et al. 2007b; Sivanesan 1977). DNA based phylogenies support the placement of *Sympoventuria* within *Venturiales*, but not *Venturiaceae* (Crous et al. 2007b, Fig. 1). Currently, only one monotypic ascomycetous genus, *Sympoventuria*, is included in *Sympoventuriaceae,* while the anamorphic genus *Veronaeopsis* and a clade containing "*Fusicladium pini*" and "*F. intermedium*" may represent distinct genera.

Venturiaceae E. Müll. & Arx ex M.E. Barr, Mycologia 71: 947 (1979). **emend**.

Habitat saprobic or parasitic on leaves or stems of dicotyledons, rarely on monocotyledons. With or without ascostroma. *Ascomata* immersed, erumpent to superficial, scattered or gregarious, sometimes composed of a well-developed subiculum, globose, subglobose, with or without setae around papilla, ostiolate. *Hamathecium* of narrowly cellular pseudoparaphyses, mostly evanescent and rarely persistent. *Asci* 8-spored, bitunicate, fissitunicate, usually obclavate to obpyriform, rarely cylindrical, usually apedicellate. *Ascospores* hyaline, yellowish, light greenish olivaceous to brown, 1-septate, symmetrical, asymmetrical or apiosporous.

Anamorphs: *Fusicladium, Pollaccia, Spilocaea* and ? *Pseudocladosporium*-like.

Type genus: *Venturia* Sacc.

Genera included in *Venturiaceae*

Based on both morphological, ecological comparisons and limited molecular phylogenetic analysis, eight genera are included within *Venturiaceae*, *viz. Acantharia*, *Apiosporina*, *Dibotryon*, *Caproventuria*, *Coleroa*, *Pseudoparodiella*, *Venturia* and *Metacoleroa*. However further molecular analysis is necessary to confirm the inclusion of some genera, such as *Acantharia*, *Coleroa* and *Pseudoparodiella*.

Key to the genera of *Venturiaceae*

1a. Ascospores apiosporous *Apiosporina* (incl. *Dibotryon*)	
1b. Ascospore septum median or submedian, but not apiosporous	2
2a. Hyphae grow inside of the substrate	3
2b. Hyphae superficial, ascomata superficial	4
3a. Ascomata superficial, produced on thin subcuticular stroma	*Coleroa*
3b. Ascomata immersed to erumpent, without subcuticular stroma	5
4a. Ascomata without subiculum, not cupulate when dry, ascospores pale brown when mature	*Pseudoparodiella*
4b. Ascomata without subiculum, cupulate when dry, ascospores dark brown when mature	*Acantharia*
4c. Ascomata produced on well defined subiculum, not cupulate when dry, ascospores olivaceous brown when mature	*Metacoleroa*
5a. Parasitic, having *Pollaccia* or *Spilocaea* anamorphs, ascospores smooth without germ slits	*Venturia sensu stricto*
5b. Saprobic, having *Pseudocladosporium* anamorphs, ascospores smooth without germ slits	*Caproventuria*
5c. Saprobic, having *Helicodendron* anamorphs, ascospores smooth or longitudinally ridged ascospores with or without germ slits	*Tyrannosorus*

Acantharia Theiss. & Syd., Annls mycol. 16: 15 (1918).

= *Zeuctomorpha* Sivan., P.M. Kirk & Govindu, Bitunicate Ascomycetes and their Anamorphs (Vaduz): 572 (1984).

Generic description:

Habitat parasitic or saprobic. *Ascomata* small-sized, gregarious, superficial, globose, subglobose to ovate, usually cupulate when dry, thickly clothed with opaque, black setae. *Peridium* comprising two-strata of cell types. *Hamathecium* of cellular pseudoparaphyses, evanescent in mature ascomata. *Asci* 8-spored, bitunicate, fissitunicate, obclavate, apedicellate. *Ascospores* obliquely uniseriate and partially overlapping at the apex and biseriate at the base, subcylindrical to ellipsoidal, with broadly to narrowly rounded or tapered ends, brown to dark brown with a greenish tint, 1-septate, constricted at the septum, the upper cell often shorter and broader than the lower one, smooth-walled.

Anamorph reported for genus: *Fusicladium*-like, *Stigmina* (Sivanesan 1984b).

Type species:

Acantharia echinata (Ellis & Everh.) Theiss. & Syd., Annls mycol. 16: 15 (1918). (Fig. 3)

≡ *Dimerosporium echinatum* Ellis & Everh., Erythea 1: 145 (1893).

Ascomata 70–157 μm high×115–186 μm diam., gregarious, forming densely crowded, orbicular patches of 3–5 mm diam., superficial, globose, subglobose to ovate, cupulate when dry, thickly clothed with opaque, black setae, 70–110 μm long, 5–7 μm thick at the base (Fig. 3a, b). *Peridium* 20–27.5 μm wide, up to 40 μm thick near the base, comprising two-strata of cell types, outer layer composed of 1–3 layers of large heavily pigmented thick-walled cells of *textura angularis*, cells 8–13 μm diam., cell wall 1–4 μm thick, basal cells smaller and walls thicker; inner layer composed of lightly pigmented cells of *textura angularis*, up to 3×12 μm diam. (Fig. 3c). *Hamathecium* of cellular pseudoparaphyses, 2–4 μm broad, embedded in mucilage, evanescent in mature ascomata. *Asci* 65–100×14–25 μm ($\bar{x}$=80.8×19.6 μm, *n*=10), 8-spored, bitunicate, fissitunicate, obclavate, without pedicel (Fig. 3d–f). *Ascospores* 17.5–22.5×9–12.5 μm ($\bar{x}$=20.3×9.8 μm, *n*=10), obliquely uniseriate and partially overlapping at the apex and biseriate at centre or sometimes at the base, broadly cylindrical to ellipsoidal with broadly to narrowly rounded or tapered ends, brown to dark brown with greenish tint, 1-septate, constricted at the septum, the upper cell often shorter and broader than the lower one, smooth-walled (Fig. 3g–i).

Material examined: USA: California, Amador County, Jackson, on living leaves of *Quercus chrysolepis*, leg. Geo. Hansen, com. Marshall A. Howe (NY, **holotype**).

Anamorph: *Fusicladium*-like sp. (Sivanesan 1984b).

Note: The folicolous habitat, superficial, setose ascomata, evanescent pseudoparaphyses, obclavate asci, and 1-septate, brown and constricted ascospores are typical of *Venturiaceae*.

Acantharia arecae (Sivan., P.M. Kirk & Govindu) Yin. Zhang & K.D. Hyde, **comb. nov.**

≡ *Zeuctomorpha arecae* Sivan., P.M. Kirk & Govindu, in Sivanesan, Bitunicate Ascomycetes and their Anamorphs (Vaduz): 572 (1984).

Material examined: INDIA: Shimogee, on *Areca catechu* L. leaf, 1 Nov. 1979, H.C. Govindu (IMI 246067, holotype of *Zeuctomorpha arecae*).

Anamorph: *Acroconidiellina arecae* (Sivanesan 1984a).

Note: The small-sized setose ascomata, obclavate to obpyriform asci, asymmetrical pigmented ascospores of *Zeuctomorpha* point to *Acantharia* (Sivanesan 1984b). The anamorphic state of *Zeuctomorpha* (*Acroconidiellina arecae*) is also comparable with that of *Acantharia* (*Fusicladium*-like). Thus we treat *Zeuctomorpha arecae* here as a synonym of *Acantharia arecae*. Similarly, *Zeuctomorpha* is treated as a synonym of *Acantharia. Zeuctomorpha arecae* however, differs in having a thickened ascal apex with a distinct ocular chamber while its occurrence on palms is also contradictory to the understanding of the *Venturiaceae* (Zhang et al. 2012). Fresh collections and molecular study are needed to confirm whether these genera are synonymous and whether *Acantharia* should be included in *Venturiaceae.*

Apiosporina Höhn., Sber. Akad. Wiss. Wien, Math.-naturw. Kl., Abt. I 119: 439 (1910).

= *Dibotryon* Theiss. & Syd., Annls mycol.13: 663 (1915).

Generic description:

Habitat parasitic (or saprobic?) on leaves or stems of dicotyledons. *Ascomata* small-sized, gregarious, superficial, globose to subglobose, developing on a hyphal mass, easily removable from the substrate, small papillate and ostiolate. *Peridium* thin, composed of several layers of heavily pigmented thick-walled cells of *textura angularis. Hamathecium* of rare, septate, pseudoparaphyses. *Asci* 8-spored, bitunicate to narrowly obclavate, cylindrical, with a short, thick, furcate or knob-like pedicel or pedicel lacking. *Ascospores* biseriate and partially overlapping, ovoid to narrowly ovoid, hyaline to pale brown, apiosporous, 1-septate near the lower end, barely constricted at the septum, smooth-walled.

Anamorph reported for genus: *Cladosporium* sp. or *Fusicladium* sp. (Sivanesan 1984a).

Type species:

Apiosporina collinsii (Schwein.) Höhn., Sber. Akad. Wiss. Wien, Math.-naturw. Kl., Abt. I 119: 439 [47 repr.] (1910). (Fig. 4)

≡ *Sphaeria collinsii* Schwein., Trans. Am. phil. Soc. 4: 211 (1832).

Ascomata 140–172 μm diam., gregarious, superficial, globose to subglobose, developing on a hyphal mass, easily removable from the substrate, black with rough and shiny surface, papillate small and ostiolate (Fig. 4a). *Peridium* 20–33 μm wide, composed of 3–4 layers of heavily pigmented thick-walled cells of *textura angularis*, cells 5–10 μm diam., cell wall up to 2.5 μm thick, the innermost layer cell-wall thinner. *Hamathecium* of rare, septate, 4–6 μm broad pseudoparaphyses. *Asci* 63–77×8–10 μm ($\bar{x}$= 70.9×9.3 μm, *n*=10), 8-spored, bitunicate, fissitunicate dehiscence not observed, cylindrical to narrowly obclavate, with a short, thick, knob-like pedicel or pedicel lacking (Fig. 4b, c). *Ascospores* 12.5–15×5–6 μm ($\bar{x}$=13.4× 5.3 μm, *n*=10), biseriate and partially overlapping, ovoid to narrowly ovoid, hyaline, 1-septate, apiosporous, slightly constricted at the septum, the upper cell often 4–5 times longer and much broader than the lower one, smooth-walled (Fig. 4d).

Material examined: CANADA: Saskatchwan, on leaves of *Cotoneaster* sp. (K(M):158702, ex herb. Broome).

Anamorph: *Cladosporium* sp. (Sivanesan 1984a).

Apiosporina morbosa (Schwein.) Arx, Acta bot. neerl. 3: 86 (1954). (Fig. 5)

≡ *Dibotryon morbosum* (Schwein.) Theiss. & Syd., Annls mycol. 13(5/6): 663 (1915).

≡ *Sphaeria morbosa* Schwein., Schr. naturf. Ges. Leipzig 1: 40 (1822).

Ascomata densely developing in branches, erumpent and form a swelling up to 1 cm thick, black, hard. *Ascomata* 160–230 μm high×170–250 μm diam., densely gregarious on the surface of ascostromata, subglobose, triangular or oblong, often flattened on the top, wall black (Fig. 5a, b). *Peridium* 30–45 μm wide, 1-layered, composed of small heavily pigmented thick-walled cells of *textura angularis*, cells 3–7 μm diam., cell wall 2–4 μm thick, cells at the base of the ascomata larger, up to 10 μm diam. (Fig. 5b). *Hamathecium* of dense, 1.5–2(−3) μm broad, septate, branched pseudoparaphyses (Fig. 5d). *Asci* 68–90×12.5–15 μm ($\bar{x}$=73×13 μm, *n*=10), 8-spored, bitunicate, fissitunicate dehiscence not seen, subcylindrical or broadly clavate, with a short, furcate pedicel which is 8–15 μm long, with an inconspicuous ocular chamber (Fig. 5c). *Ascospores* 15–18(−19)×(5-)6–7.5 μm

($\bar{x}$=17.4×6.8 μm, *n*=10), biseriate, clavate, apiosporous, tapered towards the base, apex obtusely rounded, one septate near the lower end, barely constricted at the septum, hyaline to pale brown, smooth-walled (Fig. 5e).

Material examined: USA: Pennsylvania, Bethlehem, in *Prunis cultis*, Syn. #1416. leg. L.D. von Schweinitz s.n. Det. L.D. von Schweinitz (PH-01048831, 01048832, 01048838, 01048839, 01048840, as *Sphaeria morbosa* Schw., **syntype**; PH-01048834).

Anamorph: ?*Fusicladium* sp. (Sivanesan 1984a).

Note: The anamorphic state of *A. collinsii* was reported as *Cladosporium* sp. (Sivanesan 1984a), which was assigned to *Fusicladium sensu lato* by Braun et al. (2003). A narrow concept of *Fusicladium*, however, is accepted in this study. *Dibotryon* had been treated as a synonym of *Apiosporina* (von Arx and Müller 1975; Barr 1968; Crous et al. 2007a). Although the black knots on branches of *Prunis cultis* formed by *Dibotryon morbosum* can be readily distinguished from the black spots on leaves formed by *Apiosporina*, their congeneric relationship was confirmed by molecular data (Winton et al. 2007, Figs. 1 and 2).

Caproventuria U. Braun, Monogr. *Cercosporella*, *Ramularia* Allied Genera (Phytopath. Hyphom.) 2: 396 (1998).

Generic description:

Habitat saprobic. *Ascomata* non-stromatic, subglobose, ampulliform, obpyriform, urceolate, papillate, ostiolate, pseudoparaphysate, membranaceous, dark, setose throughout. *Setae* dark brown, aseptate, simple or occasionally forked, apex acute, smooth, wall thickened below, but thin-walled towards the apex. *Peridium* pseudoparenchymatous, composed of angular to rounded, dark brown cells. *Asci* 8-spored, bitunicate, numerous, subclavate to cylindrical. *Ascospores* monostichous or distichous, ellipsoidovoid, with a single submedian septum, mostly somewhat constricted at the septum, smooth, yellowish olivaceous (from Braun 1998).

Anamorph reported for genus: *Pseudocladosporium* (Braun et al. 2003).

Type species:

Caproventuria hanliniana (U. Braun & Feiler) U. Braun, Monogr. *Cercosporella*, *Ramularia* Allied Genera (Phytopath. Hyphom.) 2: 396 (1998).

≡ *Capronia hanliniana* U. Braun & Feiler, Microbiol. Res. 150: 90 (1995).

Anamorph: *Pseudocladosporium brevicatenatum* (U. Braun & Feiler) U. Braun 1998.

Note: Braun (1998) treated *Caproventuria* as separate genus from *Venturia* based on its saprobic life style and *Pseudocladosporium* anamorphic state, compared to the parasitic life style and *Pollaccia* or *Spilocaea* anamorphic state possessed by *Venturia sensu stricto*. Crous et al. (2007b), however, treated *Pseudocladosporium* as a synonym of *Fusicladium sensu lato* based on the combined LSU and ITS *nu*rDNA sequences comparison, and considered the arrangement of the conidiophores (solitary, fasciculate, sporodochial), the proliferation of conidiogenous cells (sympodial, percurrent) and shape, size as well as formation of conidia (solitary, catenate) to be of little taxonomic value at generic level. This proposal, however, is not supported in this study, as narrow generic concepts of *Venturia* and *Fusicladium* are accepted here. In addition, according to our multigene phylogenetic analysis, species of *Caproventuria* and *Tyrannosorus* form a unambiguously supported clade

separating from the clade *Venturia sensu stricto*. Based on both the anamorph and molecular phylogeny, *Caproventuria* is a well defined genus of *Venturiaceae*.

Coleroa Rabenh., Herb. myc., ed. 1no. 1456 (1850).

Generic description:

Habitat parasitic and saprobic on dicotyledons. *Ascomata* small-sized, scattered, or in small groups, superficial, globose, subglobose, setae few to numerous, papillate, ostiolate. *Peridium* thin, composed of lightly pigmented thin-walled cells of *textura angularis. Hamathecium ca*. 2 μm broad, evanescing. *Asci* 8-spored, bitunicate, fissitunicate, fusiform to obclavate, with or without pedicel. *Ascospores* ellipsoidal with broadly to narrowly rounded ends, pale brown with greenish tint, 1-septate, constricted at the septum.

Anamorph reported for genus: none.

Type species:

Coleroa chaetomium (Kunze ex Fr.) Rabenh., Rabenh. Krypt.-Fl., Edn 2 (Leipzig) 1:198 (1850). (Fig. 6)

≡ *Dothidea chaetomium* Kunze ex Fr., Syst. mycol. (Lundae) 2: 563 (1823).

Ascomata 130–170 μm high×80–130(−160) μm diam., scattered, or in small groups of 2–4 with confluent peridium, superficial, produced on thin subcuticular stroma, globose, subglobose, wall black, setae few to numerous, septate or non-septate, variable in length, up to 130 μm, 5–7 μm thick near the base, reddish-brown, paler at the apex, ostiole short (Fig. 6a). *Peridium* 15–25 μm wide, composed of lightly pigmented thin-walled cells of *textura angularis*, cells 5–12 μm diam., cell wall <1 μm thick (Fig. 6b). *Hamathecium ca*. 2 μm broad, cellular, septate, usually evanescing in mature ascomata. *Asci* 45–58×12–16 μm ($\bar{x}$=53.3× 13.5 μm, *n*=10), 8-spored, bitunicate, fissitunicate, fusiform to obclavate, with or without pedicel, with an inconspicuous ocular chamber (Fig. 6c, d). *Ascospores* 11–14(−17) ×5.5–6 μm ($\bar{x}$=13.2×5.9 μm, *n*=10), obliquely uniseriate and partially overlapping to biseriate in centre, ellipsoidal with broadly to narrowly rounded ends, pale brown with greenish tint, 1-septate, constricted at the septum, the upper cell often longer and broader than the lower one, verrucose (Fig. 6e).

Material examined: ITALY: Treviso, Bosco Montello, on the leaf surface of *Rubus caesius*, Sept. 1876. P.A. Saccardo (L11558.30 as *Venturia kunzei* Sacc.); ROMANIA: Plopeni, on *Rubus caesius* L., Aug. 1971, leg. & det. G. Negrean (L11558.4); on *Rubus idaeus*, leg. J. Smarods, 18 Oct. 1942 (L11558.16); L11558.39, as *Dothidea chaetomium*; on leaves of *Rubus* sp., leg. Kretzschmar (L11558.38, as *Phacidium rubi* Fries); 9 Oct. 1903, leg. G. Oertel. (L11558.3).

Anamorph: none reported.

Note: The scattered, setose ascomata, deliquescing pseudoparaphyses, fusoid to obclavate asci and the 1-septate, constricted ascospores of *Coleroa chaetomium* suggest an affinity to *Venturiaceae*.

Pseudoparodiella F. Stevens, Illinois Biol. Monogr. (Urbana) 11: 166 (1927).

Generic description:

Habitat parasitic on leaf surface of dicotyledonous plants. *Ascomata* small-sized, scattered or gregarious, superficial, globose. *Peridium* thin, composed of a few layers of lightly pigmented thin-walled cells of *textura angularis. Hamathecium* of rare, 2–3 μm broad pseudoparaphyses. *Asci* 8-spored, bitunicate, fissitunicate dehiscence not observed, obclavate, with a short, thick, knob-like pedicel, with an ocular chamber. *Ascospores* biseriate and partially overlapping, broadly fusoid to ellipsoidal with broadly to narrowly rounded ends, olivaceous to pale brown, 1-septate, constricted at the septum, the upper cell slightly longer and broader than the lower one.

Anamorph reported for genus: none.

Type species:

Pseudoparodiella vernoniae F. Stevens, Illinois Biol. Monogr. (Urbana) 11: 166 (1927). (Fig. 7)

Ascomata 80–130 μm diam., scattered or gregarious, superficial, globose, easily removed from the substrate, wall black, apex opening not observed (too small to see clearly) (Fig. 7a). *Peridium* 10–15 μm wide, composed of 2–3 layers of lightly pigmented thin-walled cells of *textura angularis*, cells 4–6 μm diam., cell wall 0.5–1 μm thick, up to 2 μm thick at the outer layer (Fig. 7b). *Hamathecium* of rare, 2–3 μm broad pseudoparaphyses. *Asci* 55–72×17–22 μm ($\bar{x}$=62.5×20.3 μm, *n*=10), 8-spored, bitunicate, fissitunicate dehiscence not observed, obclavate, with a short, thick, knob-like pedicel which is usually less than 10 μm long, with an ocular chamber (Fig. 7c). *Ascospores* 16–19×6–8 μm ($\bar{x}$=17×7 μm, *n*=10), biseriate and partially overlapping, broadly fusoid to ellipsoidal with broadly to narrowly rounded ends, olive pale brown, 1-septate, constricted at the septum, the upper cell slightly longer and broader than the lower one, smooth-walled (Fig. 7d).

Material examined: SPAIN: Peralta, on leaves of *Vernonia canescens*, 7 Dec. 1923, leg. & det. F.L. Stevens (K(M):154549, **holotype**).

Anamorph: none reported.

Note: The small-sized ascomata produced on leaves of dicotyledons, rare pseudoparaphyses, obclavate asci, 1-septate olivaceous brown ascospores agree with *Venturiaceae*.

Metacoleroa Petr., Annls mycol. 25: 332 (1927).

Anamorph reported for genus: none.

Type species:

Metacoleroa dickiei (Berk. & Broome) Petr. [as 'dieckiei'], Annls mycol. 25: 332 (1927).

≡ *Sphaeria dickiei* Berk. & Broome, Ann. Mag. nat. Hist., Ser. 2 9: 317 (1852).

Material examined: UK: Carlton House, on leaves of *Linnaea borealis*, 1827, Richardson (K(M): 143928; **syntype**).

Anamorph: none reported.

Note: No mature ascoma were found on the specimen examined. Based on DNA sequence analysis, *Metacoleroa* clustered with *Venturia sensu lato*, thus was treated as synonym (Crous et al. 2007a). However the phylogeny presented in Crous et al. (2007a) was not well

resolved and our analysis did not resolve this either (Fig. 1). This proposal needs further study.

Tyrannosorus Unter. & Malloch, Mycol. Res. 99(8): 910 (1995).

Generic description:

Habitat saprobic. *Ascomata* solitary, dark brown to black, ovate to pyriform, ostiolate, covered with brown setae. *Peridium* pseudoparenchymatous. *Hamathecium* trabeculate pseudoparaphyses. *Asci* bitunicate, saccate to clavate with a thickened endotunica. *Ascospores* brown, fusoid, 1-septate, indistinctly striate, each cell with 3–5 elongate germ slits (from Untereiner et al. 1995).

Anamorph reported for genus: *Helicodendron* (Untereiner et al. 1995).

Type species:

Tyrannosorus pinicola (Petrini & P.J. Fisher) Unter. & Malloch, Mycol. Res. 99(8): 910 (1995).

≡ *Capronia pinicola* Petrini & P.J. Fisher, Trans. Br. mycol. Soc. 88(1): 68 (1987).

Anamorph: *Helicodendron pinicola* E. Müll., Petrini, P. J. Fisher, Samuels & Rossman ex Voglmayr & P.J. Fisher, Mycol. Res. 101(9): 1124 (1997).

Note: *Tyrannosorus* was separated from *Capronia* and was introduced as a monotypic genus represented by *T. pinicola* based on its helicosporous anamorph and longitudinally ridged ascospores with multiple germ slits (Untereiner et al. 1995). According to our molecular phylogenetic analysis based on five genes, i.e. *nu*LSU, *nu*SSU, *RPB*1, 2 and *TEF*1, *Caproventuria hanliniana* and *C. hystrioides* together with *Tyrannosorus pinicola* form a unambiguously supported clade separating from *Venturia sensu stricto*. Both *Tyrannosorus* and *Caproventuria* share setose ascomata, 1-septate, brown or yellowish olivaceous ascospores, which are typical of *Venturiaceae*. The helicosporous anamorph of *Tyrannosorus pinicola* (*Helicodendron pinicola*) is quite different from the *Pseudocladosporum* anamorph of *Caproventuria* species. In addition, the indistinctly striate ascospores with germ slits of *Tyrannosorus pinicola* are also quite different from species of *Caproventuria* (Braun 1998; Untereiner et al. 1995). Thus here we treat *Caproventuria* and *Tyrannosorus* as separate genera of *Venturiaceae*.

Venturia Sacc., Syll. fung. (Abellini) 1: 586 (1882).

Generic description:

Habitat parasitic on dicotyledonous leaves. *Ascomata* small-sized, solitary, scattered, or gregarious, initially immersed, becoming erumpent, globose, subglobose, wall black, papillate, ostiolate. *Peridium* thin, composed of a few layers of pigmented cells of *textura angularis. Hamathecium* rare, evanescent in mature ascomata. *Asci* 8-spored (rarely 4-spored), bitunicate, fissitunicate dehiscence unknown, oblong to obclavate, with a short, thick pedicel or pedicel lacking, with an inconspicuous ocular chamber. *Ascospores* obliquely uniseriate and partially overlapping to biseriate, especially at the base, ellipsoidal, with broadly rounded ends, pale brown, 1-septate, slightly constricted at the septum, the upper cell shorter than the lower one, smooth-walled.

Anamorph reported for genus: *Spilocaea*, *Pollaccia* (Barr 1968; Crous et al. 2007a; Sivanesan 1984a).

Type species:

Venturia inaequalis (Cooke) G. Winter, Hedwigia 36: 81 (1897) (Fig. 8)

≡ *Sphaerella inaequalis* Cooke, J. Bot. 4: 248 (1866).

Ascomata 90–180 μm high×90–200(−240) μm diam., solitary, scattered, or gregarious, initially immersed, becoming erumpent, globose, subglobose, wall black, ostiolate with a distinct papilla (Fig. 8a). *Peridium* 20–28 μm wide, 1-layered, composed of (2-)3–4 layers of pigmented cells of *textura angularis*, cells 5–10 μm diam., cell wall 0.8–1.5 μm thick (Fig. 8d). *Hamathecium* rare, *ca*. 2 μm broad, evanescent in mature ascomata (Fig. 8e). *Asci* (53-) 70–90×9.5–14 μm ($\bar{x}$=73.5×10.8 μm, *n*=10), 8-spored (rarely 4-spored), bitunicate, fissitunicate dehiscence not observed, oblong to obclavate, with a short, thick pedicel or pedicel lacking, with an inconspicuous ocular chamber (Fig. 8b, c). *Ascospores* 13–17×6–8 μm ($\bar{x}$=14.8×7.2 μm, *n*=10), obliquely uniseriate and partially overlapping to biseriate, especially at the base, ellipsoidal, with broadly rounded ends, pale brown, 1-septate, slightly constricted at the septum, the upper cell shorter than the lower one (4:5-) 2:3(−1:2), smooth-walled (Fig. 8f, g).

Material examined: CZECH REPUBLIC: Brno ('Brünn'), on leaves of *Sorbus torminalis* (*Rosaceae*). Niessl s.n., Mar. 1913, distributed in Rabenhorst, Fungi Europaei 2663, leg. de Niessl (L 0054534, **isotype** of *Didymosphaeria inaequalis* (Cooke) Nissl.).

Anamorph: *Spilocaea pomi* (Schubert et al. 2003).

Note: A relatively broad concept for *Venturia* was adopted by Sivanesan (1977), who considered the genus to comprise species having separate or aggregated ascomata with or without stroma, or forming below a blackened clypeus, symmetrical or asymmetrical, olive green, pale brown or dark brown ascospores and being parasitic on leaves or stems of dicotyledons. DNA sequence analysis had indicated that species of *Venturia* clustered together with *Apiosporina collinsii*, *Caproventuria hanliniana* and *Metacoleroa dickiei*, and thus *Caproventuria* and *Metacoleroa* were treated as synonyms of *Venturia* (Crous et al. 2007a), although their ecological, morphological or anamorphic states are distinct from each other (see the key of genera). This proposal, however, needs further consideration and study. Herein we apply a narrower generic concept for *Venturia*, which comprises parasitic species closely related to the generic type of *Venturia* (*V. inaequalis*).

Other genera included in *Venturiales*

Based on morphology, the genera *Arkoola*, *Atopospora*, *Botryostroma*, *Lasiobotrys*, *Rhizogene*, *Trichodothella* and *Trichodothis* may be related to *Venturiaceae*. Thus we provisionally include them in *Venturiaceae*, but their ordinal and/or familial status needs confirmation based on DNA sequence data.

Arkoola J. Walker & Stovold, Trans. Br. mycol. Soc. 87: 28 (1986).

Anamorph reported for genus: none.

Type species:

Arkoola nigra J. Walker & Stovold, Trans. Br. mycol. Soc. 87: 29 (1986).

Anamorph: none reported.

Note: The superficial, setose ascomata produced on mycelium and greenish-brown, asymmetrical, thin-walled ascospores fit *Venturiaceae* well. The large-sized ascomata, cylindrical asci and short pedicels of *Arkoola* however, differ from other genera of *Venturiaceae* (Walker and Stovold 1986).

Atopospora Petr., Annls mycol. 23: 100 (1925).

Anamorph reported for genus: ?*Didymochora* (Sivanesan 1984a).

Type species:

Atopospora betulina (Fr.) Petr., Annls mycol. 23: 101 (1925).

≡ *Xyloma betulinum* Fr., Observ. mycol. (Havniae) 1: 198 (1815).

Anamorph: ?*Didymochora betulina* (Sivanesan 1984a).

Note: The multiloculate ascostromata, fusoid asci and lightly pigmented, biseriate, apiosporous ascospores suggest an affinity to *Venturiales* (Müller and von Arx 1962).

Botryostroma Höhn., Sber. Akad. Wiss. Wien, Math.-naturw. Kl., Abt. 1 120: 424 [46 repr.] (1911).

Anamorph reported for genus: none.

Type species:

Botryostroma inaequale (G. Winter) Höhn. [as 'inaequalis'], Sber. Akad. Wiss. Wien, Math.-naturw. Kl., Abt. 1 120: 425 [47 repr.] (1911).

≡ *Lizonia inaequalis* G. Winter, Hedwigia 22: 261 (1883).

Anamorph: none reported.

Note: The ascomata of *Botryostroma inaequale* are produced under a clypeus, with numerous persistent pseudoparaphyses among asci. All these characters do not fit *Venturiales*. However, the obclavate or fusiform asci, lightly pigmented, apiosporous ascospores suggest an affinity to *Venturiales* (Müller and von Arx 1962).

Lasiobotrys Kunze, in Kunze & Schmidt, Mykologische Hefte (Leipzig) 2: 88 (1823).

Anamorph reported for genus: none.

Type species:

Lasiobotrys lonicerae Kunze, in Fries, Syst. mycol. (Lundae) 2: 88 (1823).

Anamorph: none reported.

Note: The most striking morphological character of *Lasiobotrys* is its ascomata produced among hyphae under a stromatal disc (forming a "roof-like" structure) (see Müller and von Arx 1962). The apiosporous, lightly pigmented ascospores, subclavate to obclavate asci are comparable with taxa of *Venturiales*.

Rhizogene Syd. & P. Syd., Annls mycol. 18: 181 (1921) [1920].

Anamorph reported for genus: none.

Type species

Rhizogene symphoricarpi (Syd. & P. Syd.) Syd. & P. Syd., Annls mycol. 18: 181 (1921) [1920].

≡ *Lasiobotrys symphoricarpi* Syd. & P. Syd., Annls mycol. 16: 244 (1918).

Anamorph: none reported.

Note: Ascomata of *Rhizogene symphoricarpi* are produced radially around the circumference of the stromatal disc, which is covered with short setae. The subclavate to somewhat obclavate asci and lightly pigmented, submedianly 1-septate ascospores are comparable with *Venturiales* (Müller and von Arx 1962).

Trichodothella Petr., in Blumer, Ergebn. wiss. Unters. schweiz. NatnParks, N.S. 14: 37 (1946).

Anamorph reported for genus: none.

Type species:

Trichodothella blumeri Petr. ex S. Blumer, Ergebn. Wiss. Unters. Schweiz. Natn Parks, N.S. 14: 37 (1946).

Anamorph: none reported.

Note: Considering the position of ascomata on the ascostromata, *Trichodothella* is a "transition" genus—the ascomata of which are produced radially around the circumference of the stromatal disc, but under the hyphae around the ascostromata (Müller and von Arx 1962).

Trichodothis Theiss. & Syd., Annls mycol. 12: 176 (1914).

Generic description:

Habitat saprobic or parasitic? on leaf surface of dicotyledonous. *Ascostromata* medium-sized, solitary, scattered, or in small groups, superficial, multilocular, discoid, with straight or flexuous aggregations of hairs sticking together and forming stellate projections around the ascostroma. *Locules* small-sized, globose to subglobose, forming one layer within the ascostroma. *Peridium* one layered, lower peridium composed of light pigmented cells of *textura angularis*, upper peridium composed of more heavily pigmented thick-walled cells of *textura angularis. Hamathecium* of dense, cellular pseudoparaphyses, septate, hyaline. *Asci* 8-spored, bitunicate, fissitunicate dehiscence not observed, saccate, without pedicel. *Ascospores* 3–4-seriate, broadly ellipsoidal with broadly rounded ends, hyaline and becoming pale brown when old, 1-septate, slightly constricted at the septum.

Anamorphs reported for genus: none.

Type species:

Trichodothis comata (Berk. & Ravenel) Theiss. & Syd., Annls mycol. 12: 176 (1914). (Fig. 9)

≡ *Asterina comata* Berk. & Ravenel, Grevillea 4 (no. 29): 10 (1875).

Ascostromata 72–157 μm high×243–529 μm diam. (excluding the stellate aggregations), solitary, scattered, or in small groups, superficial, multilocular, discoid, with straight or flexuous, septate, dark brown aggregations of hairs sticking together and forming stellate projections around the ascostromata, projections black, cylindrical, 6–8 μm broad. *Locules* 60–95 μm high×75–115 μm diam., globose to subglobose, forming a single layer within ascostromata, and extending as far as 100–214 μm out of the edge of ascostromata (Fig. 9a, c). *Peridium* 28–42 μm wide, one layered, lower peridium composed of light pigmented cells of *textura angularis*, cells 5–9 μm diam., cell wall 1.5–2.5 μm thick, apex cells smaller and walls thicker, upper peridium composed of more heavily pigmented thick-walled cells of *textura angularis* (Fig. 9b, d, e). *Hamathecium* of dense, cellular pseudoparaphyses, *ca*. 2.5–4 μm diam., septate, hyaline (Fig. 9e, f). *Asci* 55–70×15–22 μm, 8-spored, bitunicate, fissitunicate dehiscence not observed, saccate, without pedicel, ocular chamber not observed (Fig. 9g). *Ascospores* 14–23×6.5–10.5 μm, 3–4 seriate, broadly ellipsoidal with obtusely rounded ends, hyaline and becoming pale brown when old, 1-septate, slightly constricted at the septum, smooth-walled (Fig. 9h).

Material examined: USA: South Carolina, Santee Canal, on *Magnolia grandiflora* leaf, 1819; leg. H.W. Ravenel (K(M): 143933, ex herb. Berkeley, **syntype**).

Anamorph: none reported.

Note: *Trichodothis comata* is characterized by its ascostromata covered by dark brown hairs, broad pseudoparaphyses, saccate asci and hyaline, 1-septate ascospores (Müller and von Arx 1962, Fig. 9). *Trichodothis* is most comparable with *Lasiobotrys*, *Rhizogene* and *Trichodothella*, which have ascomata beneath or radially around the circumference of the stromatal disc (Müller and von Arx 1962). All these characters make it difficult to be assigned *Trichodothis* in a family or even order. Because the morphology of asci and ascospores are most comparable with *Venturiales*, we questionably accept it in *Venturiales*, until further molecular phylogenetic result is available.

Genera excluded from *Venturiales*

Crotone, *Polyrhizon*, *Lineostroma*, *Phragmogibbera*, *Platychora*, *Phaeocryptopus*, *Rosenscheldiella*, *Uleodothis* and *Xenomeris* do not share common ancestry with *Venturiales* based either on recent DNA sequence analyses or on morphological characters. Thus they are excluded from this order.

Crotone Theiss. & Syd., Annls mycol. 13: 629 (1915).

Generic description:

Habitat saprobic on lower surface of leaves of dicotyledons. *Ascostromata* large-sized, solitary, scattered, or in small groups, erumpent to nearly superficial, with basal wall remaining immersed in host tissue, flat globose to subglobose. *Locules* small-sized, globose to subglobose, forming one layer near the surface of ascostromata, area between locules of ascostromata filled with heavily pigmented, thick-walled cells of *textura angularis.* *Peridium* composed of heavily pigmented, thick-walled cells of *textura angularis*, cells of ascostromata larger, hyaline and walls thinner. *Hamathecium* appears to lack pseudoparaphyses. *Asci* 8-spored, bitunicate, broadly subclavate to obclavate, without pedicel. *Ascospores* uniseriate, biseriate to 4-seriate, broadly clavate, narrowly fusoid to fusoid with broadly to narrowly rounded ends, brown, 1-septate, constricted at the septum, the upper cell often longer and broader than the lower one, rough-walled.

Anamorph reported for genus: none.

Type species:

Crotone drimydis (Lév.) Theiss. & Syd., Annls mycol. 13: 629 (1915). (Fig. 10)

≡ *Dothidea drimydis* Lév. [as '*drymidis*'], Annls Sci. Nat., Bot., sér. 3 3: 55 (1845).

Ascostromata 230–570 μm high×615–915 μm diam., solitary, scattered, or in small groups of 2–4, erumpent to nearly superficial, with basal wall remaining immersed in host tissue, flat globose to subglobose, wall black, roughened, usually ornamented with some white collared ornaments (Fig. 10a). *Locules* 75–90 μm diam., globose to subglobose, forming one layer near the surface of ascostromata, area between locules of ascostromata filled with heavily pigmented thick-walled cells of *textura angularis,* up to 10 μm diam., cell wall 3–5 μm thick (Fig. 10b). *Peridium* 35–80 μm wide on the surface part of ascostromata, composed of heavily pigmented thick-walled cells of *textura angularis*, cells up to 10× 3.8 μm diam., cell wall 2–5 μm thick, cells of ascostromata larger, hyaline and walls thinner (Fig. 10b). *Hamathecium* appears to lack pseudoparaphyses. *Asci* 55–105×10–17.5 μm ($\bar{x}$=79.2×13.5 μm, *n*=10), 8-spored, bitunicate, broadly subclavate to obclavate, without pedicel, ocular chamber not seen (Fig. 10c, d, f, g). *Ascospores* 17.5–25 μm×4.5–7.5 μm ($\bar{x}$=20.4× 5.5 μm, *n*=10), uniseriate, biseriate to 4-seriate, narrowly clavate, narrowly fusoid to fusoid with broadly to narrowly rounded ends, brown, 1-septate, constricted at the septum, the upper cell often longer (*ca*. 2-times) and broader than the lower one, rough-walled (Fig. 10e, h).

Material examined: CHILE: on the lower side of the leaves of *Drymidis chilensis*, 1841 (K(M): 143929, ex herb. Berkeley, **syntype**).

Anamorph: none reported.

Note: Locules of *Crotone drimydis* are arranged in a layer in the hemispherical ascostromata, which forms on the lower surface of *Drymidis chilensis* leaves. The genus may belong in *Dothideaceae*, *Elsinoaceae* or *Myrangiaceae*, families in which taxa form in ascostromata with ascomata as a single layer. The saccate asci in the *Elsinoaceae* or *Myrangiaceae* are somewhat comparable with those of *Crotone drimydis*.

Gibbera Fr., Syst. orb. veg. (Lundae) 1: 110 (1825).

Anamorphs reported for genus: *Dictyodochium*, *Stigmina*-like and *Virgariella* (Sivanesan 1984a, b).

Type species:

Gibbera vaccinii (Sowerby) Fr., Summa veg. Scand., Section Post. (Stockholm): 412 (1849).

≡ *Sphaeria vaccinii* Sowerby, Col. fig. Engl. Fung. Mushr. 3: 156, tab. 373:1 (1803).

Anamorph: none reported.

Note: The narrowly fusoid ascospores, asci with furcate pedicel as well as its *Dictyodochium*, *Stigmina*-like and *Virgariella* anamorphic states (Sivanesan 1984a, b) all refute its placement within *Venturiales*. Barr (1968) has considered *Gibbera* comparable with *Phaeocryptopus* and *Xenomeris*, as they all have "erumpent basal stroma bearing the ascostromata which do not form superficial mycelium". Both *Phaeocryptopus* and *Xenomeris* have been assigned to *Capnodiales* (Schoch et al. 2009; Winton et al. 2007), thus *Gibbera* may also be closely related to *Capnodiales*. Based on the mulitigene phylogenetic

analysis, *G. conferta* nested within the clade of *Venturiales*, while *G. rosea* clustered within *Helotiales* (class *Leotiomycetes*) (Crous et al. 2007a). No firm conclusion can be reached, however, until it is possible to analyse DNA sequences of the type species, *G. vaccinii*.

Platychora Petr., Annls mycol. 23(1/2): 102 (1925)

Anamorph reported for genus: ? *Piggotia* (Hyde et al. 2011).

Type species:

Platychora ulmi Duval, Bot. Taschenbuch 6: 105 (1795).

Anamorph: unknown.

Note: The fusoid hyaline apiosporous ascospores of *Platychora ulmi* are comparable with *Dibotryon* and *Apiosporina*, but its gregarious ascomata, which are immersed at first, then becomes erumpent to superficial, are quite different from other genera in *Venturiaceae*. Based on molecular phylogenetic data, *Platychora ulmi* should reside within the family of *Didymellaceae*, *Pleosporales* (Zhang et al. 2009, Fig. 1).

Polyrhizon Theiss. & Syd., Annls mycol. 12: 281 (1914).

Generic description:

Habitat saprobic on leaves of dicotyledons. *Ascostromata* producing round, black spots in leaves. *Ascomata* gregarious in the ascostromata, immersed to erumpent, globose, subglobose, or broadly conical. *Peridium* 1-layered, composed of small, lightly pigmented, thick-walled cells of *textura prismatica. Hamathecium* of dense, long cellular pseudoparaphyses, anastomosing and branching between and above the asci. *Asci* 8-spored, bitunicate, fissitunicate, cylindrical to fusoid, with a short furcate pedicel, which is less than 10 μm long, with a small ocular chamber. *Ascospores* biseriate, broadly fusoid to subclavate with broadly to narrowly rounded ends, reddish brown, 1-septate, constricted at the septum, the upper cell often broader and shorter than the lower one, baculate.

Anamorph reported for genus: none.

Type species:

Polyrhizon terminaliae (Syd.) Syd., Annls mycol. 12: 281 (1914). (Fig. 11)

≡ *Dothidea terminaliae* Syd., in Sydow & Butler, Annls mycol. 9: 401 (1911).

Ascostromata producing round, black spots in leaves, spots up to 2.5–3 mm. *Ascomata* 150–260 μm high×(90-) 150–280 μm diam., gregarious in ascostromata, immersed to erumpent, globose, subglobose, or broadly conical (Fig. 11a). *Peridium* 10–20 μm wide laterally, up to 45 μm thick at the apex, thinner at the base, single layered, composed of small lightly pigmented thick-walled cells of *textura prismatica*, *ca*. 2×5 μm diam., cells more heavily pigmented near apex and hyaline in the base. *Hamathecium* of dense, long cellular pseudoparaphyses, 2–3 μm broad, anastomosing and branching between and above the asci. *Asci* (39-)50–67×10–16 μm ($\bar{x}$=52.1× 11.7 μm, *n*=10 μm), 8-spored, bitunicate, fissitunicate cylindrical to fusoid, with a short furcate pedicel which is less than 10 μm long, with a small ocular chamber (to 3 μm wide×2 μm high) (Fig. 11c, d). *Ascospores* 24–28× 7.5–10 μm ($\bar{x}$=25.1×8.5 μm, *n*=10 μm), biseriate, broadly fusoid to subclavate with broadly to narrowly rounded ends, reddish brown, 1-septate, constricted at the septum, the upper cell often broader and shorter than the lower one, baculate (Fig. 11b).

Material examined: INDIA: Wynaad, Cataffa, on the upper surface of leaves of *Terminalia catapha*, 14 Nov. 1909, leg. W. Mc Rae (S reg. nr F8238, as *Dothidea terminaliae*, **holotype**).

Anamorph: none reported.

Note: The persistent cellular pseudoparaphyses, broadly clavate asci with short furcate pedicels, and the almost median septate, baculate ascospores of *Polyrhizon terminaliae* refute those of *Venturiales*, but fit *Pleosporineae* (*Pleosporales*). Further study is needed for confirmation of its ordinal or familial status.

Lineostroma H.J. Swart, Trans. Br. mycol. Soc. 91: 464 (1988).

Generic description:

Habitat necrotrophic parasitic on *Banksia. Ascostromata* linear, solitary, scattered, initially immersed, becoming erumpent. *Ascomata* linearly arranged in ascostromata, wall black, roughened, globose, subglobose to triangular. *Peridium* thickness uneven, usually thinner at the base, 1-layered, composed of brown-walled cells of *textura angularis. Hamathecium* of long trabeculate pseudoparaphyses. *Asci* 8-spored, bitunicate, fissitunicate, subcylindrical to obclavate, with a short pedicel. *Ascospores* broadly fusoid to oblong, with broadly to narrowly rounded ends, dark brown, 1-septate, constricted at the septum.

Anamorph reported for genus: none.

Type species:

Lineostroma banksiae (Cooke) H.J. Swart, Trans. Br. mycol. Soc. 91: 464 (1988). (Fig. 12)

≡ *Didymosphaeria banksiae* Cooke, Grevillea 19: 90 (1890).

Ascostromata linear, 600–860 μm long, 140–240 μm broad, 55–115 μm high, solitary, scattered, initially immersed, becoming erumpent, with up to 15 locules (Fig. 12a). *Ascomata* 110–165 μm high×90–215 μm diam., linearly arranged in ascostromata, wall black, roughened, globose, subglobose to triangular (Fig. 12a, b, c). *Peridium* 13–40 μm wide, thickness uneven, usually thinner at the base, 1-layered, composed of brown-walled cells of *textura angularis*, sides and apex cells 2.5–5×2.5–9 μm diam., cell wall 1–2 μm thick, base cells smaller and walls thicker (Fig. 12b). *Hamathecium* of <1 μm broad, dense, long trabeculate pseudoparaphyses. *Asci* 50–65×7–8.5 μm, 8-spored, bitunicate, fissitunicate, subcylindrical to obclavate, with a short pedicel, 6.5–9 μm long. *Ascospores* (10-)14–17.5×5–7.5 μm, uniseriate and partially overlapping to biseriate near the base, broad fusoid to oblong, with broadly to narrowly rounded ends, dark brown, 1-septate, constricted at the septum (Fig. 12d–g).

Material examined: AUSTRALIA: Victoria, on leaves *Banksia* sp. leg. Martin (K(M): 143926, **syntype**).

Anamorph: none reported.

Note: The linearly arranged ascomata, persistent pseudoparaphyses as well as the nearly symmetrical, 1-septate ascospores indicated that is should be a species of *Pleosporineae* (*Pleosporales*). *Lineostroma banksiae* is one of the most common ascomycetes found on leaves of *Banksia* in Australia (Swart 1988).

Phragmogibbera Samuels & Rogerson, Mem. N. Y. bot. Gdn 64: 178 (1990).

Generic description:

Habitat fungicolous on *Xylariaceae. Ascostromata* erumpent from ostioles of host *Xylaria*, turbinate. *Ascomata* globose, wall black, carbonaceous, non papillate, ostiolate not sure. *Peridium* tissue continuous with the stroma, 2-layered. *Hamathecium* of rare, septate pseudoparaphyses. *Asci* 8-spored, bitunicate, fissitunicate dehiscence not observed, broadly cylindrical to narrowly clavate, with a conspicuous ocular chamber. *Ascospores* partially to completely biseriate, narrowly curved, fusoid, end cells colourless and central cells brown, multi-septate, constricted at each septum.

Anamorph reported for genus: *Stigmina*-like (Samuels and Rogerson 1990).

Type species:

Phragmogibbera xylariicola Samuels & Rogerson, Mem. N. Y. bot. Gdn 64: 178 (1990). (Fig. 13)

Ascostromata erumpent from ostioles of host *Xylaria*, turbinate, *ca*. 300 μm high×400 μm wide, comprising at first a hemisphaerical, brown head of conidia on a short, black stipe; ascomata ultimately forming in groups of 5–7 around the periphery of the stipe below the conidial hymenium after the cessation of conidial production. *Medulla* of stroma consisting of a central, obpyramidal core of colourless hyphal elements surrounded by colourless to pale yellow, pseudoparenchymatous cells measuring *ca*. 7.5 μm across, and an outer layer ca. 25 μm thick of dark brown to black, KOH blue-green pseudoparenchyma (Fig. 13a). *Ascomata* globose, wall black, roughened to nearly smooth, carbonaceous, non papillate, becoming slightly umbilicate or not collapsed when dry, method of opening of mature ascomata not observed, arising as outgrowths of the stromatal tissue, ascomatal wall ca. 75 wide, tissues continuous with the stroma. *Peridium* tissue continuous with the stroma, *ca*. 75 μm wide, 2-layered (Fig. 13b). *Hamathecium* of rare, 1–1.5 μm broad, septate pseudoparaphyses. *Asci* 125–175×12–22 μm, 8-spored, bitunicate, fissitunicate dehiscence not observed, broadly cylindrical to narrowly clavate, with a conspicuous ocular chamber (Fig. 13c). *Ascospores* 32–39×5–7.5(−10) μm ($\bar{x}$=35×6 μm, *n*=10), partially to completely biseriate, narrowly curved fusoid, end cells colourless and central cells brown, 3-septate, constricted at each septum, smooth-walled (Fig. 13d).

Anamorph: *Stigmina*-like (Samuels and Rogerson 1990).

Cells at upper surface of stroma producing conidiophores. *Conidiophores* pale brown, septate, sparingly branched, each branch terminating in a single conidium and proliferating percurrently, eventually *ca*. 100 μm long, 3–5 μm wide. *Conidia* cylindrical to narrowly clavate, 25–42×7.5–11.2 μm, (1-)2–3 distoseptate, dark brown, smooth, with a torn, circular basal abscission scar.

Material examined: VENEZUELA: Cerro de la Nelina, summit camp #5, valley at north base of Pico Phelps, 1000–1,250 m, 00º49′N, 66º00′W, cloud forest, on *Xylaria schweinitzii* ?, 12–13 Apr. 1984 (NY Gary J. Samuels 1238, **isotype**).

Note: The narrowly fusoid, 3-septate ascospores, clavate asci with a furcate pedicel all refute its placement within *Venturiales*. We assign it to *Dothideomycetes incertae sedis*.

Phaeocryptopus Naumov, Bull. Soc. mycol. Fr. 30: 424 (1915).

Anamorph reported for genus: none.

Type species:

Phaeocryptopus abietis Naumov, Bull. Soc. mycol. Fr. 30: 424 (1914).

Anamorph: none reported.

Note: Phylogenetic analysis indicates that *Phaeocryptopus nudus* nested within *Dothideales* and *P. gaeumannii* within *Mycosphaerellaceae* (Winton et al. 2007). Both of taxa however, are not the generic types. Thus the ordinal or familial status of *Phaeocryptopus* awaits molecular phylogenetic studies on *P. abietis*.

Rosenscheldiella Theiss. & Syd., Annls mycol. 13: 645 (1915).

Generic description:

Habitat parasitic? on leaves of dicotyledons. *Ascomata* tightly clustered on the surface of substrate, small-sized, superficial, globose, subglobose, wall black, roughened, ostiolate. *Peridium* 1-layered, composed of heavily pigmented thick-walled cells of *textura angularis.* *Hamathecium* composed of evanescing pseudoparaphyses. *Asci* 8-spored, bitunicate, fissitunicate obclavate, with a short, thick pedicel. *Ascospores* tri-seriate near the base, ellipsoidal to fusoid with broadly rounded ends, hyaline, 1-septate, septum median to submedian, constricted at the septum.

Anamorph reported for genus: none.

Type species:

Rosenscheldiella styracis (Henn.) Theiss. & Syd., Annls mycol. 13: 645 (1915).

≡ *Naemacyclus styracis* Henn., Hedwigia 48: 8 (1908). (Fig. 14)

Ascomata tightly clustered on the surface of substrate, cluster 0.8–1.6 mm diam., single ascoma 155–200 μm high×120–150 μm diam., superficial, globose, subglobose, wall black, roughened, ostiolate (Fig. 14a). *Peridium* 25–30 μm wide laterally, single layered, composed of heavily pigmented thick-walled cells of *textura angularis*, cells 5–6×5–9 μm diam., cell wall 1.5–3.5 μm thick (Fig. 14c). *Hamathecium* of evanescing pseudoparaphyses. *Asci* 75–90 (−105)×17.5–22.5 μm, 8-spored, bitunicate, fissitunicate, obclavate, with a short, thick pedicel which is *ca.* 5 μm long, with a small ocular chamber and an small apical apparatus (to 0.5 μm wide×2 μm high) (Fig. 14b, d, e). *Ascospores* 25–33×7.5–10 μm, tri-seriate near the base, ellipsoidal to fusoid with broadly rounded ends, hyaline, 1-septate, constricted at the septum, the upper cell often broader and shorter than the lower one, verrucose (Fig. 14f).

Material examined: BRAZIL: S. Paulo, Morro Pellado, on leaves of *Styrax* sp., July 1904, Puttemans (S reg. nr F7328, **lectotype**).

Anamorph: none reported.

Note: Based on the DNA sequence analysis *R. brachyglottidis* and *R. korthalsellae* are members of the *Mycosphaerellaceae sensu* Crous et al. (2007a) (Sultan et al. 2011).

Uleodothis Theiss. & Syd., Annls mycol. 13: 305 (1915).

Anamorph reported for genus: none.

Type species:

Uleodothis balansiana (Sacc., Roum. & Berl.) Theiss. & Syd., Annls mycol. 13: 305 (1915).

≡ *Plowrightia balansiana* Sacc., Roum. & Berl., Revue mycol., Toulouse 7: 157 (1885).

Anamorph: none reported.

Note: *Uleodothis* had been assigned to *Mycosphaerellaceae* (*Pseudosphaeriales*) by Müller and von Arx (1962). Luttrell (1973) assigned it to *Venturiaceae*. Its ascomata immersed in ascostromata, persistent pseudoparaphyses, cylindrical asci and hyaline ascospores are atypical of genera in *Venturiales*.

Xenomeris Syd., in Sydow & Werdermann, Annls mycol. 22: 185 (1924).

Anamorphs reported for genus: ?*Sclerophoma* and *Hormonema* (Sivanesan 1984a).

Type species:

Xenomeris pruni Syd., Annls mycol. 22: 185 (1924).

Anamorphs: ?*Sclerophoma* sp. and *Hormonema* sp. (Sivanesan 1984a).

Note: Molecular phylogenetic analysis indicated that *Xenomeris raetica* and *X. juniperi* (*Sthughesia juniperi*?) belong to *Capnodiales* (Winton et al. 2007). However, neither of these species are the generic type.

Discussion

Phylogeny

The phylogenetic analysis of the present study affirmed the polyphyletic nature of *Venturiaceae sensu* Barr (1979). *Phaeocryptopus gaeumannii, P. nudus, Xenomeris juniperi and X. raetica* resided in *Capnodiales* (Schoch et al. 2009; Winton et al. 2007). According to the present molecular phylogeny (Fig. 1), core taxa of *Venturiaceae*, i.e. *Apiosporina*, *Caproventuria*, *Dibotryon*, *Metacoleroa* and *Venturia*, form a well-supported monophyletic group, and placed as a distinct lineage, separate from *Botryosphaeriales*, *Jahnulales, Dothideomycetidae* and *Pleosporomycetidae*. Our second, more limited phylogenetic analysis using only LSU data corroborates the combined 5-gene data set (Fig. 2). Similar results were obtained by some recent phylogenetic studies (Crous et al. 2007a; Kodsueb et al. 2006; Kruys et al. 2006; Winton et al. 2007). Thus a new order of *Dothideomycetes—Venturiales* is introduced in this study to accommodate *Venturia s. str*. and its aggregates.

Venturia sensu Sivanesan (1977) accommodates a large number of species (250, http://www.mycobank.org/MycoTaxo.aspx, June/2011). The generic types of *Caproventuria* (*C. hanliniana*) and *Metacoleroa* (*M. dickiei*) clustered in the *Venturia* clade, which was subsequently treated as synonyms of *Venturia* by Crous et al. (2007a). *Caproventuria* was primarily distinguished from *Venturia* based on its distinct *Pseudocladosporium* anamorphs as well as its saprobic life style (Braun et al. 2003). The well-developed subiculum of *Metacoleroa* and the apiosporous ascospores of *Apiosporina* (incl. *Dibotryon*) readily distinguish them from *Venturia*. We thus choose to retain them as separate genera from *Venturia*, and to apply a narrower generic concept for *Venturia* than used in the past.

Phaeocryptopus nudus clustered in the *Dothideales*, and *P. gaeumannii* and *Xenomeris raetica* in the *Capnodiales* as reported previously (Crous et al. 2007a; Schoch et al. 2009; Winton et al. 2007). However, these assignments are not based on the study of generic types.

Some of the previous phylogenetic studies based on *nu*SSU rDNA sequence showed inconsistent placement of *Venturia liriodendri*, such as grouping with *Curreya pityophila* (Silva-Hanlin and Hanlin 1999; Olivier et al. 2000) or with *Phaeodothis winteri* (Eriksson and Hawksworth 2003). When mature, *Venturia liriodendri* has abundant pseudoparaphyses and pale-brown ascospores, instead of the deliquescing pseudoparaphyses and greenish ascospores of typical *Venturia* spp. (Hanlin 1987). It appears, therefore, that *Venturia liriodendri* would be better placed in *Pleosporineae* (*Pleosporales*).

Wu et al. (2011a) epitypified the generic type of *Tothia* Bat. (*T. fuscella* (Sacc.) Bat.), and found it nesting within the clade of *Venturiales* based on analysis of LSU and ITS or LSU and SSU *nu*rDNA sequences Wu et al. (2011a, b). The dilute brown ascospores of *T. fuscella* differ from the representatives of *Microthyriaceae* (Wu et al. 2011a, b), and agree with those of *Venturiales*. But the flat-conical and thyriothecial ascomata of *T. fuscella* are unusual within *Venturiales*. The dendrogram obtained by Wu et al. (2011b) indicated that *T. fuscella* is basal to the clade of *Venturiaceae*, but the support is inconsistent. Thus the familial status of *Tothia* cannot be determined yet.

Previous phylogenetic analysis indicated that *Venturiales* may be closely related to species of *Microthyriales* and *Phaeotrichaceae* (Schoch et al. 2009). This is corroborated here, although a relationship between *Microthyriales* and *Venturiales* is not well resolved. The 1-septate usually pigmented ascospores and deliquescing pseudoparaphyses of *Venturiales* are mostly comparable with species of *Botryosphaeriales* and *Capnodiales* as has been noticed by Crous et al. (2007a). In particular, venturialean genera such as *Phaeocryptopus*, *Xenomeris* and *Rosenscheldiella* have been assigned to *Capnodiales* (Sultan et al. 2011; Winton et al. 2007). Ecological habitats, ascospore shape and colour may help to distinguish these three orders, but DNA sequences are determinative. The poor resolution for interspecific relationships within *Venturiaceae* seen in this study and others (e.g. Crous et al. 2007a) suggests that the currently applied DNA markers will need to be expanded drastically in order to determine radiation events more precisely. This also means that generic and/or familial classification will likely remain unstable for the foreseeable future.

Morphology and ecology

Most of the venturialean genera have deliquescing or rare pseudoparaphyses. Pseudoparaphyses usually persist and are numerous in saprobic fungi, *viz*. freshwater (*Amniculicolaceae*) or marine taxa (*Aigialaceae*), while they are usually evanescent in parasitic fungi, i.e. in taxa of *Botryosphaeriales* (Schoch et al. 2006) and *Didymellaceae* (de Gruyter et al. 2009). Studies of the hamathecium have mainly focused on the presence, morphology or ontogeny, while the function of it is unclear (Eriksson 1981; Singer and Gamundi 1963). *Venturiaceae* had been placed in *Pleosporales* according to its "*Pleospora*-type centrum and bitunicate asci" (Barr 1968, 1979; Cannon and Kirk 2007). Although the "*Pleospora*-type" centrum developmental type was recorded for several species of *Venturia* (Kerr 1961; Walker and Stovold 1986), hamathecial types (*Pleospora*-type or *Sporormia*-type) has been shown to have little phylogenetic significance, at least at family level classification (Liew et al. 2000; Reynolds 1991). In particular, comparing with the centrum developmental type, the presence (or absence) of hamathecium seems be more significant in classification of *Dothideomycetes* (Schoch et al. 2006).

The shape of ascus and length of ascus pedicels might have taxonomic significance in *Dothideomycetes*. These characters have shown significance in distinguishing *Lophiostoma* and *Lophiotrema*, two morphologically comparable genera within *Pleosporales* (Hirayama and Tanaka 2011). The generic types of venturialean genera mostly have obclavate or obpyriform asci, i.e. *Pseudoparodiella vernoniae* and *Venturia inaequalis* (see Figs. 7 and 8). Compared with the cylindrical to cylindroclavate asci with short or long furcate pedicels

possessed by saprobic fungi, some dothideomycetous plant pathogens have obclavate or obpyriform asci with or without small knob-like pedicels, for instance in *Mycosphaerella* (*Mycosphaerellaceae), Macroventuria (Pleosporaceae) and Bricookea (Phaeosphaeriaceae).*

Thin-walled, mostly asymmetrical and olivaceous ascospores is another striking character of *Venturiales*. Anamorphic states are reported from some genera of *Venturiales*, especially on those plant pathogens, such as *Venturia* and *Apiospora*. The anamorphic states mostly infect and reproduce during the growing season, and the teleomorphic state helps to overwinter, which matures by the following spring when the host intiates growth. The parasitic species of *Venturiales* lacking anamorphs infect their hosts by means of ascospores, and produce ascomata on the substrates during the growing season (Kerr 1961). In this case, the ascospores as well as other reproductive structures of *Venturiaceae* play important roles to overwinter on fallen host leaves. Thus the relatively small, thin-walled and asymmetrical ascospores have an important role in this life cycle.

Summary

Based on the ITS *nu*rDNA sequences analysis results, Beck et al. (2005) accepted *Fusicladium sensu lato*, which included *Pollaccia* and *Spilocaea*. Based on 28S *nu*rDNA sequences analysis, a broader generic concept of *Fusicladium* was accepted, which included *Pseudocladosporium* as another synonym of *Fusicladium sensu lato* (incl. *Pollaccia* and *Spilocaea*) (Crous et al. 2007a). In this study, five genes are used for phylogenetic analysis, i.e. 18S, 28S *nu*rDNA sequences as well as the protein genes *RPB*1, 2 and *TEF*1, and a narrow concept of *Venturia* is accepted, which includes only some parasitic species closely related to the generic type of *Venturia* (*V. inaequalis*). Concurrently, a narrower concept of *Fusicladium* is accepted, and *Pollaccia*, *Pseudocladosporium* and *Spilocaea* are treated as separate genera herein.

The majority of economic interest in *Venturiales* is closely tied to members of the type genus *Venturia,* containing several species with host specific associations. The type species of *Venturia*, *V. inaequalis*, is the causal agent of apple scab, the most important disease on apples worldwide (Carisse and Bernier 2002). This species has been studied intensively for over 100 years with extensive genetic and epidemiological data available (MacHardy 1996). More recently it has been the focus of studies on molecular agents of host infection with whole genome sequences underway (Bowen et al. 2011). In spite of this pending increase in genetic data and long historical record, much of the phylogenetic relationships with *Venturia* as well as it relationships to other members of the newly described order remain poorly understood. A polyphasic approach by integrating morphological, ecological, biological methods and DNA and protein based sequence comparisons is critical to access a modern taxonomy that reflects evolutionary theories of *Venturiales* as well as other orders of *Dothideomycetes* (Zhang et al. 2012).

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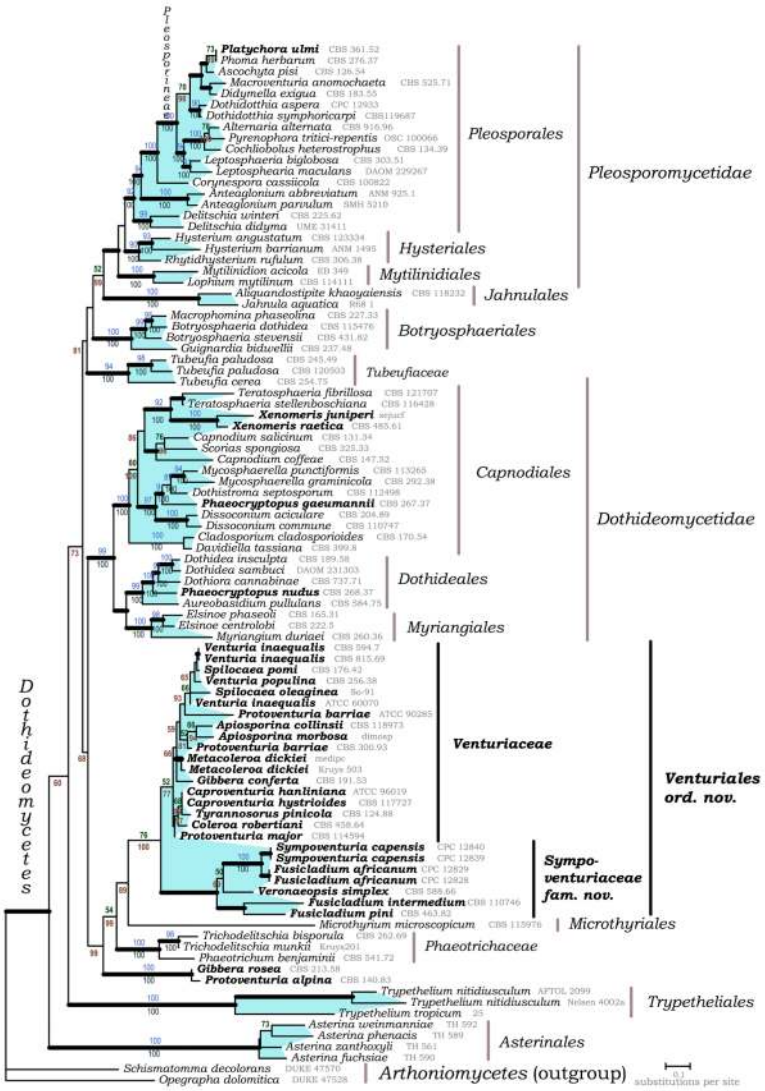

Fig. 1.

A RAxML maximum likelihood tree obtained from a data set of 94 taxa and five genes (SSU, LSU, *TEF1, RPB1, RPB2*) with *Arthoniomycetes* species as outgroup. Numbers above the nodes are bootstrap from 1000 repetitions. Only values above 50% are shown and branches recovered in more than 90% of bootstrap trees are thickened. Culture and voucher numbers are indicated after species names and relevant taxa are bolded

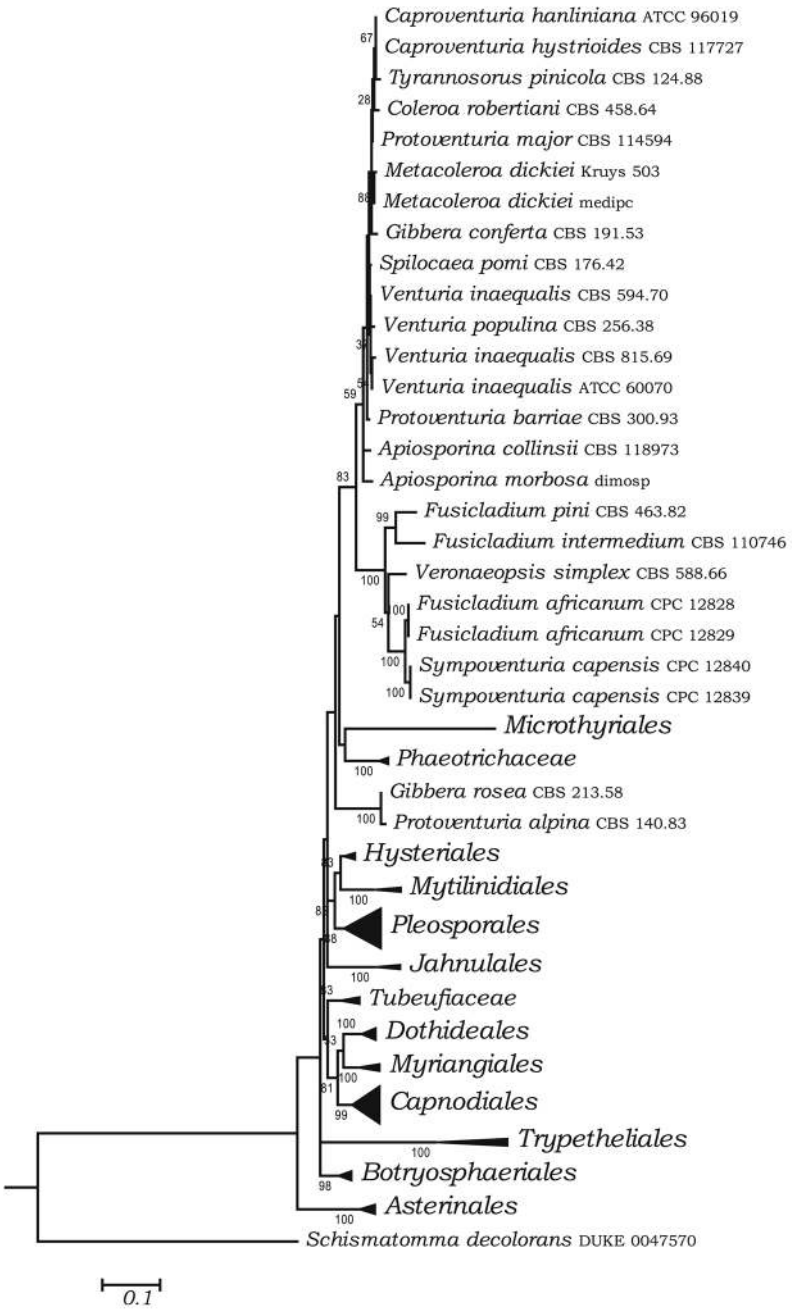

Fig. 2.

A simplified RAXML maximum likelihood tree from obtained from 90 taxa and LSU data only. All ordinal level clades were collapsed ad bootstrap numbers from 450 repetitions are shown above the nodes

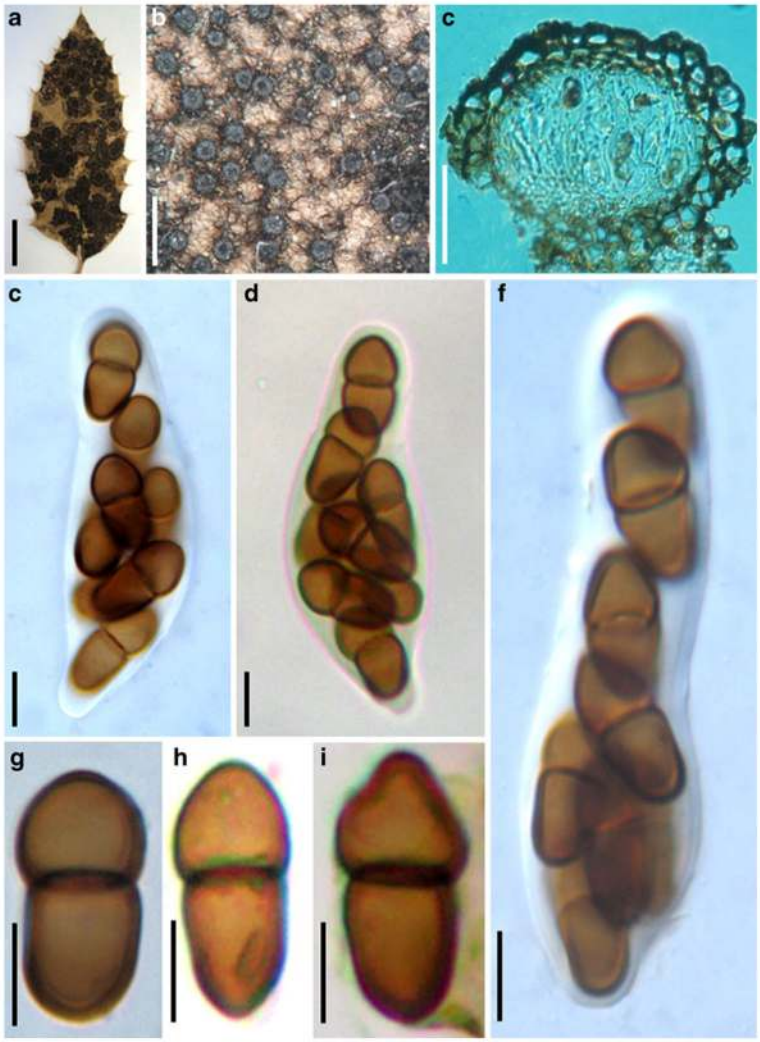

Fig. 3. ***Acantharia echinata*** **(from NY, holotype)**
a, b. Superficial ascoma gregarious on the substrate surface. **c.** Section of an ascoma. Note large heavily pigmented thick-walled cells. **d–f.** Obclavate asci. **g–i.** Released ascospores. Scale bars: a=5 mm, b=0.5 mm, c=50 μm, d–i=10 μm

Fig. 4. ***Apiosporina collinsii*** **((K(M):158702, ex herb. Broome)**
a. Ascomata gregarious on the substrate surface. **b.** Squash mounts with a large number of asci. **c.** Cylindrical 8-spored asci. **d.** Released ascospores. Scale bars: a=0.5 mm, b, c=10 μm, d=5 μm

Fig. 5. ***Dibotryon morbosa*** **(PH-01048831, syntype)**
a. Ascomata densely gregarious on the substrate surface. **b**. Section of ascomata. **c**. Asci in pseudoparaphyses. **d**. Septate pseudoparaphyses. **e**. Released apiosporous ascospores. Scale bars: a=0.5 mm, b=100 μm, c, d=10 μm

Fig. 6. ***Coleroa chaetomium*** **(L11558.38)**

a. Ascomata scattered on the substrate surface. **b.** Section of an ascoma. **c, d.** Somewhat obclavate, 8-spored asci without pedicel. **e.** Released ascospores. Scale bars: a= 0.5 mm, b=50 μm, c, d=10 μm, e=5 μm

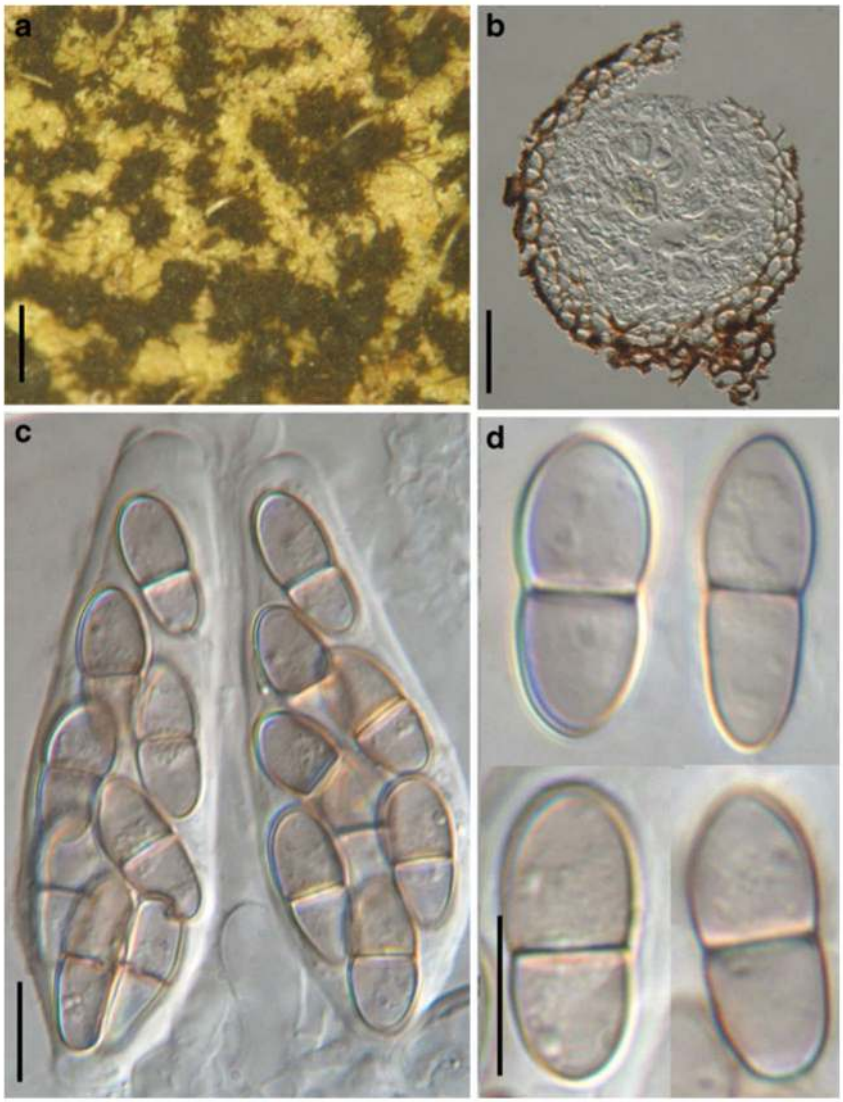

Fig. 7. ***Pseudoparodiella vernoniae*** **(K(M):154549, holotype)**
a. Setose ascomata scattered on the substrate surface. **b**. Section of an ascoma **c**. Squash mounts with two asci. **d**. Released, 1-septate ascospores. Scale bars: a=200 μm, b=20 μm, c, d=10 μm

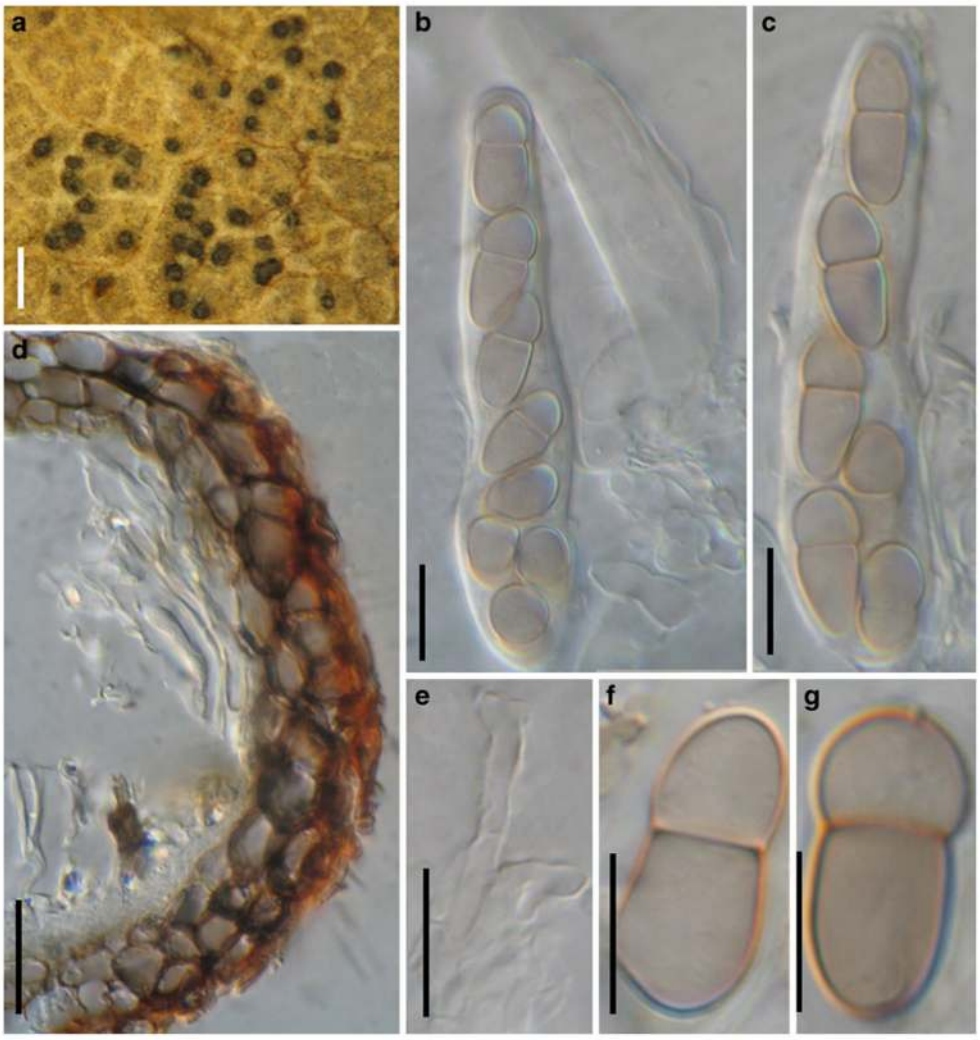

Fig. 8. ***Venturia inaequalis*** **(L 0054534, isotype of** ***Didymosphaeria inaequalis*** **(Cooke) Nissl.)**
a. Ascostroma on the surface of substrate. **b, c.** Ascus. **d.** Section of the peridium comprising a few layers of texture of angularis cells. **e.** Decomposing pseudoparaphyses. **f, g.** Ascospores with one septum. Scale bars: **a**=0.5 mm, **b, c, e – g**=10 μm, **d**=20 μm

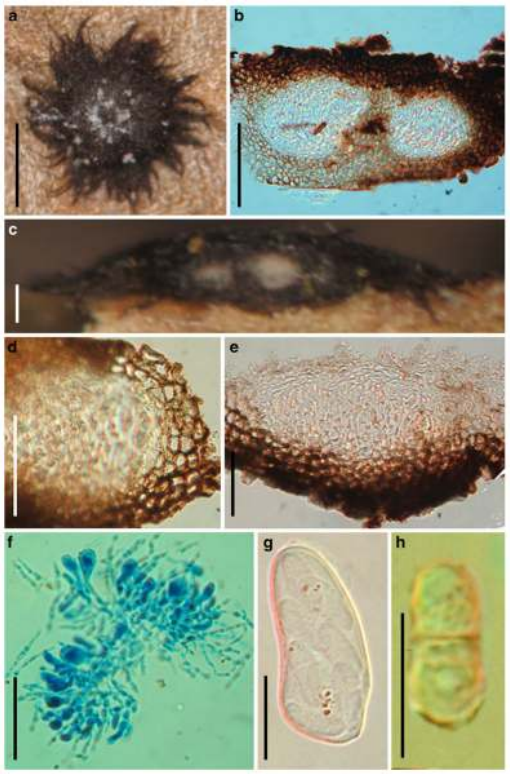

Fig. 9. ***Trichodothis comata*** **(K (M): 143933, syntype)**
a. An flattened ascostroma on the substrate surface. **b**, **c**. Section of a partial ascostroma. **d**, **e**. Section of a partial peridium comprising a few layers of texture of angularis cells. **f**. Pseudoparaphyses with immature asci. **g**. Ascus. **h**. Released 1-septate ascospore. Scale bars: a=0.5 mm, b, c=100 μm, d–f=50 μm, g, h=20 μm

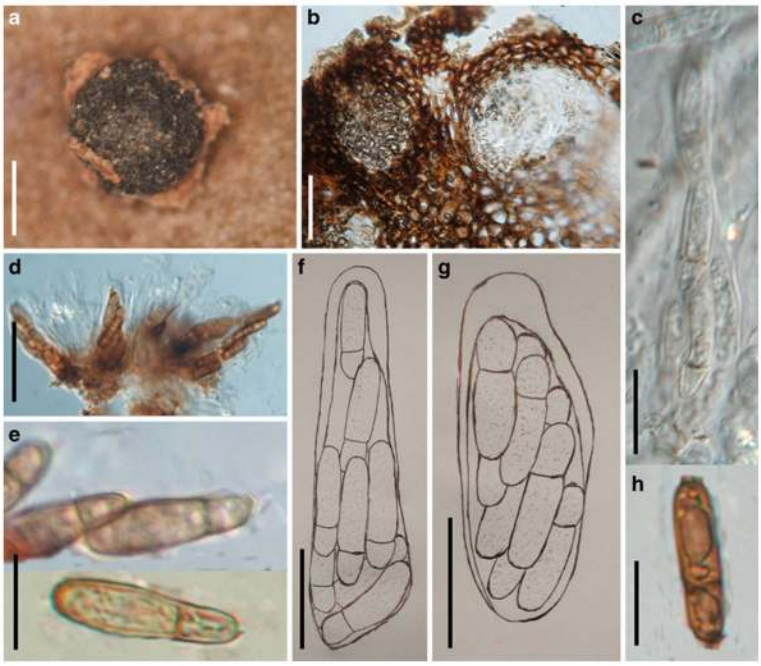

Fig. 10. ***Crotone drymidis*** **(K(M): 143929, syntype)**
a. Ascostroma on the host surface. **b**. Section of a partial ascostroma. **c**. Dehiscent ascus. **d**. Squash mounts with several asci. **e**, **h**. Released ascospores. **f**, **g**. Ascus. Scale bars: a=0.5 mm, b, d=100 μm, c, f, g=20 μm, e, h=10 μm

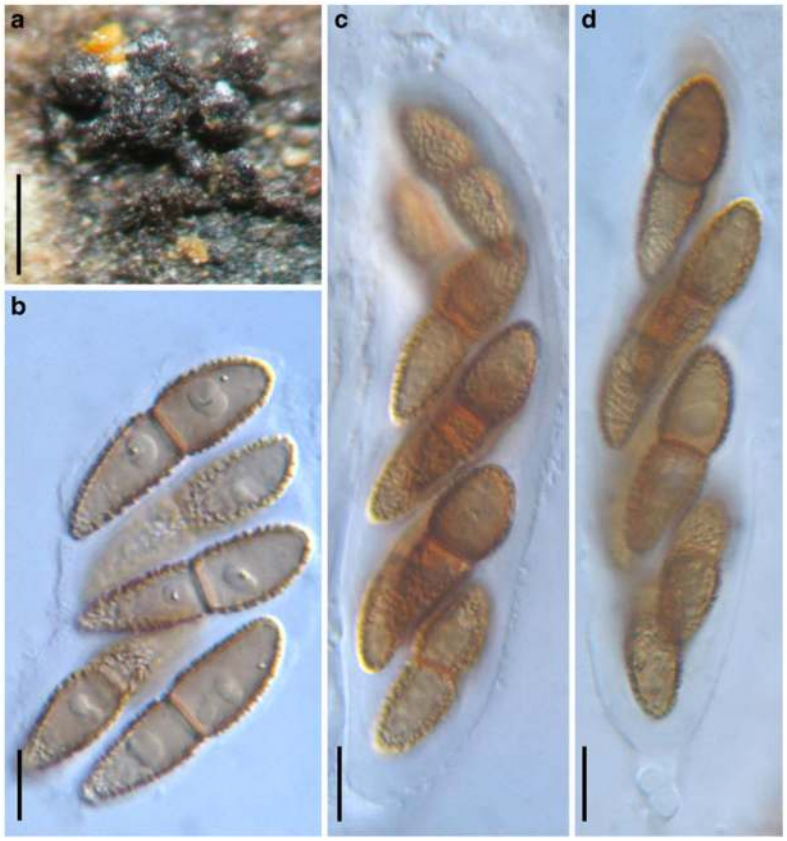

Fig. 11. ***Polyrhizon terminaliae*** **(S reg. nr F8238, holotype)**
a. A cluster of ascomata on the substrate surface. **b**. Released ascospores. **c**, **d**. Asci with short furcate pedicels. Scale bars: a=0.5 mm, b–d=10 μm

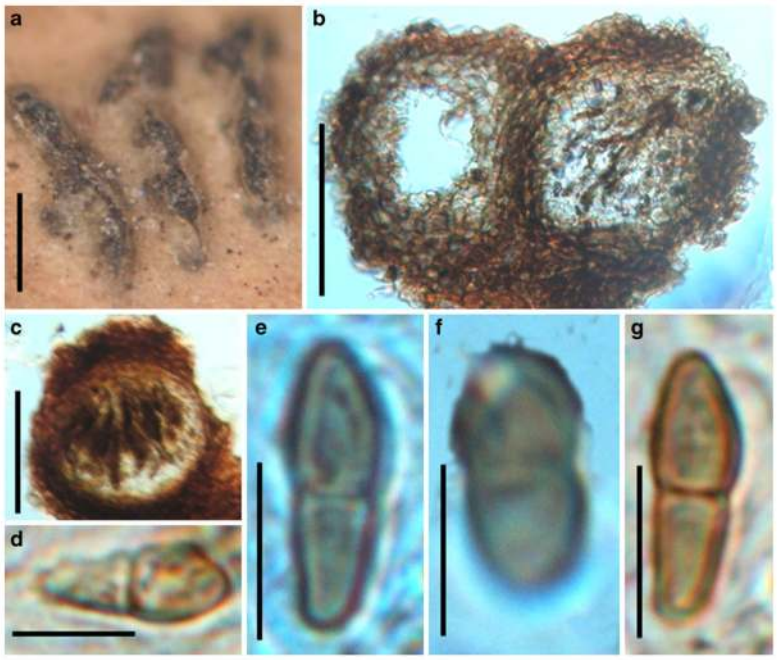

Fig. 12. ***Lineostroma banksiae*** **(K(M): 143926, syntype)**
a. Linear ascostroma on the host surface. **b**, **c**. Section of ascomata. **d**–**g**. Released ascospores. Scale bars: a=0.5 mm, b, c=100 μm, d–g=10 μm

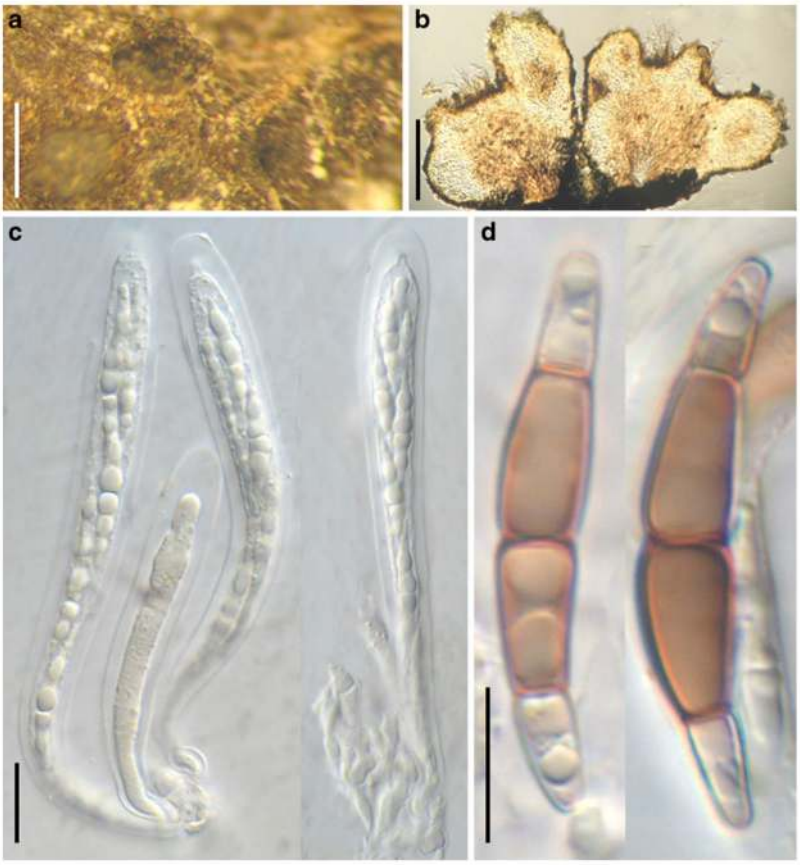

Fig. 13. ***Phragmogibbera xylariicola*** **(NY Gary J. Samuels 1238, isotype)**
a. Ascostromata erumpent from ostiole of *Xylaria*. **b**. Section of a partial ascostroma. **c**. Clavate immature asci. **d**. Narrowly fusoid ascospores. Note the hyaline end cells. Scale bars: a=0.5 mm, b=100 μm, c, d=10 μm

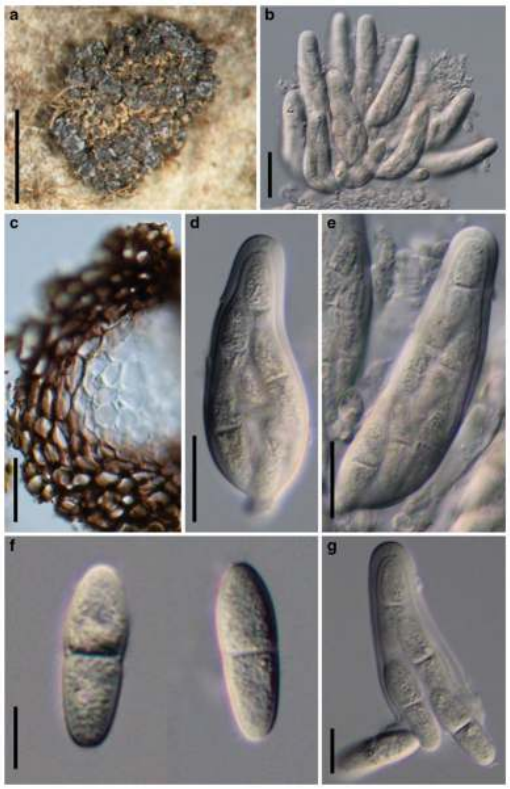

Fig. 14. ***Rosenscheldiella styracis*****(S reg. nr F7328, lectotype)**
a. Ascomata clustered on the host surface. **b, e**. Squash mounts with a large number of asci. **c**. Section of partial peridium. **d**. Obclavate ascus. **f**. Released ascospores. **g**. Broken ascus with spores releasing. Scale bars: a=1 mm, b–e=20 μm, f, g=10 μm

Table 1

Taxa used in the phylogenetic analysis and their corresponding GenBank accession numbers

Species	voucher/culture	SSU	LSU	*TEF1*	*RPB1*	*RPB2*
Aliquandostipite khaoyaiensis	CBS 118232	AF201453	GU301796	GU349048		FJ238360
Alternaria alternata	CBS 916.96	DQ678031	DQ678082	DQ677927		DQ677980
Anteaglonium abbreviatum	ANM 925.1		GQ221877	GQ221924		
Anteaglonium parvulum	SMH 5210		GQ221907	GQ221917		
Apiosporina collinsii	CBS 118973	GU296135	GU301798	GU349057	GU357778	
Apiosporina morbosa	dimosp		EF114694			
Ascochyta pisi	CBS 126.54	DQ678018	DQ678070	DQ677913		DQ677967
Asterina fuchsiae	TH 590	GU586210	GU586216			
Asterina phenacis	TH 589	GU586211	GU586217			
Asterina weinmanniae	TH 592	GU586212	GU586218			
Asterina zanthoxyli	TH 561	GU586213	GU586219			
Aureobasidium pullulans	CBS 584.75	DQ471004	DQ470956	DQ471075	DQ471148	DQ470906
Botryosphaeria dothidea	CBS 115476	DQ677998	DQ678051	DQ767637	GU357802	DQ677944
Botryosphaeria stevensii	CBS 431.82	DQ678012	DQ678064	DQ677907		DQ677960
Capnodium coffeae	CBS 147.52	DQ247808	DQ247800	DQ471089	DQ471162	DQ247788
Capnodium salicinum	CBS 131.34	DQ677997	DQ678050	DQ677889		
Caproventuria hanliniana	ATCC 96019		AF050290			
Caproventuria hystrioides	CBS 117727		EU035459			
Cladosporium cladosporioides	CBS 170.54	DQ678004	DQ678057	DQ677898	GU357790	DQ677952
Cochliobolus heterostrophus	CBS 134.39	AY544727	AY544645	DQ497603		DQ247790
Coleroa robertiani	CBS 458.64		xxx			
Corynespora cassiicola	CBS 100822	GU296144	GU301808	GU349052	GU357772	GU371742
Davidiella tassiana	CBS 399.80	DQ678022	DQ678074	DQ677918	GU357793	DQ677971
Delitschia didyma	UME 31411	AF242264	DQ384090			
Delitschia winteri	CBS 225.62	DQ678026	DQ678077	DQ677922		DQ677975
Didymella exigua	CBS 183.55	GU296147			GU357800	GU371764
Dissoconium aciculare	CBS 204.89	GU214523	GQ852587			
Dissoconium commune	CBS 110747	GU214525	GQ852589			
Dothidea insculpta	CBS 189.58	DQ247810	DQ247802	DQ471081	DQ471154	AF107800

Species	voucher/culture	SSU	LSU	*TEF1*	*RPB1*	*RPB2*
Dothidea sambuci	DAOM 231303	AY544722	AY544681	DQ497606		DQ522854
Dothidotthia aspera	CPC 12933	EU673228	EU673276			
Dothidotthia symphoricarpi	CBS119687	EU673224	EU673273			
Dothiora cannabinae	CBS 737.71	DQ479933	DQ470984	DQ471107	DQ471182	DQ470936
Dothistroma septosporum	CBS 112498	GU214533	GQ852597			
Elsinoë centrolobi	CBS 222.50	DQ678041	DQ678094	DQ677934	GU357798	
Elsinoë phaseoli	CBS 165.31	DQ678042	DQ678095	DQ677935	GU357799	
Fusicladium africanum	CPC 12829		EU035424			
Fusicladium africanum	CPC 12828		EU035423			
Fusicladium intermedium	CBS 110746		EU035432			
Fusicladium pini	CBS 463.82		EU035436			
Gibbera conferta	CBS 191.53	GU296150	GU301814	GU349041	GU357758	
Gibbera rosea	CBS 213.58		xxx			
Guignardia bidwellii	CBS 237.48	DQ678034	DQ678085		GU357794	DQ677983
Hysterium angustatum	CBS 123334	FJ161167	FJ161207	FJ161111		FJ161129
Hysterium barrianum	ANM 1495	GU323182	GQ221885			
Jahnula aquatica	R68-1	EF175633	EF175655			
Leptosphaeria biglobosa	CBS 303.51		GU301826	GU349010		
Leptosphearia maculans	DAOM 229267	DQ470993	DQ470946	DQ471062	DQ471136	DQ470894
Lophium mytilinum	CBS 114111	EF596819	EF596819			
Macrophomina phaseolina	CBS 227.33	DQ678037	DQ678088	DQ677929		DQ677986
Macroventuria anomochaeta	CBS 525.71		GU456315	GU456262		GU456346
Metacoleroa dickiei	medipc	EF114719	EF114695			
Metacoleroa dickiei	Kruys 503	DQ384100	DQ384100			
Microthyrium microscopicum	CBS 115976	GU296175	GU301846	GU349042		GU371734
Mycosphaerella graminicola	CBS 292.38	DQ678033	DQ678084			DQ677982
Mycosphaerella punctiformis	CBS 113265	DQ471017	DQ470968	DQ471092	DQ471165	DQ470920
Myriangium duriaei	CBS 260.36	AY016347	DQ678059	DQ677900		DQ677954
Mytilinidion acicola	EB 0349	GU323185	GU323209			GU371757
Opegrapha dolomitica	DUKE 0047528	DQ883706		DQ883732	DQ883717	DQ883714
Phaeocryptopus gaeumannii	CBS 267.37	EF114722	EF114698		GU357770	

Species	**voucher/culture**	**SSU**	**LSU**	***TEF1***	***RPB1***	***RPB2***
Phaeocryptopus nudus	CBS 268.37	GU296182	GU301856	GU349034	GU357745	
Phaeotrichum benjaminii	CBS 541.72	AY016348	AY004340	DQ677892	GU357788	DQ677946
Phoma herbarum	CBS 276.37	DQ678014	DQ678066	DQ677909	GU357792	DQ677962
Platychora ulmi	CBS 361.52	EF114726	EF114702			
Protoventuria alpina	CBS 140.83	EU035444				
Protoventuria barriae	ATCC 90285		EF114728			
Protoventuriabarriae	CBS 300.93		xxx			
Protoventuria major	CBS 114594		xxx			
Pyrenophora tritici	OSC 100066		AY544672	DQ677882		
Rhytidhysteron rufulum	CBS 306.38	GU296191	FJ469672	GU349031	FJ238444	
Schismatomma decolorans	DUKE 0047570	AY548809	AY548815	DQ883725		DQ883715
Scorias spongiosa	CBS 325.33	DQ678024	DQ678075	DQ677920		DQ677973
Spilocaea oleaginea	So-91	AF338393	AF338397			
Spilocaea pomi	CBS 176.42		GU348998	GU349089		
Sympoventuria capensis	CPC 12839		DQ885905			
Sympoventuria capensis	CPC 12840		DQ885904			
Teratosphaeria fibrillosa	CBS 121707	GU296199	GU323213		GU357767	
Teratosphaeria stellenboschiana	CBS 116428	GU214583	EU019295			
Trichodelitschia bisporula	CBS 262.69	GU349000	GU348996	GU349020	GU371812	GU371802
Trichodelitschia munkii	Kruys201	DQ384070	DQ384096			
Trypethelium nitidiusculum	Nelsen 4002a		GU327728			
Trypethelium nitidiusculum	AFTOL 2099		FJ267701	GU327732		
Trypethelium tropicum	25		GU327730			
Tubeufia cerea	CBS 254.75	DQ471034	DQ470982	DQ471105	DQ471180	DQ470934
Tubeufia paludosa	CBS 120503	GU296203	GU301877	GU349024	GU357754	GU371731
Tubeufia paludosa	CBS 245.49	DQ767649	DQ767654	DQ767638		DQ767643
Tyrannosoru spinicola	CBS 124.88	DQ471025	DQ470974	DQ471098	DQ471171	DQ470928
Venturia inaequalis	ATCC 60070	EF114737	EF114712			
Venturia inaequalis	CBS 815.69	GU296204	GU301878	GU349023	GU357756	
Venturia inaequalis	CBS 594.70	GU296205	GU301879	GU349022	GU357757	
Venturia populina	CBS 256.38	GU296206	GU323212		GU357769	

Species	voucher/culture	SSU	LSU	*TEF1*	*RPB1*	*RPB2*
Veronaeopsis simplex	CBS 588.66		EU041877			
Xenomeris juniperi	xejucf	EF114734	EF114709			
Xenomeris raetica	CBS 485.61	EF114741	EF114716			