Mycoscience 39: 97–104, 1998

Review

The order Phyllachorales: Taxonomic review

Denise M. W. Silva-Hanlin[1] and Richard T. Hanlin[2]

[1] Universidade Federal Rural de Pernambuco, DEPA/Área de Fitossanidade, 52.171–900, Recife-PE, Brazil
[2] Department of Plant Pathology, University of Georgia, Athens, GA 30602–7274, USA

Accepted for publication 29 January 1998

The order Phyllachorales contains ascomycetous fungi of considerable economic importance. The group is represented mostly by foliar parasites which produce perithecia under a clypeus, inside a stroma, or do not produce any stromatic tissue. A major taxonomic problem with this order is the lack of reliable morphological characters that clearly delimit the entire group. The main purpose of this review is to provide a clear picture of the taxonomic relationships of the order Phyllachorales, along with a key to the most important genera in the family Phyllachoraceae.

Key Words——Loculoascomycetes; phyllachoraceae; phyllachorales; taxonomy.

The Phyllachorales is a small order of mostly tropical perithecial ascomycetes (pyrenomycetes), and has generally been treated as comprising only one family, the Phyllachoraceae (=Polystigmataceae) (Eriksson and Hawksworth, 1993; Hawksworth et al., 1995). Most of the members of the family are obligate parasites, making it difficult experimentally to connect anamorphs and teleomorphs. As a consequence their complete life cycle is practically unknown (Cannon, 1991).

The family Phyllachoraceae, with controversial taxonomic position, has been placed in several orders, including the Dothideales (Horst, 1990), Sphaeriales (Nannfeldt, 1932; Miller, 1949; Müller and Arx, 1962; Wehmeyer, 1975), Xylariales (Luttrell, 1951; Barr, 1990), Glomerellales (Chadefaud, 1960; Locquin, 1984), Phyllachorales (Barr, 1976a, b, 1983), Polystigmatales (Eriksson, 1982; Hawksworth et al., 1983), and Diaporthales (Cannon, 1988).

In general, members of the Phyllachoraceae produce an ascocarp embedded in the host tissue, mostly within a stroma or beneath an epidermal clypeus. The type of development is ascohymenial, and the ascus has an apical ring, normally not turning blue in iodine reagent (J−). Paraphyses are usually present and thin-walled, ascospores are mostly one-celled, ovoid and hyaline, and anamorphs are coelomycetes, spermatial or disseminative (Hawksworth et al., 1995). Munk (1957) and Barr (1990) had a different concept of the family and also accepted forms whose ascus apical ring turns blue in iodine (J+).

It is difficult to characterize the species in the family using the general description given above. *Glomerella* Spauld. & H. Schrenk is not an obligate, but a necrotrophic parasite, and does not produce conspicuous stromatic tissue as do the others. *Sphaerodothis* (Sacc. & P. Syd.) Shear has dark spores covered by a mucilaginous sheath, and has an undifferentiated ascus tip. In *Ophiodothella* (Henn.) Höhn. the ascus tip reacts positively to iodine, and ascospores are mostly filiform.

Wehmeyer (1975) did not consider the characters used to delimit the family well defined, and suggested that the Phyllachoraceae might include genera more closely related to other orders than to each other. Another factor that suggests that the family may be artificial is the emphasis that has been placed on only a few characters, such as ascospore shape, color, and septation, as well as on the extent of stromatic tissue (Cannon, 1991).

A detailed study of the peridial anatomy of several pyrenomycetes was undertaken by Jensen (1985), who found high variation in peridial structure of the four genera sampled for the Polystigmataceae (Phyllachoraceae), *Phyllachora* Nitschke ex Fuckel, *Glomerella*, *Physalospora* Niessl, and *Polystigma* DC. Based on this single character, he questioned the monophyly of this family.

The number of genera recognized within the family varies according to the authority. Hawksworth (1985) recognized 23 genera of Phyllachoraceae, which he placed in the Polystigmatales, whereas Barr (1990) provided a key to genera of Phyllachoraceae which included only 12 genera. Eriksson and Hawksworth (1993) recognized 39 genera in the family Phyllachoraceae, and recently Hawksworth et al. (1995) accepted 42 genera and 59 synonyms.

Despite the relatively high number of genera included in the family, only six have been commonly reported and cited in the literature searched: *Coccodiella* Hara (=*Coccostroma* Theiss. & Syd.), *Glomerella*, *Ophiodothella*, *Phyllachora*, and *Sphaerodothis*. The sixth genus, *Magnaporthe* R. A. Krause & R. K. Webster is considered by only a few investigators as a member of the Phyl-

lachorales (Barr, 1977; Farr et al., 1989) or Polystigmatales (Hawksworth et al., 1983), while other authors have placed it in the Diaporthales (Krause and Webster, 1972; Yaegashi and Udagawa, 1978).

Economic importance and distribution

Despite their widespread nature, *Phyllachora*, *Coccodiella*, *Ophiodothella*, and *Sphaerodothis* rarely cause economic losses, due to the small amount of damage inflicted on the host. On the contrary, *Glomerella* and *Magnaporthe* are destructive plant pathogens.

Phyllachora species are responsible for leaf tar spot diseases on Leguminosae (Cannon, 1991) and *Duranta* spp. in the tropics (Hanlin and Tortolero, 1991), small scabby leafspots or "lixa-pequena" on coconut palms in Brazil (Subileau et al., 1993), and leaf-spots on grasses and sedges in northern regions (Seaver, 1928). One of the most important species, *P. graminis* (Pers.) Fuckel, causes tar spots, mostly on grasses. The symptoms are visualized on both leaf surfaces by elongated grayish violet to dark green spots which later become glossy black (Horst, 1990).

Coccodiella (*Bagnisiopsis* Theiss. & Syd.) is also a weak leaf parasite, forming erumpent stromata mostly on *Miconia* (Melastomataceae) leaves in South and Central America (Miller and Burton, 1943), as well as on bamboos and grass bamboos in Japan (Katumoto, 1968).

Glomerella species have a worldwide distribution, especially in the tropics and subtropics (Shear and Wood, 1913; Mordue, 1971). Although some saprotrophic strains have been reported, most of them are necrotrophic and produce their fruiting structures after killing the plant tissue (Cannon, 1991). They cause diseases referred to as anthracnose (Shear and Wood, 1913; Sutton, 1992), and they are able to cause quiescent infections, which make these fungi important post-harvest pathogens (Sutton, 1992). They can attack all parts of the host, causing leaf spots and diebacks, root rots, blossom rots and fruit rots. Seedling blights in the earliest stages of development are also observed (Mordue, 1971).

Ophiodothella also causes tar spot diseases. The species *O. vaccinii* E. S. Boyd is a common parasite on *Vaccinium arboreum* Marsh. leaves in the southern states of the USA (Boyd, 1934). This fungus produces an unusual anamorph, *Acerviclypeatus* Hanlin, which produces an acervulus covered by a clypeus. Also produced is a "pore-puncher," a vertical column of hyphae that perforates the clypeus (Hanlin, 1990a).

Sphaerodothis is a stromatic foliar parasite. It is probably a heterogeneous genus, formed by species with dark, ornamented or smooth ascospores (Cannon, 1989), with some species producing a gelatinous sheath or envelope (Joly, 1961). The species *S. acrocomiae* (Mont.) Arx & E. Müll. is an important parasite of palms (Joly, 1961). In Brazil it is the causal agent of big scab or the "lixa grande" of coconut leaves (Bezerra, 1991; Subileau et al., 1993).

Magnaporthe is a necrotrophic parasite, mostly of roots and stems of Gramineae and Cyperaceae (Cannon, 1994). The type species, *M. salvinii* (Catt.) R. A. Krause & R. K. Webster causes stem rot of rice (*Oryza sativa*), and it is widespread along with the host (Ellis and Holliday, 1972).

Taxonomic controversy in the Phyllachorales

There has been disagreement among taxonomists in recent years concerning the limits of the family Phyllachoraceae. Most of the early classification schemes were artificial and based on few characters, such as the gross appearance of the ascoma, asci, and ascospores (Wehmeyer, 1975). The presence or absence of a stroma also has been used in the past to delimit orders, which led to the separation of several genera of fungi supposedly phylogenetically related (Orton, 1924).

Nannfeldt (1932) separated the euascomycetes according to their ascomal development. He defined two types of ontogeny: the ascolocular type, comprised of fungi that produce asci in locules of a preformed stroma (typical of the Dothideales); and the ascohymenial type, in which he placed fungi forming asci in a hymenium or fascicle surrounded by a distinct wall (typical of the Phyllachorales). Luttrell (1951) noted the connection between the ascolocular type of development and the bitunicate ascus, as well as between the ascohymenial type of development and unitunicate asci.

The family Phyllachoraceae was first proposed by Theissen and Sydow (1915). They placed it in the order Dothideales, which was characterized by ascomata produced in locules without true walls. However, the presence of a true perithecial wall, pseudoparenchymatous in texture, in members of the Phyllachoraceae was demonstrated by Orton (1924), and Miller (1951, 1954).

In the meantime, Petrak (1924) also noticed that *Phyllachora* and other closely related genera were distinct from the Dothideales based mainly on stromatic features. He observed that *Polystigma* was not a member of the family Hypocreaceae, but a close relative of *Phyllachora*, despite its bright colored ascomata, characteristic of the order Hypocreales (Cannon, 1991).

Miller (1949) treated the Phyllachoraceae as a family in the order Sphaeriales (pyrenomycetes), which was comprised of perithecial ascomycetes with an ascomatal wall, ascocarps opening by a pore or slit, asci forming in a hymenium, and paraphyses with a free apex.

The ascomatal wall had been possibly ignored in the past because it is not well differentiated and is difficult to see in some histological preparations (Orton, 1924). Another possible reason for the inclusion of members of the Phyllachoraceae in the order Dothideales of the subclass Loculoascomycetidae is the superficial similarity of the stroma in certain genera in these two orders. For instance, *Physalospora*, a member of the Phyllachorales with unitunicate asci, is easily confused with *Botryosphaeria* Ces. & De Not., a loculoascomycete with bitunicate asci. Those two genera, despite their placement in different subdivisions, share several superficial features, differing mainly in ascus characteristics (Can-

non, 1991). The genus *Physalospora* also resembles *Glomerella*, except for its larger ascomata and ascospores, fusoid ascus (instead of cylindrical), and the absence of anamorphs (Hanlin, 1990c). Several species of *Botryosphaeria*, e.g., *B. obtusa* (Schwein.) Shoem., *B. rhodina* (Berk. & Curt.) Arx, and *B. zeae* (Stout) Arx & E. Müll., have been transferred from *Physalospora*.

Another genus with uncertain affinities is *Trabutia* Sacc. et Roum., which is referred to as bitunicate by Arx and Müller (1954) and placed in the Botryosphaeriaceae. In contrast, Barr (1987) treated *Trabutia* as a unitunicate genus and suggested its connection with *Phyllachora*.

Luttrell (1951), after defining eight types of centrum development, demonstrated that *Phyllachora*, *Ophiodothella*, and *Catacauma* Theiss. & Syd. (now included in *Phyllachora*) have the "Xylaria" type of ontogeny, typical of the order Xylariales.

Barr (1976b) raised the Phyllachoraceae to ordinal rank on the basis of their biotrophic relationships with the host, ascocarp type, and ascus tip features. At the same time Barr (1976a) separated the Phyllachorales into four families: the Phacidiaceae, comprising apothecioid or cleistothecioid forms; the Porinaceae, with lichenized forms; the Melogrammataceae (=Phyllachoraceae), comprising parasitic forms with small apical nonamyloid annulus and narrow paraphyses; and the Physosporellaceae, which includes saprobic and parasitic forms, some with amyloid apical annulus and broad deliquescent paraphyses.

Later, Barr (1983) proposed a new classification scheme in which she stressed features of the centrum and stroma. She included in the Phyllachoraceae parasitic, hemibiotrophic, or lichenized forms, and retained the family under the order Phyllachorales. She also placed the order in the subclass Edaphomycetidae (centrum with hymenial paraphyses). The Diaporthales was included in the subclass Parenchymatomycetidae (centrum pseudoparenchymatous, without true paraphyses)

After revising her previous classification (Barr, 1976a, b; 1983), she did not find consistent differences between the Phyllachorales and Xylariales when she compared the following morphological characters: centrum structure, absence or presence and type of hamathecial (interascal) tissues, and peridium structure. This motivated her to reduce the Phyllachorales back to family level under the order Xylariales (Barr, 1990).

Based primarily on the mode of nutrition, Cannon (1988) suggested that the Phyllachorales is closely related to the Diaporthales, and not to the Xylariales, thus he proposed the merging of the two former orders. His theory did not receive much support due to the differences in centrum structure of Diaporthales ("Diaporthe" type, without true paraphyses and with pseudoparenchyma), and Phyllachorales ("Xylaria" type, with true paraphyses, and without pseudoparenchyma) as defined by Luttrell (1951).

An alternative scheme of classification of the ascomycetes was proposed by Chadefaud (1960), based primarily on the features of the ascus tip and stroma texture. He created the order Glomerellales. This order was characterized by fungi with a thickening of the ascus tip, and without pronounced ring structures. He further divided the order into two groups: "Eu-Glomerellales," which included species with a non-fleshy black stroma (*Glomerella*, *Phyllachora*, *Physalospora*, and *Gibellina* Pass. ex Roum.), like the diaporthaceous fungi. The second group, the Polystigmatales or "Glomerellales nectrioides" was comprised of one genus, *Polystigma*, with a red to orange, fleshy stroma, like the Hypocreales (=Nectriales). It has subsequently been suggested that the ascus tip is not a good character to delimit certain genera in the Phyllachorales, such as *Phyllachora*, due to the variation of its ring structure and difficulty in observing it (Swart, 1982; Cannon, 1991). Other members of the order (e.g., the species *Sphaerodothis acrocomiae* and *Glomerella septospora* Sivan. & W. H. Hsieh) do not possess any distinctive apical structure.

Locquin (1984) raised the two groups suggested by Chadefaud (1960), the Polystigmatales and Glomerellales, to ordinal level. Despite using the ascus tip to delimit orders, Locquin described both orders as having an ascus with a lenticular disc at the apex, and differentiated them by stroma characteristics. In the Polystigmatales, with fleshy stroma, he accepted one family with 26 genera. In Glomerellales, with one family (Glomerellaceae) and two genera, he included species with ascoma not fleshy. However, he did not provide a Latin description of the family which automatically made it a nom. inval. or invalid name under Art. 36.1 of the International Code of Botanical Nomenclature (Hawksworth and David, 1989).

The confusion about the taxonomic position of the Phyllachorales has been increased by different schemes of classification adopted by mycologists and plant pathologists. Horst (1990), in a book elaborated for plant pathologists, accepts the genera *Phyllachora*, *Glomerella*, and *Ophiodothella* under the order Dothideales of the subclass Loculoascomycetidae, apparently unaware of the transfer of the family to the Sphaeriales by Miller (1949). He described the genera *Phyllachora* and *Ophiodothella* as having "asci in locules, immersed in groups in a stroma covered by host tissue at maturity." The only difference between the two genera pointed out by that author was the filiform ascospore and the absence of paraphyses in *Ophiodothella*. However, paraphyses have been previously reported in *Ophiodothella* (Boyd, 1934; Hanlin, 1990b), and asci have been demonstrated not to be produced in locules, but within a centrum surrounded by a true ascomal wall (Boyd, 1934).

Taxonomic considerations of genera in the Phyllachorales

One of the problems of dealing with taxonomy of the Phyllachorales is that few or no detailed morphological studies are available in the order, and most of the information available is based on only a few species or genera. Detailed studies on spermatia/anamorph/teleomorph connections, ascomal ontogeny, ascus structure/function, cytology, metabolic products, phytogeography, and cell

wall chemistry still need to be carried out (Hawksworth, 1985). This knowledge might help to elucidate the controversy and conflicting information on this group. A summary of the taxonomic status of the most common genera in the order is provided below.

Phyllachora Detailed monographs of the genus are available for the species parasitic on Gramineae (Parbery, 1967), and Leguminosae (Cannon, 1991). *Phyllachora* is the type genus of the family Phyllachoraceae, and about 600 species of *Phyllachora* had been reported on Gramineae by the time Parbery monographed the genus (Parbery, 1967). What contributed to the high number of species in the genus is that species with similar characters have been given different names if they occurred on a different host (Cannon, 1988). This genus is separated from most of the others by the development of the perithecia beneath a subcuticular or epidermal clypeus (Dennis, 1981). *Catacauma*, now a synonym of *Phyllachora*, used to be considered distinct from *Phyllachora* in that it produced ascomata embedded between a clypeus and epidermis, instead of below the epidermis (Cannon, 1991). However, it has been shown that differences in depth of ascomata can be influenced by the consistency of the host tissue (Cannon, 1991), thus this is not a valid character on which to distinguish genera.

Coccodiella This genus is mostly known by its synonym, *Coccostroma*, and has been extensively studied by Miller and Burton (1943) (as *Bagnisiopsis* Theiss. & Syd.), as well as by Arx and Müller (1954). *Coccodiella arundinaria* Hara, found on bamboos in Japan, is the type species. A striking distinction between *Coccodiella* and *Phyllachora* is the nature of the stroma. *Phyllachora* produces a perithecium immersed beneath a pseudostromatic clypeus, and *Coccodiella* produces an erumpent-superficial pulvinate eustroma that contains the perithecia (Cannon, 1991). Several species of *Coccodiella* as well as *Phyllachora* produce mostly filiform, hyaline spermatia. The spermagonium can be produced in the same or in a separate stroma in *Coccodiella* (Miller and Burton, 1943) or under the same or separate clypeus in *Phyllachora* (Cannon, 1991).

Glomerella Sutton (1992) recognized eight species in the genus *Glomerella*. It differs from the other genera in the Phyllachorales in that it does not produce a stroma or pseudostroma (Alexopoulos et al., 1996). The genus *Glomerella* can be easily recognized by morphological and cultural characteristics of its anamorph, *Colletotrichum* Corda (Cannon, 1991; Sutton, 1992), which is not produced by any other fungus. However, the taxonomy at the species level is confusing (Sutton, 1992), since both anamorph and teleomorph have great molecular variation even within the same species (Sherriff et al., 1994). Shear and Wood (1913) emphasized that the same species of *Glomerella* has received different names, depending on whether it occurs on fruits or foliage. Due to these problems, the identification of isolates of *Glomerella* and *Colletotrichum* to species is difficult (Sutton, 1992).

Ophiodothella *Ophiodothella* was previously placed in the family Phyllachoraceae of the order Dothideales by Clements and Shear (1931) based on the absence of perithecial walls. However, ontogenic studies by Boyd (1934) proved not only the presence of a wall in the genus, but also the formation of an ostiole and paraphyses which are characteristic of the order Sphaeriales. This combination of characters motivated the author to transfer the genus *Ophiodothella* from the Dothideales to the Sphaeriales. At that time Boyd (1934) could not determine with certainty into which family the genus should be placed, so she temporarily placed it within the Clypeosphaeriaceae (a family currently placed in the Xylariales by Barr (1990)), due to the presence of a clypeus, until more detailed studies in the genus were available. Later on, Müller and Arx (1962) transferred *Ophiodothella* to the Phyllachorales despite its filiform ascospores which are not typical of the order.

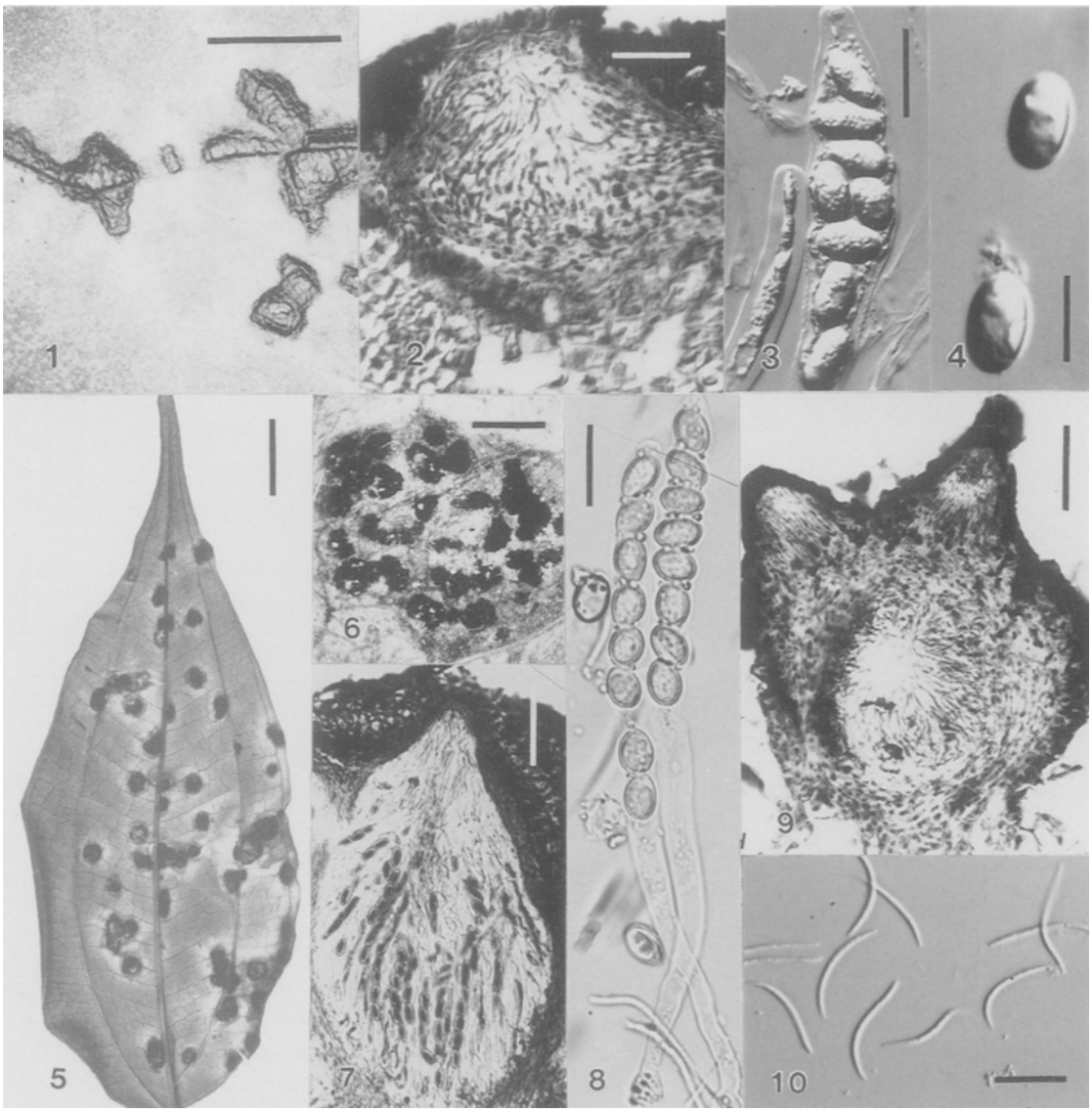
Sphaerodothis *Sphaerodothis* is probably a heterogenous genus (Cannon, 1991). When this genus was first described it was thought to belong to the order Dothideales. Joly (1961) reviewed the genus and recognized eight species, mostly on palms. The color of the ascospores of *Sphaerodothis* is brown before being released from the ascus, an unusual feature for members of the Phyllachorales, which have hyaline spores. However, in *Phyllachora*, ascospores can turn brown in older herbarium specimens after being released from the ascus, and the same phenomenon has been observed in *Coccodiella* (personal observations). Cannon (1989) attributed this change to "degeneration" of the ascospores. Certain species of *Sphaerodothis* have ornamented ascospores, atypical of the order Phyllachorales. For example, *S. danthoniae* (McAlpine) Jane Walker & S. M. Francis has ascospores which are slightly verrucose, and *S. arxii* P. F. Cannon produces ascospores which are highly verrucose or spinose (Cannon, 1989). Nevertheless, like certain species of *Phyllachora* and *Coccodiella*, species of *Sphaerodothis* can produce spermatia, characteristic of the Phyllachorales.

Magnaporthe This genus has an equivocal taxonomic position. The ascoma and ascus features recall *Diaporthe* Nitschke. Both *Magnaporthe* and *Diaporthe* have the endothia-type of ascus as delimited by Luttrell (1951), with asci having a non-amyloid refractive ring and deliquescent bases (Krause and Webster, 1972). Krause and Webster (1972) and Yaegashi and Udagawa (1978) treated *Magnaporthe* as a member of the order Diaporthales. However, Barr (1977) placed this genus in the Physosporellaceae, whereas Hawksworth et al. (1983), and Farr et al. (1989) placed it under the Phyllachoraceae. Recently, Cannon (1994) reviewed the genus *Magnaporthe* and placed it, together with *Gaeumannomyces* Arx & D. L. Olivier and five other genera, in the family Magnaporthaceae. However he did not give the ordinal status of this family and stressed that its relationships with other families are uncertain.

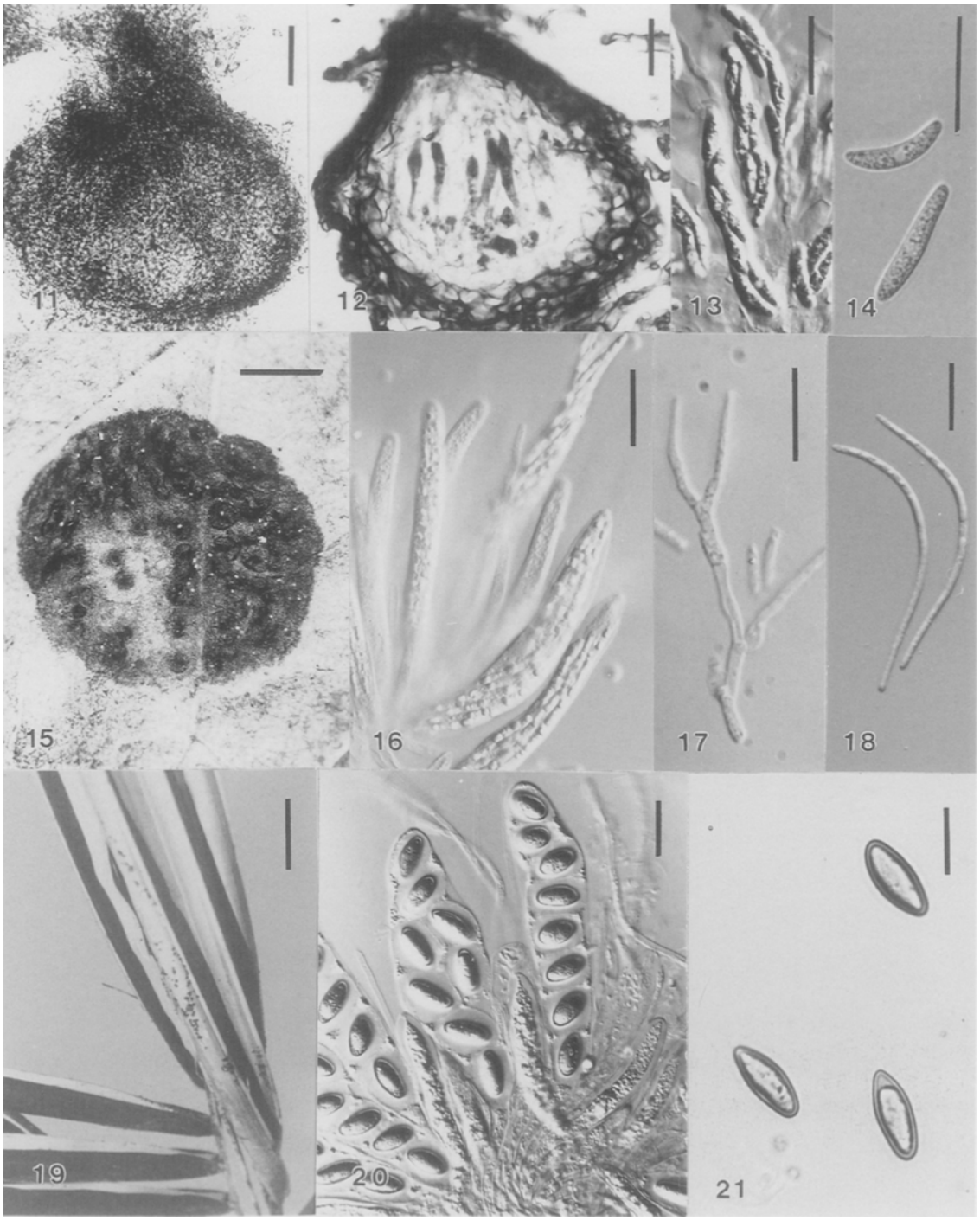
Other genera Two new genera have been recently added to the order Phyllachorales, *Retroa* P. F. Cannon and *Vitreostroma* P. F. Cannon, based on examination of herbarium specimens (Cannon, 1991). *Retroa*, with only two species, was created to accommodate species of

Phyllachora having ascomata with long necks beneath a clypeus. The genus *Vitreostroma*, with only one species and three subspecies, includes one species formerly placed in *Phyllachora* and another formerly placed in *Diachora* Müll. Arg. *Vitreostroma* produces asci in an equatorial ring within the ascoma, which is formed by refractive thick-walled cells. *Rikatlia* P. F. Cannon has been previously described by Cannon (1993) to accommodate *Phyllachora lungusaensis* Henn., which has an anamorph producing conidia with two horizontal pale bands. He placed this fungus in the Phyllachorales based on its biotrophic nature and the presence of a clypeus, although its ascus structure, the absence of paraphyses, and coelomycetous anamorph suggest a closer relationship to the Diaporthales.

18S rDNA studies of the Phyllachorales, including *Phyllachora*, *Coccodiella*, *Glomerella*, *Ophiodothella*, and *Sphaerodothis*, suggest that the order is polyphyletic (Silva, 1996). *Phyllachora* was the closest relative of *Coccodiella* and both genera are apparently the only true Phyllachorales sampled for this study. This will probably result in future realignments of the genera presently included in the order. Details of these studies will be published elsewhere.



Figs. 1–10. 1–4. *Phyllachora* sp. on *Bauhinia* sp. 1. Mature lesions on upper surface of leaf. 2. Section through perithecium immersed in leaf. 3. Ascus with ascospores. 4. Mature ascospores. 5–10. *Coccodiella* spp. on *Miconia* sp. 5. Mature lesions and stromata of *Coccodiella melastomatum* on upper leaf surface. 6. Close-up of lesion with stromata. 7. Section through ascoma of *C. melastomatum* on leaf surface. 8. Mature asci of *C. toledoi*. 9. Section through spermogonium of *C. toledoi*. 10. Mature spermatia of *C. melastomatum*. Bars: 1 = 2mm; 2 = 20 μm; 3, 4 = 10 μm; 5 = 8 mm; 6 = 0.5 mm; 7 = 30 μm; 8–10 = 10 μm.



Figs. 11–21. 11–14. *Glomerella* spp. 11. Ascoma of *G. glycines* on V-8. 12. Vertical section of *G. glycines* ascoma. 13. Asci of *G. cingulata*. 14. Ascospores of *G. cingulata*. 15–18. *Ophiodothella vaccinii*. 15. Lesion on upper surface of *Vaccinium arboreum* leaf with clypeus. 16. Mature asci with ascospores. 17. Branched paraphysis. 18. Mature ascospores. 19–21. *Sphaerodothis acrocomiae*. 19. Stromata on upper surface of *Cocos nucifera* leaflets. 20. Mature asci with ascospores. 21. Mature ascospores. Scale bars: 11–14 = 10 μm; 15 = 2 mm; 16–18 = 20 μm; 19 = 1.5 cm; 20 = 30 μm; 21 = 10 μm.

Key to common genera in the Phyllachoraceae

1. Stromatic tissue generally absent, parasite or saprobe on vascular plant tissues, ascospores unicellular or multiseptate[a], spermatia absent, anamorph *Colletotrichum* ..... *Glomerella*
1'. Stromatic tissue present, mostly biotrophs, ascospores unicellular, spermatia present or absent, anamorph absent or other than above 2
2. Clypeus (pseudostroma) dark and surrounding perithecial neck 3
2'. Eustroma dark and superficial 4
3. Ascospores mostly filiform, ascus apex blueing in iodine (J+), ananorph coelomycetous, spermatia absent ..... *Ophiodothella*
3'. Ascospores cylindrical, obovoid or fusiform, ascus apex not blueing in iodine (J-), anamorph absent, spermatia present ..... *Phyllachora*
4. Ascospores hyaline ..... *Coccodiella*
4'. Ascospores dark before being released from ascus, wall smooth or ornamented ..... *Sphaerodothis*

a) In only one species, *G. septospora*.

Literature cited

Alexopoulos, C. J., Mims, C. W. and Blackwell, M. 1996. Introductory mycology, 4th ed. John Wiley and Sons, New York.

Arx, J. A. von and Müller, E. 1954. Die Gattungen der Amerosporen Pyrenomyceten. Beitr. Kryptogamenfl. Schweiz **11**: 1–434.

Barr, M. E. 1976a. *Buergenerula* and the Physosporellaceae. Mycologia **68**: 611–621.

Barr, M. E. 1976b. Perspectives in the Ascomycotina. Mem. New York Bot. Gard. **28**: 1–8.

Barr, M. E. 1977. *Magnaporthe*, *Telimenella* and *Hyponectria* (Physosporellaceae). Mycologia **69**: 952–966.

Barr, M. E. 1983. The ascomycete connection. Mycologia **75**: 1–13.

Barr, M. E. 1987. Prodomus to Class Loculoascomycetes, Published by the author, Amherst, MA.

Barr, M. E. 1990. Prodomus to nonlichenized, pyrenomycetous members of class Hymenoascomycetes. Mycotaxon **39**: 43–184.

Bezerra, J. L. 1991. Taxonomia dos fungos causadores de Lixa no coqueiro. Fitopatol. Brasil **16**: 36.

Boyd, E. S. 1934. A developmental study of a new species of *Ophiodothella*. Mycologia **26**: 456–468.

Cannon, P. F. 1988. Proposal to merge the Phyllachorales with the Diaporthales, with a new family structure. System. Ascom. **7**: 23–43.

Cannon, P. F. 1989. Notes on *Sphaerodothis* species parasitic on Gramineae. Stud. Mycol. **31**: 49–59.

Cannon, P. F. 1991. A revision of *Phyllachora* and some similar genera on the host family Leguminosae. Mycol. Pap. **163**: 1–302.

Cannon, P. F. 1993. Ascomycetes with banded spores. The genus *Rikatlia* gen. nov. System. Ascom. **11**: 83–93.

Cannon, P. F. 1994. The newly recognized family Magnaporthaceae and its interrelationships. System. Ascom. **13**: 25–42.

Chadefaud, M. 1960. Les végétaux non vasculaires (Cryptogamie). In: Traité de botanique systématique. Tome I, (ed. by Chadefaud, M. and Emberger, L.), pp. 613–616. Masson et Cie, Paris.

Clements, F. E. and Shear, C. L. 1931. The genera of fungi. H. W. Wilson, New York.

Dennis, R. W. G. 1981. British ascomycetes, Rev. ed. J. Cramer, Varduz.

Ellis, M. B. and Holliday, P. 1972. *Leptosphaeria salvinii*. CMI descriptions of pathogenic fungi and bacteria. No. 344. CMI, Kew, Surrey, U.K.

Eriksson, O. 1982. Outline of the ascomycetes-1982. Mycotaxon **15**: 203–248.

Eriksson, O. E. and Hawksworth, D. L. 1993. Outline of the ascomycetes-1993. Syst. Ascom. **12**: 51–257.

Farr, D. F., Bills, G. F., Charmuris, G. P. and Rossman, A. Y. 1989. Fungi on plants and plant products in the United States. APS Press, St. Paul, USA.

Hanlin, R. T. 1990a. *Acerviclypeatus*, a new genus for the anamorph of *Ophiodothella vaccinii*. Mycotaxon **37**: 379–384.

Hanlin, R. T. 1990b. Icones ascomycetum Georgiae: *Ophiodothella vaccinii*. Mycotaxon **39**: 1–8.

Hanlin, R. T. 1990c. Illustrated genera of ascomycetes. APS Press, USA.

Hanlin, R. T. and Tortolero, O. 1991. Icones ascomycetum Venezuelae: *Phyllachora fusicarpa*. Mycotaxon **41**: 19-26.

Hawksworth, D. L. 1985. Problems and prospects in the systematics of the Ascomycotina. Proc. Indian Acad. (Sci.) **94**: 319–339.

Hawksworth, D. L. and David, J. C. 1989. Family names – Index of Fungi Supplement. CAB International Mycological Institute, Kew, U.K.

Hawksworth, D. L., Sutton, B. C. and Ainsworth, G. C. 1983. Ainsworth & Bisby's Dictionary of the fungi, 7th ed. CMI, Kew, Surrey, U.K.

Hawksworth, D. L., Kirk, P. M., Sutton, B. C. and Pegler, D. N. 1995. Ainsworth & Bisby's Dictionary of the fungi, 8th ed. CAB International, Wallingford, U.K.

Horst, R. K. 1990. Westcott's plant disease handbook, 5th ed. AVI Book, USA.

Jensen, J. D. 1985. Peridial anatomy and pyrenomycete taxonomy. Mycologia **77**: 688–701.

Joly, P. 1961. Le genre *Sphaerodothis* Shear. Bull. Res. Council Israel **10D**: 187–193.

Katumoto, K. 1968. On the genus *Coccodiella* Hara. J. Jpn. Bot. **43**: 277–284.

Krause, R. A. and Webster, R. K. 1972. The morphology, taxonomy, and sexuality of the rice stem rot fungus, *Magnaporthe salvinii* (*Leptosphaeria salvinii*). Mycologia **64**: 103–114.

Locquin, M. V. 1984. Mycologie Généra le et Structurale. Masson S.A., Paris.

Luttrell , E. S. 1951. Taxonomy of the Pyrenomycetes. Univ. Missouri Stud. **24**: 1–120.

Miller, J. H. 1949. A revision of the classification of the as-

comycetes with special emphasis on the pyrenomycetes. Mycologia **41**: 99–127.

Miller, J. H. 1951. Studies in the Phyllachoraceae I. *Phyllachora ambrosiae* (Berk. and Curt.) Sacc. Amer. J. Bot. **38**: 830–834.

Miller, J. H. 1954. Studies in the Phyllachoraceae II. *Phyllachora lespedezae*. Amer. J. Bot. **41**: 825–828.

Miller, J. H. and Burton, M. G. 1943. Study of *Bagnisiopsis* species on the Melastomaceae (sic!). Mycologia **35**: 312–334.

Mordue, J. E. M. 1971. *Glomerella cingulata*. CMI descriptions of pathogenic fungi and bacteria. No. 315. CMI, Kew, Surrey, U.K.

Müller, E. and Arx, J. A. von. 1962. Die Gattungen der didymosporen Pyrenomyceten. Wabern, Bern.

Munk, A. 1957. Danish Pyrenomycetes. A preliminary flora. Dansk Bot. Ark. **17**: 1–491.

Nannfeldt, J. A. 1932. Studien über die morphologie und systematik der nicht-lichenisierten inoperculaten discomyceten. Nova Acta Regiae Soc. Sci. Upsal. Ser. IV. **8**: 1–368.

Orton, C. R. 1924. Studies in the morphology of the ascomycetes I. The stroma and the compound fructification of the Dothideaceae and other groups. Mycologia **16**: 49–95.

Parbery, D. G. 1967. Studies on graminicolous species of *Phyllachora* Nke. in Fckl. V. A taxonomic monograph. Austr. J. Bot. **15**: 271–375.

Petrak, F. 1924. Mykologische notizen No. 301. Über die phylogenetischen beziehungen der gattung *Phyllachora* Nit. und ihre bedeutung für das system der dothidealean pilze. Ann. Mycol. **22**: 1–10. (Original not seen.)

Seaver, F. J. 1928. Studies in tropical Ascomycetes-V. Species of *Phyllachora*. Mycologia **20**: 214–225.

Shear, C. L. and Wood, A. K. 1913. Studies of fungus parasites belonging to the genus *Glomerella*. U.S.D.A. Bur. Pl. Industry. Bull. **252**: 1–110.

Sherriff, C., Whelan, M. J., Arnold, G. M., Lafay, J.-F., Brygoo,Y. and Bailey, J. A. 1994. Ribosomal DNA sequence analysis reveals new species groupings in the genus *Colletotrichum*. Exper. Mycol. **18**: 121–138.

Silva, D. M. W. 1996. Phylogenetic relationships of the Phyllachorales and related genera. PhD thesis, The University of Georgia, Athens, Georgia.

Subileau, C., Renard, J. L. and Dennetiere, B. 1993. *Phyllachora torrendiella* (Batista) comb. nov., responsable de la maladie verruqueuse du cocotier. Mycotaxon **49**: 175–185.

Sutton, B. C. 1992. The genus *Glomerella* and its anamorph *Colletotrichum*. In: *Colletotrichum*: Biology, pathology and control, (ed. by Bailey, J. A. and Jeger, M. J.), pp. 1–26. CAB International, Wallingford, U.K.

Swart, H. J. 1982. Australian leaf-inhabiting fungi. XV. *Ophiodothella longispora* sp. nov. Trans. Br. Mycol. Soc. **79**: 566–568.

Theissen, F. and Sydow, H. 1915. Die Dothideales. Ann. Mycol. **13**: 147–746 + 6 pl.

Wehmeyer, L. E. 1975. The pyrenomycetous fungi. Mycol. Mem. **6**: 1–250.

Yaegashi, H. and Udagawa, S. 1978. The taxonomical identity of the perfect state of *Pyricularia grisea* and its allies. Can. J. Bot. **56**: 180–183.