

Chaetosphaeriaceae, a new family for *Chaetosphaeria* and its relatives

Martina Réblová¹, Margaret E. Barr² & Gary J. Samuels³

¹ Institute of Botany, Academy of Sciences, 252 43 Pruhonice, Czech Republic

² 9475 Inverness Road, Sidney, BC V8L 5G8, Canada

³ USDA-ARS, Systematic Botany and Mycology Lab., Rm. 304, 8-011A, BARC-W, Beltsville, Maryland 20705-2350, USA

Réblová, M., M. E. Barr & G. J. Samuels (1999). Chaetosphaeriaceae, a new family for *Chaetosphaeria* and its relatives. – *Sydowia* 51(1): 49–70.

The systematic position of the genus *Chaetosphaeria* among pyrenomycetous ascomycetes is discussed. The families Lasiosphaeriaceae, Helminthosphaeriaceae and Trichosphaeriaceae are rejected as possible families for *Chaetosphaeria*. A new family, Chaetosphaeriaceae (Sordariales) is introduced for *Chaetosphaeria* and for other closely related genera, including *Ascocodinaea*, *Melanochaeta*, *Melanopsammella*, *Porosphaerella*, *Porosphaerellopsis* and *Striatosphaeria*. Anamorphs are dematiaceous and phialidic; they include the genera *Catenularia*, *Cylindrotrichum*, *Chalara*, *Chloridium*, *Cordana*, *Custingophora*, *Dictyochaeta*, *Gonytrichum*, *Menispora*, *Phialophora*, *Sporoschisma*, *Sporoschismopsis* and *Zancluspora*. A dichotomous key to genera of the Chaetosphaeriaceae is provided. The accepted genera are listed along with synonymy, brief descriptions and other references.

Keywords: Ascomycotina, *Chaetosphaeria*, wood-inhabiting fungi, systematics.

Chaetosphaeria Tul. & C. Tul. (Tulasne & Tulasne, 1863) accommodates pyrenomycetous ascomycetes that commonly occur on decaying wood or on the inner side of bark of deciduous and coniferous trees and shrubs. Perithecia are superficial, globose to subglobose, and are typically associated with conspicuous dematiaceous anamorphs. Ascospores are always hyaline and have 1–3 transverse septa. On the basis of gross morphology alone, it is difficult to distinguish *Chaetosphaeria* from many other pyrenomycetous fungi that have black perithecia.

Chaetosphaeria has been placed in various orders and families over the past century. The Tulasne brothers (Tulasne & Tulasne, 1863) included the genus in the group “Sphaeriei”. Fuckel (1870) did not have the type species, *Chaet. innumera* Berk. & Broome ex Tul. & C. Tul., but he included *Chaetosphaeria phaeostroma* (Durieu & Mont.) Fuckel and *Chaet. fusca* Fuckel, both with versicolored ascospores and pyriform perithecia, in the “Sphaeriacei” subgroup

“Cucurbitariae.” These species are today considered to belong to *Chaetosphaerella* (Müller & Booth, 1972). Saccardo (1883) modified the concept of *Chaetosphaeria*, including it in the “Sphaeriaceae, Phaeophragmiae,” and included several species having dark ascospores along with the type species, that has colorless ascospores. He accepted the two species that Fuckel included. Thus the concept of *Chaetosphaeria* was considerably expanded before the end of the 19th century. *Zignoëlla* was distinguished from *Chaetosphaeria* by Saccardo (1883) on the basis of ascospore color; species with hyaline ascospores were included in the former and those with pigmented ascospores in the latter. However, the type species of *Chaetosphaeria*, *Chaet. innumera*, has hyaline ascospores but was not included by Saccardo in *Zignoëlla*. Today *Zignoëlla* is considered to be a synonym of *Chaetosphaeria* (Booth, 1957). Munk (1953) distinguished between *Chaetosphaeria* and *Zignoëlla* Sacc. He included *Chaetosphaeria phaeostroma* among the loculoascomycetes, and *Z. fallax* (Sacc.) Sacc. along with *Trichosphaeria* Fuckel and *Niesslia* Auersw. were placed in an uncertain position among the pyrenomyces. Later Munk (1957) placed *Z. fallax* and *Z. pulviscula* (Currey) Sacc. in the subfamily Rhamphorioideae Munk, of the Diaporthaceae Höhnelt ex Wehmeyer *sensu* Munk (order Diaporthales Nannf.). Müller & von Arx (1962) included *Chaetosphaeria* in the broadly conceived Sphaeriaceae. Locquin (1984), without discussion or explanation, proposed the family Chaetosphaeriaceae M. V. Locq. for *Chaetosphaeria* and included four other genera, *Zignoëlla* Sacc., *Niesslia* Auersw., *Rhagadostoma* Körb. and *Loramyces* W. Weston. He referred the Chaetosphaeriaceae to the order Chaetosphaeriales (Lanier & al., 1978; not validly published, Art. 36.1, Greuter & al., 1994). The Chaetosphaeriaceae M. V. Locq. is not validly published (Hawksworth & David, 1989; Art. 36.1, Greuter & al., 1994). Barr (1990) and Eriksson & Hawksworth (1993) placed *Chaetosphaeria* in the Lasiosphaeriaceae (Sordariales Chadeff. ex D. Hawksw. & O.E. Erikss.).

The Lasiosphaeriaceae Nannf. is a broadly conceived family of the Sordariales. The family was introduced by Nannfeldt (1932) to accommodate species that have a plasmatic globule at the top of the ascus and more or less cylindrical ascospores that become transversely septate with increasing age. Genera such as *Lasiosphaeria* Ces. & De Not., *Bizzozzeria* Berl. & Sacc., *Leptospora* Fuckel, *Bombardia* (Fr.) P. Karst., *Bombardiella* Höhnelt, *Eosphaeria* Höhnelt, *Podospora* Ces. and *Zopfiella* G. Winter were originally included. Lundqvist (1972) divided the large family Sordariaceae G. Winter into two smaller families, the Lasiosphaeriaceae and the highly restricted Sordariaceae. He emended the Lasiosphaeriaceae Nannf. and included two subfamilies, the Lasiosphaerioideae Lundq. and the Po-

dosporoideae Lundq. The Lasiosphaerioideae included three genera, viz. *Lasio-sphaeria*, *Bombardia* and *Cercophora* Fuckel. The Podosporoideae included typically sordariaceous genera such as *Sordaria* Ces. & De Not. and *Podospora*. The ascospores of the Podosporoideae are variable in form. They are typically unicellular, sometimes 2–4-celled, and opaque brown to black, and have 1–4 germ pores and may be surrounded by a gelatinous sheath. Ascospores of fungi in the Podosporoideae always germinate by germ tubes, not by phialides which is a common feature of the Lasiosphaerioideae. Species are typically fimicolous. In the Lasiosphaerioideae the ascospores are typically aseptate to multiseptate, cylindrical, vermiform, occasionally fragmenting, geniculate, rarely ellipsoidal to allantoid or strongly asymmetrical, hyaline or finally partly pigmented. Species are lignicolous, fimicolous, herbicolous or rarely terricolous. The peridium of members of both subfamilies is leathery to partly carbonaceous in the outer layers and lightly pigmented brown; it is generally greater than 50 µm wide and often comprises two or more cell regions. Anamorphs of the Lasiosphaeriaceae in the sense of Lundqvist (1972) are typically *Phialophora*-like, being reduced to solitary dematiaceous phialides producing minute, unicellular conidia. A somewhat more complex anamorph is found in *Cercophora samala* (Subram. & Lodha) Mouchacca & W. Gams which has a *Cladorrhinum* anamorph (Mouchacca & W. Gams, 1993).

Barr (1990) elevated the two subfamilies of the Lasiosphaeriaceae to familial rank, the Lasiosphaeriaceae and the Tripterosporeaceae Cain emend. M. E. Barr, which is equivalent to Lasiosphaeriaceae/Podosporoideae. The Tripterosporeaceae was distinguished from the Lasiosphaeriaceae and the Sordariaceae on the basis of the ascus apex. The apical ring of the Tripterosporeaceae is nonfunctional and may even be lacking, whereas in the other two families the apical ring is functional and pronounced. Barr (1990) expanded the concept of the Lasiosphaeriaceae by including a diversity of genera that could not be accommodated in either the Tripterosporeaceae or the Sordariaceae. The twenty-one genera that she included in the family Lasiosphaeriaceae, including *Chaetosphaeria*, do not appear to be morphologically, anatomically or biologically homogeneous. There is a wide diversity of perithecial anatomies, anamorphs have either phialidic or holoblastic conidiogenous cells (including the basauxic *Arthrimum* anamorph of *Apiospora*) and biologies are also distinct. Eriksson & Hawksworth (1993) did not accept Barr's emendation of the Tripterosporeaceae (Barr 1990) and reported the family as a synonym of the Lasiosphaeriaceae Nannf. following Lundqvist's somewhat broader concept of the latter.

The core genera of the Lasiosphaeriaceae, viz. *Apiosordaria* von Arx & W. Gams, *Lasio-sphaeria*, *Cercophora*, *Bombardia* and *Eo-*

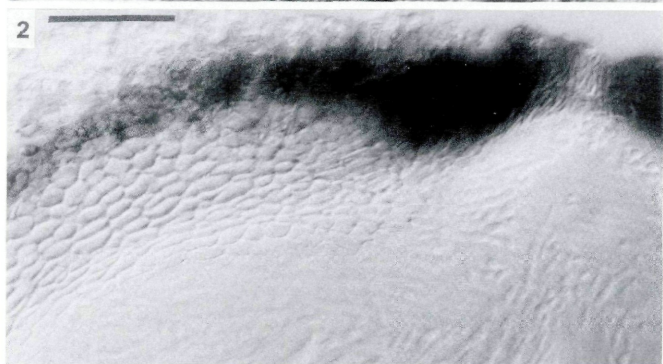
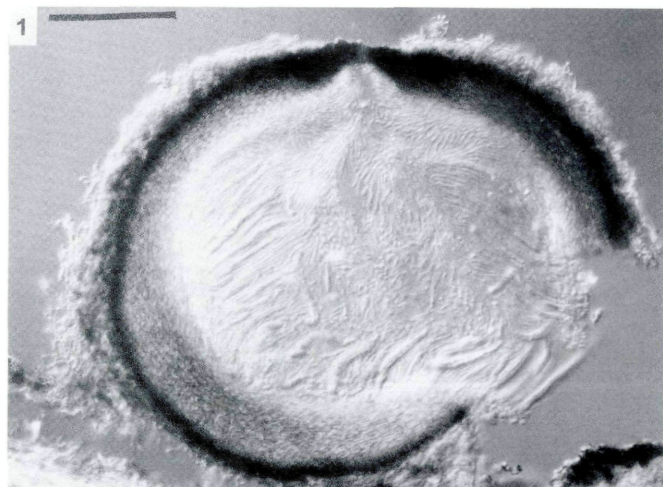
sphaeria, form a homogeneous unit that is characterized by the perithecial peridium (Figs. 1, 2), hamathecium anatomy (cylindrical paraphyses, Fig. 3), ascus anatomy (with a subapical globulus; Figs. 3, 4, 13a), ascospore anatomy (cylindrical, bent in the lower third, sometimes becoming inflated and darker in the upper part; Figs. 3, 4, 13a) and anamorphs. However, the Lasiosphaeriaceae, as broadly perceived by Barr (1990) and Eriksson & Hawksworth (1993), does not appear to be monophyletic.

Chaetosphaeria differs from the core genera of the Lasiosphaeriaceae in the anatomy of the perithecial wall that is narrower (ca. 15 µm wide), brittle, comprises opaque, brick-like cells (Figs. 11, 12), tapering paraphyses (Fig. 5), asci that lack a plasmatic globule in the apex (Figs. 6, 13b) and ellipsoidal to fusiform, septate ascospores that germinate by a germ tube (Figs. 5, 13b). Perithecia are typically associated with conspicuous dematiaceous anamorphs that form long, macronematous, brown conidiophores that are densely disposed around the perithecia. Perithecia are typically glabrous, but in species where the anamorph is associated with long sterile setae on the substratum, similar setae arise from the perithecial surface. Anamorph genera include *Catenularia* Grove, *Cylindrotrichum* Bonorden, *Chalara* (Corda) Rabenh., *Chloridium* Link: Fr., *Custingophora* Stolk & al., *Dictyochaeta* Speg., *Menispora* Pers.: Fr., *Phialophora* Medlar and *Zanclospora* S. Hughes & B. Kendrick.

Several genera share these characters, including *Ascocodinaea* Samuels & al., *Chaetosphaeria* Tul. & C. Tul., *Melanochaeta* E. Müll. & al., *Melanopsammella* Höhnelt, *Porosphaerella* E. Müll. & Samuels, *Porosphaerellopsis* Samuels & E. Müll. and *Striatosphaeria* Samuels & E. Müll. These genera form a homogeneous group that is easily distinguished from the core genera of the Lasiosphaeriaceae s. str.

Small, black perithecia that are also sometimes setose are also found in genera of the Trichosphaeriaceae G. Winter and Helminthosphaeriaceae Samuels & al. Thus either of these families might be considered to be appropriate for *Chaetosphaeria* and its allies. Despite superficial similarities in perithecial morphology, *Chaetosphaeria* does not seem to be closely related to *Helminthosphaeria* Fuckel emend. Samuels & al., the only known genus of the Helminthosphaeriaceae (Samuels & al., 1997). Species of *Helminthosphaeria* are fungicolous, occurring on members of the Aphyllophorales. They have a wide, dark perithecial peridium; the

Figs. 1–3. *Lasio-sphaeria ovina*. – 1. Median, longitudinal section of perithecium, note the three-layered peridium. – 2. Ostiolar canal lined with paraphyses. – 3. Ascus with ascospores and cylindrical paraphyses. – Figs. 1, 2 from BPI 624133; Fig. 3 from BPI 624132. – Figs. 1–3: DIC. – Figs. 1, 2: 100% lactic acid; 3: water. – Scale bars: 1 = 100 µm; 2, 3 = 50 µm.

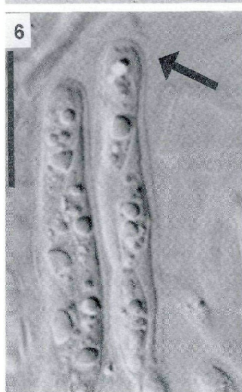


perithecial apex is formed of a palisade of distinct hyphal elements that terminate at a single level to form a truncate perithecial apex. Ascospores are ellipsoidal, gray-brown and have an inconspicuous pore at one or both ends. Anamorphs are typically holoblastic-tretic (*Diplococcium*). The peridium, ascus and ascospore anatomy of the Helminthosphaeriaceae is illustrated for *Helminthosphaeria* by Samuels & al. (1997). On the basis of these characters, *Chaetosphaeria* does not appear to belong to the Helminthosphaeriaceae.

It is more difficult to distinguish *Chaetosphaeria* from *Trichosphaeria*. Barr included the latter genus in the Trichosphaeriaceae. Perithecia in *Trichosphaeria pilosa* (Pers.: Fr.) Fuckel, the type of the genus, are small, black, setose and have a peridium 15–25 µm wide, but the upper part of the peridium around the ostiolum tends to be wider and comprises darker cells that have opaque contents, whereas the peridium at the perithecial base tends to be much thinner and is only lightly pigmented, comprising small brick-like cells (Fig. 10). Setae are always present on perithecia of *Trichosphaeria* and are always short (<25 µm long), thick-walled, aseptate, acute and are never conidigenous. Setae are not associated with the anamorphs. Periphyses of *Trichosphaeria pilosa* arise from a meristem of thin-walled cells in the perithecial apex that is distinct from a meristem from which the paraphyses arise (Fig. 10). Paraphyses arise among asci; they are cylindrical, infrequently branched, anastomosing and septate (Figs. 8, 13c). Ascospores are ellipsoidal and non-septate (Figs. 9, 13c). The few known anamorphs of the Trichosphaeriaceae have holoblastic-denticulate conidigenous cells (*Rhamphoria*, Müller & Samuels, 1982a).

Despite superficial similarities, we do not believe that *Chaetosphaeria* is closely related to *Trichosphaeria*. The phialidic anamorphs, at least, suggest to us a closer relationship of *Chaetosphaeria* to *Lasiosphaeria* and the Lasiosphaeriaceae than to *Trichosphaeria* and the Trichosphaeriaceae. *Chaetosphaeria*, however, cannot be accommodated in the Lasiosphaeriaceae or in any other family that is known to us. We note with regret the invalidly proposed family Chaetosphaeriaceae M. V. Locq. Although Locquin (1984) did not discuss the basis for the family that he proposed, and

Figs. 4–7. – 4. *Lasiosphaeria ovina*. – 5, 6. *Chaetosphaeria callimorpha*. – 7. *Trichosphaeria pilosa*. – 4. Ascus containing ascospores, arrow indicates the ascial apex containing a plasmatic globule. – 5. Asci with ascospores and paraphyses, arrow indicates tapering paraphyses. – 6. Ascial apex, arrow indicates the top that lack a plasmatic globule. – 7. Ascial apices, arrow indicates the top with a distinct apical annulus. – Fig. 4 from BPI 624132; Figs 5, 6 from BPI 744743; Fig. 7 from BPI 600294. – Figs. 4–7: DIC. – Figs. 4–6: water; 7: 1% (aq.) phloxine. – Scale bars: 4 = 50 µm; 5, 6 = 20 µm; 7 = 10 µm.



although we do not accept most of the genera that he included in it, we do acknowledge the need for the family. Thus, we propose below the new family, Chaetosphaeriaceae in the order Sordariales.

Material and methods

Dry specimens were rehydrated in 3% (aq.) KOH and the mounts were then flooded with water. Photographs were taken of ascospores, asci mounted in water mounts or 1% (aq.) phloxine. Photographs of perithecial sections were taken from material mounted in 100% lactic acid. Two types of microscopy were used in this study. These are indicated in the legends to the illustrations as bright field (BF) and differential interference contrast (DIC).

The characteristics for the narrowly delimited Lasiosphaeriaceae and its core genera are illustrated by *Lasiosphaeria ovina* (Pers.: Fr.) Ces. & de Not. (BPI 624132, BPI 624133; Figs. 1–4, 13a), the type species of *Lasiosphaeria*; for *Chaetosphaeria* and the Chaetosphaeriaceae by *Chaetosphaeria callimorpha* (Mont.) Sacc. (BPI 744743; Figs. 5, 6, 11, 12, 13b) and for *Trichosphaeria* and the Trichosphaeriaceae by *Trichosphaeria pilosa*, the type of the genus (BPI 600294; Figs. 7–10, 13c).

Taxonomic part

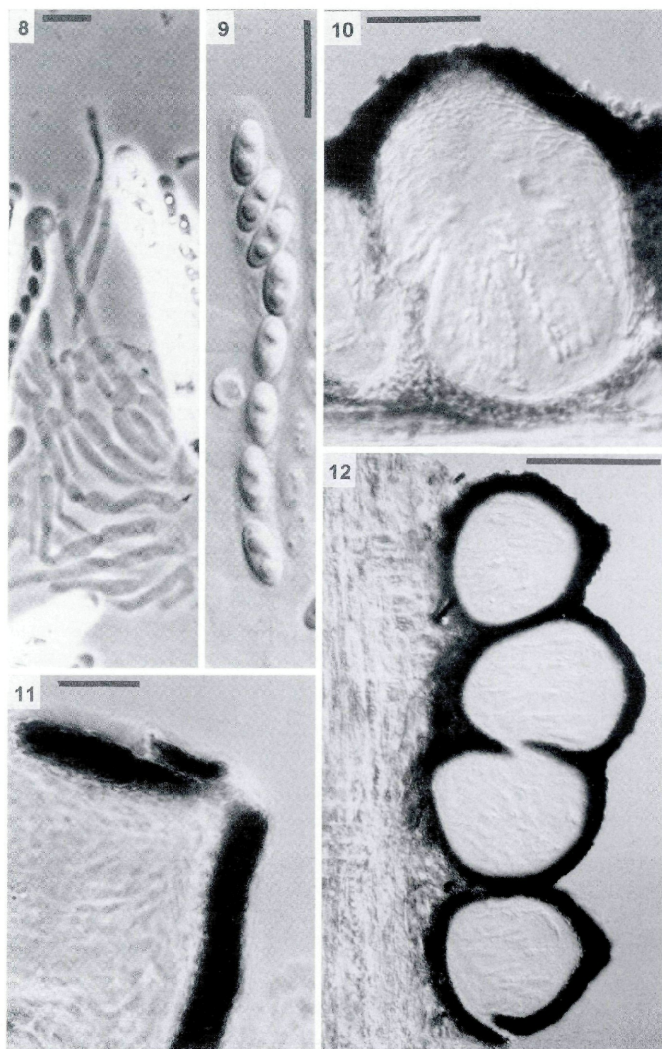
Chaetosphaeriaceae Réblová, M.E. Barr & Samuels, fam. nov.

Perithecia superficialia vel basi immersa, stromate basali vel subiculo sparso vel subiculo nullo insidentia, glabra vel setosa, non collabescentia, apice a peridio haud divergente. Pariete ascomatibus fragili, 2–3-stratoso. Periphyses atque paraphyses adsunt. Asci unitunicati, 8-sporei, annulo apicali J-, refractivo praediti. Ascospores septatae, hyalinae, bicoloratae vel totae obscure coloratae. Anamorphosis: conidiis modo enteroblastico-phialidico orientibus.

Genus typicum. – *Chaetosphaeria* Tul. & C. Tul., Sel. Fung. Carp. 2: 253, 1863.

Perithecia superficial or basally immersed, on a thin basal stroma or on a sparse subiculum or the subiculum is lacking, globose, subglobose to conical, 100–350 µm wide and 100–450 µm high,

Figs. 8–12. – 8–10. *Trichosphaeria pilosa*. – 11, 12. *Chaetosphaeria callimorpha*. – 8. Branching and anastomosing paraphyses. – 9. Ascus containing ascospores. – 10. Longitudinal section of perithecium, note the ostiolar canal lined with paraphyses. – 11. Perithecial apex, note the ostiolar canal lined with paraphyses. – 12. Longitudinal section of a group of perithecia. – Figs 8–10 from BPI 600294; Figs. 11, 12 from BPI 744743. – Figs 8, 11: BF; 9, 10, 12: DIC. – Figs. 8: water; 9: 1% (aq.) phloxine; 10–12: 100% lactic acid. – Scale bars: 8, 9 = 10 µm; 10 = 50 µm; 11 = 20 µm, 12 = 100 µm.



papillate, glabrous or setose, perithecial apex not differentiated from the rest of the peridium. – Peridium thin, fragile, usually comprising two layers, the outer layer of thin-walled, brown, opaque brick-like cells or of cells that form a network (*textura epidermoidea*), the inner layer of non-pigmented, flattened cells, occasionally a third brightly colored layer is formed on the outside of the dark layer, it comprises either cells that disintegrate at the surface or interwoven hyphae that form a compact cover. – Ostiolar canal periphysate, periphyses formed from the same meristem as the paraphyses. – Paraphyses abundant, tapering or cylindrical. – Asci unitunicate, 8-spored, ascus apex J-, apical ring pronounced, refractive. – Ascospores transversely septate, ellipsoidal to fusiform, non-fragmenting or fragmenting into part spores, dark pigmented or hyaline or becoming dark colored in part, germinating by germ tubes. – Anamorphs with enteroblastic-phialidic conidiogenesis.

Type genus. – *Chaetosphaeria* Tul. & C. Tul., Sel. Fung. Carp. 2: 253, 1863.

Key to genera of the Chaetosphaeriaceae

1. Ascospores versicolored, the middle cells becoming brown, the end cells remaining hyaline 2
1. Ascospores completely hyaline or brown 3
2. Ascospores with 3 transverse septa, smooth; perithecia setose; setae dark, acute; peridium two-layered; *Dictyochaeta* anamorph *Ascocodinaea*
2. Ascospores with 3–5 transverse septa, smooth or verrucose; perithecia setose; setae capitate; peridium three-layered; *Sporoschisma* and *Chalara* synanamorphs *Melanochaeta*
3. Ascospores hyaline, germ pores not pronounced; perithecia glabrous or setose; peridium two-layered 4
3. Ascospores brown, germ pores pronounced; perithecia glabrous, peridium two- or three-layered 5
4. Ascospores 1-septate, disarticulating into parts; *Chloridium* and *Gonytrichum* anamorphs *Melanopsammella*
4. Ascospores 1–3-septate, not fragmenting; *Catenularia*, *Cylindrotrichum*, *Chalara*, *Chloridium*, *Custingophora*, *Dictyo-*

Fig. 13a–c. – a. *Lasiosphaeria ovina*. – b. *Chaetosphaeria callimorpha*. – c. *Trichosphaeria pilosa*. – a–c. Ascus with ascospores and paraphyses. – a from BPI 624132; b from BPI 744743; c from BPI 600294. – Scale bars: a–c = 10 µm.



- chaeta*, *Menispora*, *Phialophora* and *Zanclospora* anamorphs *Chaetosphaeria*
5. Ascospores 3-septate, smooth, germ pores at each end, peridium three-layered; *Sporoschismopsis* anamorph .. *Porosphaerellopsis*
5. Ascospores 1-septate, peridium two-layered 6
6. Ascospores striate, germ pore in the median septum; *Dictyochaeta* anamorph *Striatosphaeria*
6. Ascospores smooth, germ pores at both ends; *Cordana* anamorph *Porosphaerella*
1. **Ascocodinaea** Samuels, Candoussau & Magni, Mycologia 89: 156, 1997.

Perithecia superficial, basally immersed on hymenium of old aphyllorphaceous basidiomata, setose; setae brown, acute, thick-walled, never conidiogenous, covering the upper part of the perithecia and also arising on the substratum among the conidiophores. – Peridium two-layered, the region around the ostiolum can be formed of enlarged cells arranged in files (*A. stericola*) or the upper part of lateral perithecial wall having a \pm hyphal appearance (*A. polyporicola*). – Ostiolar canal periphysate. – Paraphyses abundant, cylindrical, branching, anastomosing. – Asci 8-spored, apical annulus thin, pierced by a pore. – Ascospores ellipsoidal with narrow ends, with 3 transverse septa, versicolored, smooth.

Fungicolous ascomycetes on the hymenium surface of old basidiomata of Aphyllorphales.

Anamorph. – *Dictyochaeta*.

Accepted species. – *A. polyporicola* Samuels & al., *A. stericola* Samuels & al.

References. – Samuels & al. (1997).

The character of the upper part of the perithecium of *A. stericola* is unusual in the Chaetosphaeriaceae and suggests the apex of the perithecium of *Helminthosphaeria* species that is formed of diverging, thick-walled hyphal elements. However, the apex in the Helminthosphaeriaceae is always truncate because the hyphae grow to the same level. Despite the atypical peridium characters of *A. stericola*, the genus *Ascocodinaea* is placed in the Chaetosphaeriaceae based on the asci, ascospores and perithecial anatomy and the enteroblastic *Dictyochaeta* anamorph.

2. ***Chaetosphaeria*** Tul. & C. Tul., Sel. Fung. Carp. 2: 252, 1863.
= *Zignoëlla* Sacc., *Michelia* 1: 346, 1878.

Perithecia superficial, non-stromatic or basally immersed in a thin basal stroma, conical, globose to subglobose, papillate, glabrous or covered by setae of the associated anamorph. – *Peridium* two-layered, brittle, narrow, ca. 15 µm wide, the outer layer comprising thin-walled, brown, opaque brick-like cells or small cells that form a network (*textura epidermoidea*), the inner layer comprising thin-walled, non-pigmented, flattened cells. – *Perithecial* apex not differentiated from the rest of the perithecium. – *Ostiole* canal periphysate. – *Paraphyses* abundant, cylindrical, septate, branching, anastomosing, apically free, tend to be wider in the lower part and to taper towards the top, arising from the inner layer of the peridium. – *Asci* unitunicate, 8-spored, thin-walled, cylindrical clavate, short stipitate. The ascus apex non-amyloid; the apical annulus small, distinct and refractive, a plasmatic globule never present. – *Ascospores* generally hyaline, 1–3 transversely septate, narrowly to broadly ellipsoidal with narrow or broadly rounded ends, germinating by germ tube.

Lignicolous ascomycetes on decaying wood or inner side of rotten bark of deciduous and coniferous trees and shrubs. The genus is cosmopolitan in distribution but is more common in temperate zones.

Anamorphs. – *Catenularia*, *Cylindrotricum*, *Chalara*, *Chloridium*, *Custingophora*, *Dictyochaeta*, *Menispora*, *Phialophora* and *Zanclospora*.

Accepted species. – *C. abietis* (Höhnelt) W. Gams & Hol.-Jech., *C. aspergilloides* M. E. Barr & Crane, *C. aterrима* (Fuckel) Réblová, *C. barbicineta* (Ellis & Everh.) M. E. Barr, *C. bramleyi* C. Booth, *C. brevispora* Shoemaker, *C. callimorpha* (Mont.) Sacc., *C. chalaroides* Hol.-Jech., *C. cubensis* Hol.-Jech., *C. cupulifera* (Berk. & Broome) Sacc., *C. dingleyae* S. Hughes & al., *C. innumera* Tul. & C. Tul., *C. fusiformis* W. Gams & Hol.-Jech., *C. lentomita* W. Gams & Hol.-Jech., *C. montana* Réblová, *C. myriocarpa* C. Booth, *C. novae-zelandiae* S. Hughes & Shoemaker, *C. ovoidea* (Fr.) Constant. & al., *C. pulchriseta* S. Hughes & al., *C. pulviscula* (Currey) C. Booth, *C. pygmaea* (P. Karst.) Constant. & al. and *C. talbotii* S. Hughes & al.

References. – Barr (1991); Barr & Crane (1979); Booth (1957, 1958); Constantinescu & al. (1995); Gams & Holubová-Jechová

(1976); Holubová-Jechová (1973); Hughes (1965); Hughes & Kendrick (1968); Müller & von Arx (1962); Réblová (1998a,b).

Zignoëlla became the generic synonym of *Chaetosphaeria* when Booth (1957) transferred *Z. pulviscula* (Currey) Sacc., the type of the generic name *Zignoëlla* (Clements & Shear, 1931), to *Chaetosphaeria*. Müller & von Arx (1962) included in the synonymy of *Chaetosphaeria* another six generic names, viz. *Chaetolentomita* Maubl., *Didymopsamma* Petr., *Lentomita* Niessl, *Melanopsamma* Niessl, *Montemartinia* Curzi and *Urnularia* P. Karst. None of these generic names proposed by Müller & von Arx (1962) are accepted as synonyms of *Chaetosphaeria* by the present authors for they have no affinity with either *Chaetosphaeria* or the *Chaetosphaeriaceae*.

Similar to *Lasiosphaeria*, the periphyses that line the ostiolar canal appear to be a continuation of the paraphyses rather than to arise from a distinct plexus such as is found in many other pyrenomyces (e.g. *Hypocrea*, Hanlin, 1965, or *Trichosphaeria*, Samuels, unpublished observations). The perithecial apex, as in *Lasiosphaeria*, is not formed of distinct hyphal elements or otherwise differentiated from the rest of the peridium.

The perithecia are typically glabrous, but when the setae are present they belong to the anamorphs and are associated with the conidiophores arising from the perithecial surface and from the substratum surface, e.g. *Dictyochaeta* and *Catenularia*. In *Dictyochaeta* the apical cell of setae can be acute, dark brown, opaque and is never conidiogenous (*C. pulchriseta*) or it is blunt at the top and lighter in color than the other cells of the setae and may develop into a thin-walled, hyaline phialide (*C. callimorpha*, *C. montana*). Conidiophores of the *Catenularia* anamorphs of *Chaetosphaeria cubensis*, *C. cupullifera* and *C. novae-zelandiae*, are typically associated with capitate hyphae arising from the peridium surface and from the substratum among the conidiophores. Capitate hyphae are also found in the *Sporoschisma* anamorph of *Melanochaeta*.

Conidiogenous cells are enteroblastic, phialidic, terminal, usually cylindrical, thick-walled and darker in the lower part, paler (*Chalara*) or even hyaline to subhyaline (*Cylindrotrichum*, *Dictyochaeta*) in the upper part, ending in a shallow (*Cylindrotrichum*, *Chloridium virescens*) or deep (*Catenularia*, *Chalara*, *Chloridium clavaeforme*) collarette. The conidia form either by a 'ring building' process where the new wall material forms at the tip of the conidiogenous cell, or by a diffuse ring process where conidia form deeply within a long tube (Minter & al., 1983).

Based on the phialidic structure and conidium ontogeny the known anamorphs of *Chaetosphaeria* combine with the dematiaceous anamorphs of other taxa of the *Chaetosphaeriaceae* to form a

homogeneous group. Similar conidiogenesis and phialides are also typical *Cacumisporium* Preuss, which is an anamorphic member of the Chaetosphaeriaceae (Réblová & Gams, 1999).

Because species of *Chaetosphaeria* are uniform in anatomy and form of perithecia, hamathecium, asci and ascospores, it is difficult to impossible to distinguish species only through the teleomorph and in the absence of the anamorph.

We exclude four species from *Chaetosphaeria* that have 1-septate, fragmenting ascospores and transfer them to the genus *Melanopsammella*.

3. ***Melanochaeta*** Müller & al., Rev. Mycol. 33: 377, 1968.

Perithecia superficial, setose; setae capitate, arising from the whole perithecial surface, similar setae associated with conidiophores arising on the substratum. – Peridium typically three-layered, the third outer layer formed of grayish to whitish cover of densely interwoven hyphae that grow out of the median, fragile, dark layer and covers the perithecial surface except for the black, glabrous papilla. – Ostiolar canal periphysate. – Paraphyses abundant, unbranched. – Asci 8-spored, apical annulus pronounced. – Ascospores ellipsoidal with narrow ends to slightly navicular with broadly rounded ends, with 3–5-transverse septa, rarely with 1 or 2 longitudinal septa in the middle cells (*M. aotearoae*), smooth or finely roughened, versicolorous.

Lignicolous ascomycetes commonly found on decaying wood and bark in subtropical and tropical regions of Central and South America and Asia and in the temperate zones of southern hemisphere (New Zealand). In contrast, the anamorph genera are cosmopolitan in distribution.

Synanamorphs. – *Sporoschisma*, *Chalara*.

Accepted species. – *M. aotearoae* (S. Hughes) E. Müll. & al., *M. hemipsila* (Berk. & Broome) E. Müll. & al.

References. – Hughes (1966); Müller & al. (1968); Müller & Samuels (1982c); Réblová (1997).

Melanochaeta is easily distinguished from all the genera of the Chaetosphaeriaceae by the unique combination of versicolored ascospores, the bright hyphal perithecial cover, the capitate setae and the *Sporoschisma* and *Chalara* synanamorphs. Holubová-Jechová & Hennebert (1972) observed that the first phialidic conidia of *Spor-*

oschisma are formed basipetally in the cylindrical portion of the phialide, with the first conidium to mature near the top of the phialide and the last-formed conidium near the base. Following their release, subsequently formed conidia arise from a conidiogenous locus in the base of the tubular phialide. The authors reported that phialides of *Chalara*, the anamorph genus of two *Chaetosphaeria* species (Gams & Holubová-Jechová, 1976; Holubová-Jechová, 1984), are anatomically similar to those of *Sporoschisma*, and all exhibit the same pattern of conidial development, maturation and discharge.

4. ***Melanopsammella*** Höhnelt, Ann. Mycol. 17: 121, 1919.

Perithecia superficial, basally slightly immersed or seated on a thin basal stroma, subiculum lacking, globose to subglobose, papillate, glabrous or setose; setae short, dark brown, thin-walled, tapered, several septate, never conidiogenous. – Peridium two-layered. – Ostiolar canal periphysate. – Paraphyses abundant, tapering towards the apex. – Asci 8-spored, apical annulus pronounced. – Ascospores ellipsoidal with narrow ends, 1-septate, disarticulating into part-spores, hyaline, smooth or minutely roughened.

Lignicolous ascomycetes on strongly decayed wood and bark; cosmopolitan but most common in temperate zones.

Melanopsammella Höhnelt was described (Höhnelt, 1919) for lignicolous ascomycetes having dark, papillate, glabrous perithecia from which long hyphae arise at the base, a brittle peridium, narrow paraphyses, 8-spored asci and hyaline, two-celled, fragmenting ascospores. *Melanopsammella* was originally monotypic for *M. inaequalis* (Grove) Höhnelt, which has a *Gonytrichum* anamorph. Müller & von Arx (1962) included *Melanopsammella inaequalis* in *Trichosphaerella* Bomm. & al., a genus characterized by typically setose perithecia and 2-celled fragmenting ascospores. However, *Trichosphaerella*, with *T. decipiens* Bomm. & al. as its type, is a genus of the Niessliaceae Kirchst. (Hypocreales) (Samuels & Barr, 1998).

Gams & Holubová-Jechová (1976) did not accept *Melanopsammella* as an independent genus but considered it to be a section of *Chaetosphaeria* characterized by having 1-septate, fragmenting ascospores. Those authors concluded that the formation of *Chloridium* anamorphs by ascomycetes that differed only in disarticulation of ascospores was reason to synonymize the genera.

Based on the similarities in teleomorphs and anamorphs, *Melanopsammella* is certainly very closely related to *Chaetosphaeria*. We do not think that those taxa are congeneric and we prefer to separate

them based on the ascospore anatomy. We transfer four species from *Chaetosphaeria* to *Melanopsammella*.

Anamorphs. – *Chloridium*, *Gonytrichum*.

Accepted species. – *M. chloroconia*, *M. inaequalis*, *M. preussii*, *M. vermicularioides*.

Melanopsammella chloroconia (W. Gams & Hol.-Jech.) Réblová, M. E. Barr & Samuels, comb. nov.

= *Chaetosphaeria chloroconia* W. Gams & Hol.-Jech., Stud. Mycol. 13: 86, 1976. (basionym).

Anamorph. – *Gonytrichum chlamydosporium* Barron & Bhatt, Mycopath. Mycol. appl. 32: 126, 1967.

Melanopsammella inaequalis (Grove) Höhnelt, Ann. Mycol. 17: 121, 1919.

= *Eriosphaeria inaequalis* Grove, J. Bot., London 24: 132, 1886.

= *Lasiosphaeria inaequalis* (Grove) Massee, Grevillea 16: 37, 1887.

= *Trichosphaerella inaequalis* (Grove) E. Müll. in Müller & von Arx, Beitr. Kryptogamenfl. Schweiz 11(2): 575, 1962.

= *Chaetosphaeria inaequalis* (Grove) W. Gams & Hol.-Jech., Stud. Mycol. 13: 79, 1976.

Anamorph. – *Gonytrichum caesium* C. G. Nees & F. Nees, Nova Acta Acad. Leop. – Carol. Nat. Cur. 9: 244, 1818.

Melanopsammella preussii (W. Gams & Hol.-Jech.) Réblová, M. E. Barr & Samuels, comb. nov.

= *Chaetosphaeria preussii* W. Gams & Hol.-Jech., Stud. Mycol. 13: 34, 1976. (basionym).

Anamorph. – *Chloridium preussii* W. Gams & Hol.-Jech., Stud. Mycol. 13: 35, 1976.

Melanopsammella vermicularioides (Sacc. & Roum.) Réblová, M. E. Barr & Samuels, comb. nov.

= *Eriosphaeria vermicularioides* Sacc. & Roum., Rev. Mycol. 5: 235, 1883. (basionym).

= *Chaetosphaeria vermicularioides* (Sacc. & Roum.) W. Gams & Hol.-Jech., Stud. Mycol. 13: 15, 1976.

Anamorph. – *Chloridium virescens* (Pers.) W. Gams & Hol.-Jech., Stud. Mycol. 13: 17, 1976.

References. – Höhnelt (1919), Gams & Holubová-Jechová (1976), Constantinescu & al. (1995).

5. ***Porosphaerella*** E. Müll. & Samuels, Sydowia 35: 151, 1982.

Perithecia superficial, basally slightly immersed, seated on a basal stroma, globose, papillate, glabrous. – Peridium two-layered. – Ostiolar canal periphysate. – Paraphyses abundant, filiform, unbranched. – Asci 8-spored, apical annulus pronounced. – Ascospores ellipsoidal with narrowly to broadly rounded ends, 1-septate, brown, with a germ pore at each end, smooth or finely roughened.

Lignicolous ascomycetes on decaying woody substrata; known from Argentina, New Zealand, Switzerland and the Czech Republic (unpublished record, Herb. M. Réblová 1150/97).

Anamorph. – *Cordana*.

Accepted species. – *P. cordanophora* E. Müll. & Samuels, *P. setosa* Romero & Samuels.

References. – Müller & Samuels (1982b), Romero & Samuels (1991).

The anamorph of *Porosphaerella setosa* is unknown. *Cordana pauciseptata* Preuss is the only species of *Cordana* known to have a teleomorph, *P. cordanophora*. Conidiogenesis is enteroblastic. Scanning electron microscopy (Müller & Samuels, 1982b) reveals that the apex of the conidiogenous cell proliferates percurrently and that conidia are produced successively from cylindrical protrusions on the proliferated apex. There is no doubt that the conidiophore forms a phialidic collarete on the proliferated apex, although this collarete is inconspicuous. This kind of conidial development is highly suggestive of that of *Chloridium virescens*, the anamorph of *Melanopsammella vermicularioides*, and that of *Cylindrotrichum zignoëllae* (Höhnelt) W. Gams & Hol.-Jech., the anamorph of *Chaetosphaeria abietis* where the conidia are produced in sympodial succession on the proliferated apex of the conidiogenous cell.

6. ***Porosphaerellopsis*** Samuels & E. Müller, Sydowia 35: 143, 1982.
= *Porosphaeria* Samuels & E. Müller, Sydowia 31: 127, 1978 non *Porosphaeria* B. C. J. Dumortier, Commentaires Botaniques p.31, 1822.

Perithecia superficial, basally slightly immersed in a basal stroma, ovate, non-papillate, glabrous. – Peridium three-layered, the third superficial layer comprising hyaline to light brown cells that disintegrate at the surface. – Ostiolar canal periphysate. – Paraphyses abundant, branching, anastomosing. – Asci 8-spored, apical annulus pronounced. – Ascospores ellipsoidal with

narrow ends to fusiform, with 3 transverse septa, brown, with a germ pore at each end, smooth.

Lignicolous ascomycetes on decorticated, rotten, dicotyledoneous wood; known from Brazil only.

Anamorph. – *Sporoschismopsis*.

Accepted species. – *Porosphaerellopsis sporoschismophora* (Samuels & E. Müll.) E. Müll. & Samuels.

References. – Samuels & Müller (1978), Müller & Samuels (1982b).

The light colored cellular, disintegrating layer on the perithecial surface is unusual in the family. The light-colored surface layer of perithecia of *Melanochaeta* species is not homologous, it is formed of interwoven hyphae and is more or less easily separable from the dark middle layer.

Sporoschismopsis, the anamorph genus linked to *Porosphaerellopsis*, is superficially very similar to *Sporoschisma*, the anamorph genus linked to *Melanochaeta*. *Sporoschismopsis* is most readily distinguished from *Sporoschisma* by the absence of capitate setae, the anatomy of the conidia and by the presence of proliferating phialides (Holubová-Jechová & Hennebert, 1972). The conidia in *Sporoschismopsis* develop endogenously in basipetal succession at the apical end of the stalked phialide. According to Holubová-Jechová & Hennebert (1972), *Sporoschismopsis* is more closely related to *Catenularia* than to *Sporoschisma* because of the same successive proliferation of the phialides and conidial ontogeny. Three *Catenularia* species are known to be the anamorphs of *Chaetosphaeria*, viz. the type species *Cat. cuneiformis* (Richon) Mason anamorph of *Chaet. cupulifera* (Booth, 1958; Hughes, 1965), *Cat. cubensis* anamorph of *Chaet. cubensis* (Holubová-Jechová, 1982) and the *Catenularia* anamorph of *Chaet. novae-zelandiae* (Hughes, 1965). Analogous conidial ontogeny found in *Sporoschismopsis* and *Catenularia* is also characteristic of *Chloridium*, e.g. *Chl. claviforme* (Preuss) W. Gams & Hol.-Jech., the anamorph of *Chaet. myriocarpa* (Booth, 1957; Gams & Holubová-Jechová, 1976), and *Phialophora*, e.g. *P. phaeophora* W. Gams the anamorph of *Chaet. pygmaea* (Constantinescu & al., 1995).

7. *Striatosphaeria* Samuels & E. Müll., Sydowia 31: 132, 1978.

Perithecia superficial, basally slightly immersed in a basal stroma, ovate to obpyriform, apex acute, glabrous. – Peridium two-layered. – Ostiolar canal periphysate. – Paraphyses

abundant, cylindrical, unbranched. – Asci unitunicate, 8-spored, apical annulus pronounced. – Ascospores ellipsoidal with narrowly rounded ends, 1-septate, with a germ pore in the median septum, brown, with longitudinal dark ridges running the entire length of the ascospore.

Lignicolous ascomycetes on bark of dead angiospermous trees; known from Brazil and Puerto Rico (unpublished record, Herb. M. Réblová 1230/98).

Anamorph. – *Dictyochoeta*.

Accepted species. – *Striatosphaeria codinaeophora* Samuels & E. Müll.

References. – Samuels & Müller (1978).

The *Dictyochoeta* anamorph suggests a relationship of *Striatosphaeria* with *Chaetosphaeria* and *Ascocodinaea*. *Chaetosphaeria* is distinguished from *Striatosphaeria* by hyaline, several-septate, smooth or finely verruculose ascospores. Five species of *Chaetosphaeria* are known to produce *Dictyochoeta* anamorph (Hughes & Kendrick, 1968; Réblová, 1998). *Ascocodinaea* differs in having 3-septate, versicolored ascospores and in occurring on the hymenium of old basidiocarps of Aphyllophorales.

The longitudinally furrowed, brown ascospores with a pore in the median septum is a distinctive character of the genus. Similar ascospores are not known in other members of the Chaetosphaeriaceae.

Acknowledgments

We wish to thank Dr. Mirko Svrček for providing the Latin diagnosis.

References

- Barr, M. E. (1990). Prodrum to nonlichenized, pyrenomycetous members of class Hymenoascomycetes. – Mycotaxon 39: 43–184.
— (1991). Redisposition of some taxa described by J. B. Ellis. – Mycotaxon 46: 45–76.
— & J. L. Crane (1979). Another conidial state for a species of *Chaetosphaeria*. – Canad. J. Bot. 57: 835–837.
Booth, C. (1957). Studies on pyrenomycetes I. and II. – Mycol. Pap. 68: 1–27.
— (1958). The genera *Chaetosphaeria* and *Thaxteria* in Britain. – Naturalist 1958: 83–90.
Clements, F. E. & C. L. Shear (1931). The genera of fungi. – New York, 496 pp.

- Constantinescu, O., K. Holm & L. Holm (1995). Teleomorph-anamorph connections in Ascomycetes: anamorphs of three species of *Chaetosphaeria*. – Mycol. Res. 99: 585–592.
- Eriksson, O. E. & D. L. Hawksworth (1993). Outline of the Ascomycetes – 1993. – Syst. Ascom. 12: 51–257.
- Fuckel, L. (1870). Symbolae Mycologicae. – Jahrb. Nassauischen Ver. Naturk. 23–24: 1–459.
- Gams, W. & V. Holubová-Jechová (1976). *Chloridium* and some other dematiaceous hyphomycetes growing on decaying wood. – Stud. Mycol. 13: 1–99.
- Greuter, W. & al. (1994). International Code of Botanical Nomenclature. – Reg. Veg. 131: [1–18], 1–389.
- Grove, W. B. (1886). New or noteworthy fungi 3. – J. Bot. Brit. Foreign 24: 129–137.
- Hanlin, R. T. (1965). Morphology of *Hypocrea schweinitzii*. – Amer. J. Bot. 52: 570–579.
- Hawksworth, D. L. & J. C. David (1989). Family names. Index of Fungi Suppl. – C.A.B. International. Wallingford, U.K.
- Holubová-Jechová, V. (1973). Lignicolous hyphomycetes from Czechoslovakia 4. *Menispora*. – Folia Geobot. Phytotax. 8: 317–336.
- (1982). New or interesting phialidic hyphomycetes from Cuba. – Mycotaxon 15: 277–292.
- (1984). Lignicolous hyphomycetes from Czechoslovakia 7. *Chalara*, *Erochalara*, *Fusichalara* and *Dictyochaeta*. – Folia Geobot. Phytotax. 19: 387–438.
- & G. L. Hennebert (1972). *Sporoschismopsis*, a new genus of lignicolous Hyphomycetes. – Bull. Jard. Bot. Nat. Belg. 42: 385–391.
- Höhnelt, F. von (1919). Mykologische Fragmente. – Ann. Mycol. 17: 114–133.
- Hughes, S. J. (1965). New Zealand fungi 3. *Catenularia* Grove. – New Zealand J. Bot. 3: 136–150.
- (1966). New Zealand fungi 6. *Sporoschisma* Berk. – New Zealand J. Bot. 4: 77–85.
- & W. B. Kendrick (1968). New Zealand fungi 12. *Menispora*, *Codinaea*, *Menisporopsis*. – New Zealand J. Bot. 6: 323–375.
- Lanier, L., P. Bodoux, P. Joly & A. Bellemère (1978). Mycologie et pathologie forestières. I. Mycologie forestière. – Masson, Paris.
- Locquin, M. V. (1984). Mycologie Générale et Structurale. – Masson, Paris.
- Lundqvist, N. (1972). Nordic Sordariaceae s. lat. – Symb. Bot. Upsal. 20: 1–374.
- Minter, D. W., P. M. Kirk & B. C. Sutton (1983). Thallic phialides. – Trans. Brit. Mycol. Soc. 80: 39–66.
- Mouchacca, J. & W. Gams (1993). The hyphomycete genus *Cladorrhinum* and its teleomorph connections. – Mycotaxon 48: 415–440.
- Müller, E. & J. A. Arx von (1962). Die Gattungen der didymosporen Pyrenomyceten. – Beitr. Krypt.-Fl. Schweiz 11(2): 1–922.
- , J. Harr & P. Sulmont (1968). Deux Ascomycètes dont le stade conidien présente des conidies phaeo-phragmiées endogènes. – Rev. Mycol. 33: 369–378.
- & C. Booth (1972). Generic position of *Sphaeria phaeostroma*. – Trans. Brit. Mycol. Soc. 58: 73–77. 1972.
- & G. J. Samuels (1982a). Anamorphs of pyrenomycetous Ascomycetes I. *Rhamphoria* Niessl and *Trichosphaerella* Bommer, Rousseau & Sacc. – Sydowia 35: 143–149.
- , — (1982b). Anamorphs of pyrenomycetous Ascomycetes II. *Poro-sphaerella* gen. nov. and its *Cordana* anamorph. – Sydowia 35: 150–154.
- , — (1982c). Anamorphs of pyrenomycetous Ascomycetes III. The *Sporoschisma* and *Chalara* anamorphs of *Melanochaeta aotearoae*. – Sydowia 35: 155–161.
- Munk, A. (1953). The system of Pyrenomycetes. – Dansk Bot. Arkiv 15: 1–163.

- (1957). Danish Pyrenomycetes. A preliminary flora. – Dansk Bot. Arkiv 17: 1–491.
- Nannfeldt, J. A. (1932). Studien über die Morphologie und Systematik der nichtlichenisierten inoperculaten Discomyceten. – Nova Acta Reg. Soc. Sci. Upsal., Ser. IV., 8: 1–368.
- Réblová, M. (1997). Revision and reclassification of some *Chaetosphaeria* species. – Czech Mycol. 50: 73–83.
- (1998a). A new *Chaetosphaeria* with a *Dictyochaeta* anamorph. – Czech Mycol. 50: 151–159.
- (1998b). Revision of three *Melanomma* species described by L. Fuckel. – Czech Mycol. 50: 161–179.
- & W. Gams (1999). Teleomorph-anamorph connections in Ascomycetes 1. *Cylindrotrichum* and *Cacumisporium* anamorphs of *Chaetosphaeria*. – Czech Mycol. 51: 1–40.
- Romero, A. I. & G. J. Samuels (1991). Studies on xylophilous fungi from Argentina. VI. Ascomycotina on *Eucalyptus viminalis* (Myrtaceae). – Sydowia 43: 228–248.
- Saccardo, P. A. (1883). Pyrenomyceteae. – Sylloge Fungorum omnium hucusque cognitorum 2: 1–813, Padova.
- Samuels, G. J. & E. Müller (1978). Life-History Studies of Brazilian Ascomycetes 1. Two new genera of the Sphaeriaceae having, respectively, *Sporoschisma*-like and *Codinaea* anamorphs. – Sydowia 31: 126–136.
- , F. Candoussau & F. Magni (1997). Fungicolous pyrenomycetes 2. *Ascocodinaea*, gen. nov., and reconsideration of *Litschaueria*. – Mycologia 89: 156–162.
- & M. E. Barr (1998). Notes on and additions to the Niessliaceae (Hypocreales). – Canad. J. Bot. 75: 2165–2176.
- Tulasne, L. R. & C. Tulasne (1863). Selecta Fungorum Carpologia, Vol. 2. – Paris, 319 pp.

(Manuscript accepted 27th December 1998)

ZOBODAT - www.zobodat.at

Zoologisch-Botanische Datenbank/Zoological-Botanical Database

Digitale Literatur/Digital Literature

Zeitschrift/Journal: [Sydowia](#)

Jahr/Year: 1999

Band/Volume: [51](#)

Autor(en)/Author(s): Reblova Martina, Barr Margaret E., Samuels Gary J.

Artikel/Article: [Chaetosphaeriaceae, a new family for Chaetosphaeria and its relatives. 49-70](#)