

The genus *Chaetosphaeria* and its anamorphs

Martina Réblová

Institute of Botany, Academy of Sciences, CZ–252 43 Průhonice, Czech Republic

Correspondence: <reblova@ibot.cas.cz>

Abstract: The teleomorph genus *Chaetosphaeria* is redefined and divided into four natural groups of taxa based on morphological, cultural and molecular studies. Each group includes anamorphs of several morphologically distinct, though closely related genera, and represents a certain pattern of variability. The patterns of variation, the diagnostic value of characters of the anamorph genera corresponding to each group, and the relationships among the groups are discussed in detail. Proposals are made for future systematic studies of *Chaetosphaeria* and its anamorphs. Keys to species of *Chaetosphaeria* and genera of associated anamorphs are provided.

Key words: *Chaetosphaeriaceae*, dematiaceous hyphomycetes, *Melanopsammella*, morphogenesis, life-history, systematics.

Introduction

The genus *Chaetosphaeria* Tul. & C. Tul. was introduced by Tulasne & Tulasne (1863) based on the type species, *Chaetosphaeria innumera* Berk. & Broome ex Tul. & C. Tul. About 30 species are now accepted in *Chaetosphaeria* by the present author. The genus is placed in the *Chaetosphaeriaceae*, *Sordariales* (Réblová *et al.*, 1999).

Fundamental to an understanding of the systematics of *Chaetosphaeria* is an acknowledgement that, while several species produce both perithecia and conidia, several apparently only produce conidia. Moreover, among those species for which both sexual and asexual morphs are known, species differences are more readily seen in the anamorphs than in the perithecia. Thus, the taxonomy of *Chaetosphaeria* requires knowledge of the whole life-history and recognition and documentation of patterns of variation manifested by the anamorphs. The diagnostic taxonomic value of individual morphological characters of anamorphs, particularly those of conidia and conidiogenous cells, have been discussed several times (e.g. Gams & Holubová-Jechová, 1976; Kendrick, 1980; DiCosmo *et al.*, 1983; Cabello & Arambarri, 1989; Holubová-Jechová, 1990). In this paper, the discussion of the value of particular morphological characters of anamorphs continues. Based on results from detailed morphological, cultural and

molecular studies, four natural groups can be distinguished in *Chaetosphaeria* and are outlined below.

Historical résumé and taxonomic treatment of *Chaetosphaeria*

Chaetosphaeria species are characterized by small, glabrous or setose, non-collapsed perithecia, unitunicate asci and hyaline, two- to several-celled ascospores. Although this rather simple generic concept of *Chaetosphaeria* seems clear, about 100 species have been described and classified in the genus. Most of these, however, differ in critical taxonomic characters and are incompatible with the concept initiated by Tulasne & Tulasne (1863).

Apart from the morphological characters of ascus, hamathecium and perithecium, the characters of ascospore shape, colour and septation are generally considered the main delimiting characters in ascomycete systematics (Saccardo, 1883, 1886; Barr, 1990). These criteria were very useful in a revision of *Chaetosphaeria sensu lato* and served as a background for the subdivision of the genus into three working groups of species:

(i) Species currently placed in *Chaetosphaeria sensu lato* with superficial, dark perithecia, unitunicate asci and 4–8-celled, bicolourous ascospores with brown middle cells and hyaline end-cells (twenty-eight species); the anamorphs have been classified in

Oedemium Link, *Sporidesmium* Link, and *Veramykina* Subram. Detailed partial revisions of this group were made by Müller *et al.* (1968), Müller & Booth (1972), and Rěblová (1997, 1999a–d);

(ii) Species with glabrous or setose perithecia, unitunicate asci, 2–7-celled, hyaline ascospores and anamorphs belonging to dematiaceous hyphomycetes that produce conidia on phialidic conidiogenous cells (thirty species). These species are discussed below as *Chaetosphaeria sensu stricto*;

(iii) Virtually all taxa that do not fit the concepts of either the first or the second group. A preliminary revision (Rěblová, 1997) showed that many possess bitunicate asci and some, despite a similar appearance of dark perithecia, unitunicate asci and hyaline, septate ascospores, are unrelated to *Chaetosphaeria*. This group requires further investigation.

Two other genera, *Melanomma* Nitschke ex Fuckel and *Zignoëlla* Sacc., include another ca 200 potential species (Fuckel, 1870, 1872; Saccardo, 1878, 1883, 1886), some of which might be placed in *Chaetosphaeria* after revision (Booth, 1957, 1958; Rěblová, 1998b; Rěblová & Gams, 1999).

The concept of *Chaetosphaeria sensu stricto* presented here, in accordance with the type species, is concordant with the concepts of Booth (1957, 1958), who carried out morphological, developmental and cultural studies of six *Chaetosphaeria* species found in Great Britain, namely *Chaetosphaeria bramleyi* C. Booth, *Chaet. callimorpha* (Mont.) Sacc., *Chaet. cupulifera* (Berk. & Broome) Sacc., *Chaet. innumera* sensu C. Booth (= *Chaet. lentomita* W. Gams & Hol.-Jech; Gams & Holubová-Jechová, 1976), *Chaet. myriocarpa* C. Booth (Constantinescu *et al.*, 1995) and *Chaet. pulviscula* (Currey) C. Booth. Booth (1957, 1958) reported four associated anamorph genera, viz. *Catenularia* Grove, *Chloridium* Link, *Dictyochoeta* Speg. (as *Codinaea* Maire), and *Menispora* Pers.

Müller & von Arx (1962) included *Chaetosphaeria* in their broadly conceived 'Sphaeriaceae'. They accepted seven didymosporous species of *Chaetosphaeria* and included another six generic synonyms under *Chaetosphaeria*, viz. *Chaetolentomita* Maubl., *Didymopsamma* Petr., *Lentomita* Niessl, *Melanopsamma* Niessl, *Montemartinia* Curzi, and *Urnularia* P. Karsten. No cultural studies were made by these authors, nor did they give information about associated anamorphs.

Detailed morphological and cultural studies on the dematiaceous hyphomycete genera *Dictyochoeta*, *Menispora*, *Catenularia*, and *Zancluspora* S. Hughes & W.B. Kendr., made by Hughes (1965), Hughes & Kendrick (1963, 1968) and Holubová-Jechová

(1973a, b), considerably expanded the known diversity of anamorphs and established additional teleomorph relationships within *Chaetosphaeria*.

Gams & Holubová-Jechová (1976) approached the concept of *Chaetosphaeria* from an anamorph standpoint and based their investigation on cultural studies. The authors distributed species of the anamorph genus *Chloridium* into the sections *Chloridium*, *Gongromeriza* and *Psilobotrys*, according to the structure of phialides and conidium ontogeny. They did not accept *Melanopsammella* Höhn., characterized by 1-septate ascospores that disarticulate at the septum, as an independent genus, but rather as a section of *Chaetosphaeria*, correlating with anamorphs classified in *Chloridium* section *Chloridium*. Furthermore, the dematiaceous hyphomycete genera *Cylindrotrichum* Bonord. and *Gonytrichum* C.G. Nees & F. Nees were shown by cultural studies to be anamorphs of *Chaetosphaeria* (Gams & Holubová-Jechová, 1976).

An attempt to partially solve the question of the large number of anamorph genera associated with *Chaetosphaeria* was made by DiCosmo *et al.* (1983). They emphasized the shapes of conidia and conidiogenous cells, and the distinction between mono- or polyphialides, as the main delimiting characters. DiCosmo *et al.* (1983) transferred the type species of *Cylindrotrichum*, *Cyl. oligospermum* (Corda) Bonord., to the older genus *Chaetopsis* Grev. and redispersed the other species of *Cylindrotrichum* into other genera. Thus, several closely related anamorph genera of *Chaetosphaeria* were distinguished, such as *Chaetopsis*, *Dictyochoeta*, *Kylindria* DiCosmo, Berch & W.B. Kendr. and *Xenokylindria* DiCosmo, Berch & W.B. Kendr., although they shared a number of morphological, developmental and ecological characteristics.

Cabello & Arambarri (1988) considered *Cylindrotrichum* a distinct genus, which they reinstated based on *Cyl. oligospermum*. They misunderstood the proposal made by DiCosmo *et al.* (1983) to adopt the older genus *Chaetopsis* with *Cylindrotrichum* as its generic synonym, incorrectly suggesting that the proposal was nomenclaturally contrary to Art. 52 of the Botanical Code 1983. Cabello & Arambarri (1988) reamalgamated species previously placed in *Cylindrotrichum* into a single genus, but considered neither phylogeny nor links to teleomorphs.

Constantinescu *et al.* (1995) emphasized the significance of cultural studies as one possible way to identify indistinguishable *Chaetosphaeria* teleomorphs using their anamorphs. The authors employed cultural studies to establish the connection of *P. phaeophora* W. Gams, the anamorph of *Chaetosphaeria*

pygmaea (P. Karsten) O. Constant., K. Holm & L. Holm, with another anamorph genus, *Phialophora* Medlar; they also found a *Phialophora* sp. and *Menispora glauca* Pers. to be synanamorphs of *Chaetosphaeria ovoidea* (Fr.) O. Constant., K. Holm & L. Holm

Beside the main papers cited above, many other minor papers, dealing with *Chaetosphaeria* or chaetosphaeria-like fungi and their life-histories, have been published (e.g. Hino, 1932, 1961; Kohlmeyer, 1963; Barr & Crane, 1979; Kalani, 1964; Holubová-Jechová, 1973a, b, 1982, 1984; Fisher & Petrini, 1983; Kaur, 1991; Barr, 1993; Sivanesan & Chang, 1995, 1997; Teng, 1996; Réblová, 1998a, b; Réblová & Gams, 1999, 2000; Fernández *et al.*, 1999).

Réblová & Winka (2000) performed phylogenetic analyses on 25 representatives of *Chaetosphaeria* and eight anamorph genera. The results of their phylogenetic analyses were congruent with certain morphological features. The authors concluded that *Chaetosphaeria* and *Melanopsammella* are paraphyletic and do not represent separate genera. In the phylogenies inferred from the LSU rDNA sequence data, species of *Chaetosphaeria* formed four main groups, which are elaborated below.

Concept of *Chaetosphaeria* and its anamorphs

The concept of *Chaetosphaeria* and its anamorphs developed here is based on morphological characters, cultural studies and molecular data. Taxonomic work with *Chaetosphaeria* is complicated by problems resulting from the simple morphological characters of the teleomorphs and the frequent absence of anamorphs in herbarium material, which then must be interpreted without the benefit of cultural work or ex-type cultures.

In some cases, host specificity can be used as a differentiating character. Several species show strong host specificity, e.g. *Chaet. abietis* (Höhn.) W. Gams & Hol.-Jech. or *Chaet. fusiformis* W. Gams & Hol.-Jech. on *Abies alba*. Other examples are *Chaetosphaeria crustacea* (Sacc.) Réblová & W. Gams or *Chaet. fennica* (P. Karsten) Réblová & W. Gams, which are known exclusively from conifer wood, while their counterparts, *Chaet. decastyla* (Cooke) Réblová & W. Gams and *Chaet. acutata* Réblová & W. Gams, fruit on wood of deciduous trees only. However, their anamorphs differ considerably.

Nomenclature and synonymy

Chaetosphaeria Tul. & C. Tul., Sel. Fung. Carpol. 2: 252. 1863.

= *Zignoëlla* Sacc., *Michelia* 1: 346. 1878.

= *Melanopsammella* Höhn., *Ann. Mycol.* 17: 121. 1919.

Type: *Chaetosphaeria innumera* Berk. & Broome ex Tul. & C. Tul., Sel. Fung. Carpol. 2: 252. 1863 [non *Chaetosphaeria innumera* sensu C. Booth, *Mycol. Pap.* 68: 2. 1957 = *Chaetosphaeria lentomita* W. Gams & Hol.-Jech., *Stud. Mycol.* 13: 24. 1976].

= *Sphaeria innumera* Berk. & Broome, in Berkeley, *Outl. Br. Fungol.* p. 395. 1860 [nomen nudum, not validly published, Art. 32.1.c] = *Lasiosphaeria innumera* (Berk. & Broome ex Tul. & C. Tul.) Stevenson, *Mycol. Scot.* p. 391. 1879 = *Bysosphaeria innumera* (Berk. & Broome ex Tul. & C. Tul.) Cooke, *Grevillea* 15: 123. 1887.

Booth (1957) proposed *Zignoëlla* as a taxonomic synonym of *Chaetosphaeria* and transferred *Z. pulviscula* (Currey) Sacc., the lectotype species (Clements & Shear, 1931), to *Chaetosphaeria*.

Müller & von Arx (1962) extended the synonymy of *Chaetosphaeria* with another six generic names, including *Chaetolentomita*, *Didymopsamma*, *Lentomita*, *Melanopsamma*, *Montemartinia*, and *Urnularia*. Upon critical inspection, all these generic names with the exception of *Lentomita* (discussed below) turned out to be unrelated to *Chaetosphaeria*.

According to Müller & von Arx (1962), *Chaetolentomita lignorum* Maubl., the only described species of *Chaetolentomita* (Maublanc & Rangel, 1915), is synonymous with *Chaetosphaeria brasiliensis* (Höhn.) E. Müll. The type material of *Chaetolentomita lignorum* was unavailable for the present study. The type material of *Lentomita brasiliensis* Höhn. (FH 3148), on which the name *Chaetosphaeria brasiliensis* is based, has the following features: perithecia long-beaked, globose, glabrous, embedded in the host tissue with only the beak erumpent above the surface, surrounded by a hyphal mat growing from the perithecial wall; perithecial wall two-layered: outer layer rather thick, consisting of thick-walled, polyhedral cells; asci long-stipitate, floating in the centrum, provided with a large, J-, refractive apical annulus; paraphyses broadly cellular, deliquescent; ascospores 2-celled, fusiform and hyaline. No associated anamorph was found. This fungus has no affinity to *Chaetosphaeria* or other genera of the *Chaetosphaeriaceae* and should be classified in *Ceratostomella* Sacc. (*Clypeosphaeriaceae*).

Didymopsamma moravica Petr., the only described species of *Didymopsamma* (Petraik, 1925), was synonymized with *Chaetosphaeria brevicollis* (Niessl) E. Müll. (Müller & von Arx, 1962). Exami-

nation of the type material of *D. moravica* (PRM 17364) revealed that ascomata are semi-immersed, glabrous, subglobose; ascomatal wall very thick (33–44 µm), consisting of thick-walled, polyhedral cells, heavily pigmented in the outer part; hamathecium consisting of interthelial filaments that are sparsely distributed among the asci and deliquescing early; periphysoids abundant; asci conspicuously thickened at the top, without any visible discharge mechanism; ascospores 2-celled, ellipsoidal and hyaline. No associated anamorph was found. This fungus has no affinity with *Chaetosphaeria* and the *Chaetosphaeriaceae*. I am still uncertain about its position among the pyrenomycetous ascomycetes.

Lentomita brevicollis Niessl, the type of the generic name *Lentomita* (Niessl, 1876), was transferred by Müller & von Arx (1962) to *Chaetosphaeria*, as *Chaet. brevicollis* (Niessl) E. Müll. The type material from Niessl's original herbarium could not be located at M (Gams & Holubová-Jechová, 1976), or by the present author at BRU or OP. Gams & Holubová-Jechová (1976) described *Chaetosphaeria lentomita*, a species with ascospore size similar to *Lentomita brevicollis*. These authors chose the generic name *Lentomita* for the epithet of their new species. Judging from the protologue of *L. brevicollis*, it could be a member of *Chaetosphaeria*. I agree with conclusions made by Gams & Holubová-Jechová (1976).

Melanopsamma (Niessl, 1876) is a member of the *Niessliaceae* (Barr, 1990; Samuels & Barr, 1997). The genus is easily distinguished from *Chaetosphaeria* by its glabrous, collapsing perithecia, reddish-brown, three-layered perithecial wall, the presence of periphysoides and its *Stachybotrys* Corda anamorph.

The type material of *Montemartinia myriadea* Curzi (1926), the type of its genus, was unavailable for the present study. *Montemartinia myriadea* was placed in *Chaetosphaeria*, as *Chaet. myriadea* (Curzi) E. Müll. (Müller & von Arx, 1962). In the protologue of *M. myriadea*, the ascomata are described as globose, glabrous, sitting in a hyphal subiculum; paraphyses lacking; asci cylindrical, 35–45 × 3–4 µm, ascospores ellipsoidal, 3.5–4.5 × 2–2.5 µm, 2-celled and hyaline. Curzi (1926) described the associated anamorph as belonging to *Ramularia* Unger, a hyphomycete genus now generally associated with teleomorphs in *Mycosphaerella* Johanson. If *M. myriadea* were accepted as a member of *Chaetosphaeria*, it would be clearly distinct from other species in size of asci and ascospores. I hesitate to accept *Montemartinia* as a generic synonym of *Chaetosphaeria* without examining type material.

Müller & Arx (1962) also synonymized *Urnularia* with *Chaetosphaeria*. The reference to *Ur-*

nularia was based on a citation of a different fungus, described by Ellis & Everhart (1893) as *Melanopsamma borealis* Ellis & Everh., made by Saccardo (Saccardo in Mussat, 1901). *Urnularia boreëlla* P. Karsten (Karsten, 1866), the type of the genus, was placed by Karsten in the family 'Phacidiacei', and later synonymized with *Valsa boreëlla* (P. Karsten) Ellis & Everh. by Ellis & Everhart (1892).

Réblová *et al.* (1999) separated *Melanopsammella* from *Chaetosphaeria* on the basis of ascospore morphology and restricted it to species with ascospores that fragment into part-spores at an early stage within the ascus. According to large subunit rDNA sequences (Réblová & Winka, 2000), species of *Melanopsammella* did not separate clearly from the rest of *Chaetosphaeria* species. The character of fragmenting ascospores, formerly considered to separate these taxa (Réblová *et al.*, 1999), is probably insufficient for their delimitation at generic level. Therefore, *Melanopsammella* should be treated as a heterotypic generic synonym of *Chaetosphaeria*.

Taxonomy

Morphology of *Chaetosphaeria sensu stricto*

TELEOMORPH

Perithecia superficial, non-stromatic or immersed at the base in a thin, superficial stroma, conical, globose to subglobose, papillate, glabrous, occasionally covered with sterile perithecial setae or setae that are similar to those found on the substratum in association with conidiophores, which may be sterile or may end in a mono- or polyphialide. Perithecial wall two-layered, brittle, narrow, ca 15–25 µm thick, the outer layer comprising thin-walled, brown, opaque, brick-like cells or small cells with some tendency to form a *textura epidermoidea*, the inner layer comprising thin-walled, non-pigmented, flattened cells. Perithecial apex not differentiated from the rest of the perithecium. Ostiolar canal periphysate. Hamathecium consisting of abundant, septate, branching, anastomosing, apically free paraphyses that tend to be wider in the lower part and to taper distally, arising from the inner layer of the perithecial wall. Asci unitunicate, 8-spored, thin-walled, cylindrical-clavate, short-stipitate. The ascus apex with an inamyloid (J–), refractive apical annulus; plasmatic globule characteristic of the *Lasio-sphaeriaceae* never present. Ascospores generally hyaline, transversely 1–6-septate, formation of septa typically delayed, narrowly to broadly ellipsoidal with tapering or broadly rounded ends, fusiform, fusiform-cylindrical or cylindrical,

germinating by germ tube, sometimes fragmenting into part-spores.

ANAMORPH

Colonies slow-growing, velvety or felty, of different shades of grey and brown, at times zonate. Aerial mycelium scant or well-developed, substrate mycelium usually well-developed; hyphae light-coloured, septate, branched, smooth or slightly rugose. Setae when present straight or slightly flexuous, cylindrical, septate, dark brown and usually paler towards the apex, rounded or pointed at the top or sometimes developing as a monophialide. Conidiophores macronematous, mononematous, solitary, erect, straight or slightly flexuous, unbranched or branched, arising from both aerial and substrate mycelium, occasionally forming two distinct layers, proliferating percurrently or sympodially. Conidiogenous cells mono- or polyphialides, lateral or integrated, terminal or intercalary, with one terminal or several lateral phialidic openings arising from sympodial elongation. Collarettes generally hyaline, more or less pronounced, their depth, shape and pigmentation varying with species. Conidia phialidic, cylindrical to clavate, wedge-shaped, reniform, falcate, setulose or lacking setulae, straight or curved, transversely 1- to multiseptate or non-septate, rounded at one or both ends, or rather asymmetrical and then tapering towards one end and truncate at the other, smooth, hyaline or bicolorous.

Anamorph genera: *Cacumisporium* Preuss, *Catenularia*, *Cylindrotrichum pro parte*, *Chalara* (Corda) Rabenh., *Chloridium*, *Dictyochaeta*, *Gonytrichum*, *Menispora*, *Phialophora*, and *Zanclospora*.

THE GROUPS OF CHAETOSPHAERIA

In a phylogenetic analysis based on large subunit rDNA sequence data, *Chaetosphaeria sensu stricto* separated into two major clades, each clade having two subclades (Réblová & Winka, 2000). These subclades coincide with certain morphological features and are regarded here as natural groups within *Chaetosphaeria*. The groups are named here informally, according to the associated anamorph genera.

The *Menispora*-group – Fig. 1

Representative species: *Chaetosphaeria brevispora* R. Shoemaker, *Chaet. dingleyae* S. Hughes, W.B. Kendr. & Shoemaker., *Chaet. montana* Réblová, *Chaet. ovoidea*, *Chaet. pulchriseta* S. Hughes, W.B. Kendr. & Shoemaker, *Chaet. pulviscula* and *Chaet. talbotii* S. Hughes, W.B. Kendr. & Shoemaker; *Striatosphaeria codinaeophora* Samuels & E. Müll.

Anamorph genera: *Menispora* Pers., Mycol. Europ. 1: 32, 1822; *Codinaea sensu stricto* Maire, Publ. Inst. Bot. Barcelona 3: 15, 1937; *Codinaeopsis* Morgan-Jones, Mycotaxon 4: 166, 1976.

Conidia oblong, fusiform, falcate, symmetrical or asymmetrical, straight or curved, hyaline or brown, septate or non-septate, usually provided with fine setulae at both ends; often forming small, slimy droplets attached at the tip of the conidiogenous cells. Conidiogenesis on a single conidiogenous locus within the collarette. Conidiogenous cells mono- or polyphialides, lateral, borne singly or in whorls, or integrated, terminal and intercalary, the distal part strongly recurved or straight; collarette narrow or flaring.

Two morphologically distinct teleomorph genera are associated with this group: *Chaetosphaeria* species possessing fusiform, 1–3-septate, hyaline, non-fragmenting ascospores. The ascospores usually range from 11–26(–29) μm in length. *Striatosphaeria* Samuels & E. Müll. species have fusiform, 1-septate, brown, non-fragmenting ascospores 23–26 μm long, with longitudinal ridges.

Most of numerous species originally described in *Codinaea* (as *Dictyochaeta* in Kuthubutheen & Nawawi, 1991) with oblong to fusiform, falcate, setulose conidia probably belong to this group. Other species of *Dictyochaeta sensu stricto* with non-setulose conidia, mono- or polyphialides integrated in the conidiophore and conidiogenesis on a single locus are discussed here as the *Gongromeriza*-group.

The morphology of conidiophores, phialides and conidia of *Dictyochaetopsis* Arambarri & Cabello and *Zanclospora* suggest affinities with this group.

The *Chloridium*-group – Fig. 2

Representative species: *Chaetosphaeria chloroconia* W. Gams & Hol.-Jech., *Chaet. inaequalis* (Höhn.) W. Gams & Hol.-Jech., and *Chaet. vermicularioides* (Sacc. & Roum.) W. Gams & Hol.-Jech.

Anamorph genera: *Chloridium* Link Mag. Ges. naturf. Freunde, Berl. 3: 13, 1809, section *Chloridium pro parte* [including the type species, *Chloridium virescens* (Pers.) W. Gams & Hol.-Jech.]; *Gonytrichum* C.G. Nees & F. Nees, Nova Acta Acad. Caes. Leop.-Carol. German. Nat. Cur. 9: 244, 1818.

Conidia small, rounded, hyaline, non-septate, without setulae. Conidiogenous cells monophialides, lateral, single or in whorls, or integrated and terminal; colla-

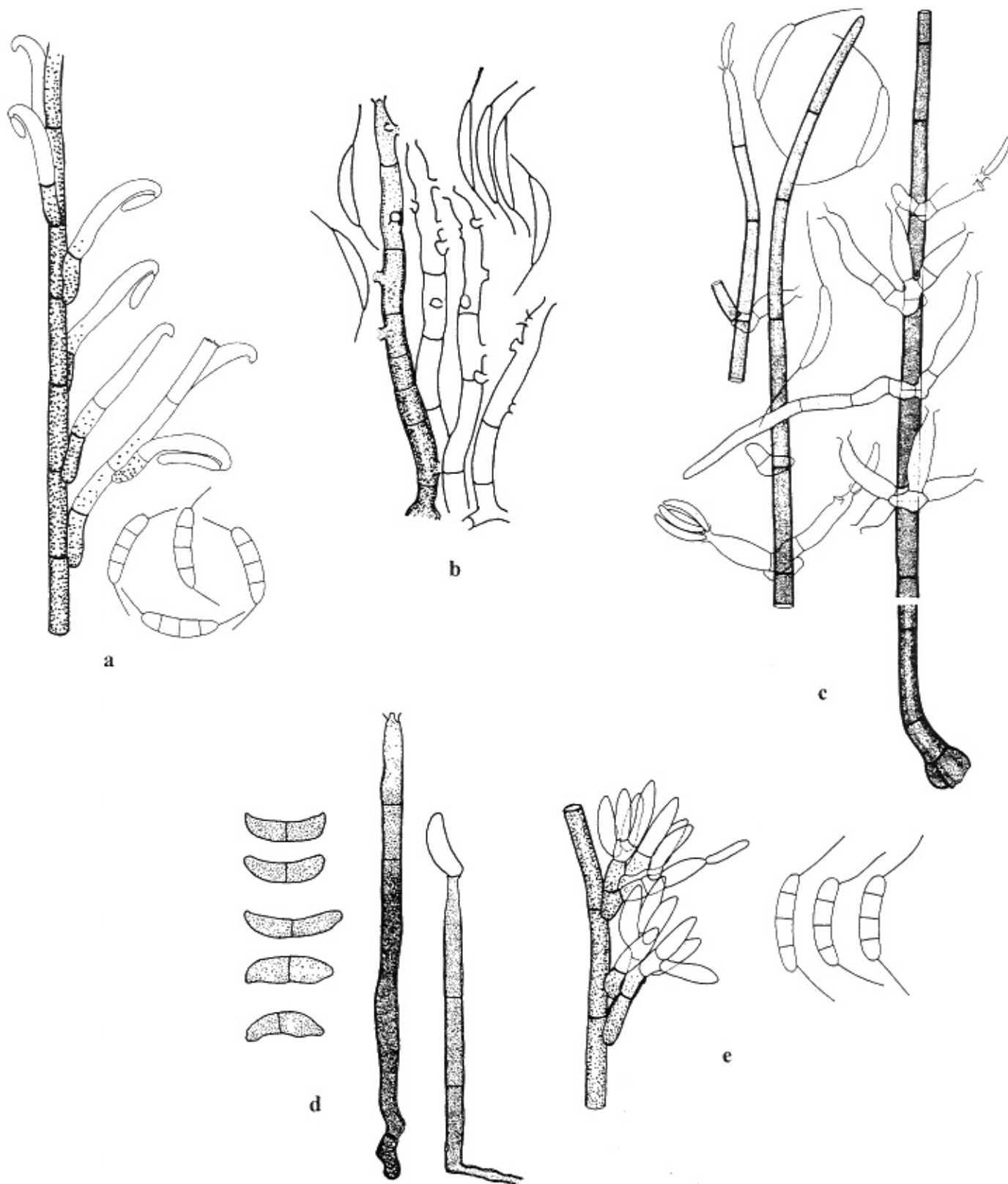
The *Menispora*-group

Fig 1. a–e. The *Menispora*-group. Habit sketch of members of the group. a. *Chaetosphaeria ovoidea* (anamorph = *Menispora glauca*); b. *Dictyochaeta simplex*; c. *Codinaeopsis gonytrichoides*; d. *Striatosphaeria codinaeophora*; e. *Menispora tortuosa* [a, e after Hughes & Kendrick (1963); b after Holubová-Jechová (1984); c after Morgan-Jones (1976); d after Samuels & Müller (1978)].

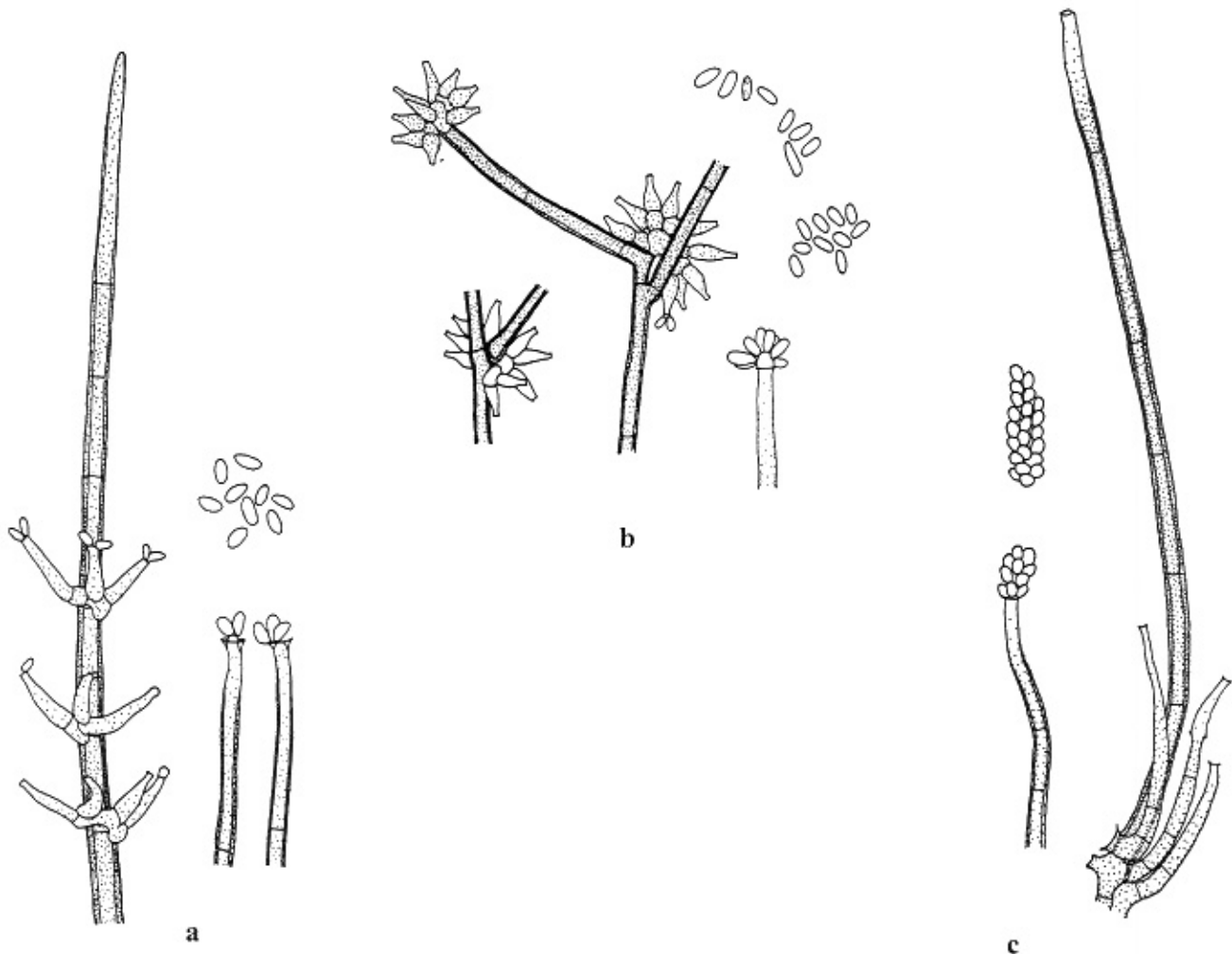
The *Chloridium*-group

Fig 2. a–c. The *Chloridium*-group. Habit sketch of members of the group. a. *Chaetosphaeria chloroconia* (anamorph = *Gonytrichum chlamydosporium* Barron & Bhatt); b. *Chaetosphaeria inaequalis* (anamorph = *Gonytrichum caesium*); c. *Chaetosphaeria vermicularioides* (anamorph = *Chloridium virescens*), [a–c after Gams & Holubová-Jechová (1976)].

rette shallow. Conidiogenesis on multiple conidiogenous loci within the collarette.

The *Chaetosphaeria* teleomorphs have ellipsoidal to short-fusiform, 1-septate, hyaline ascospores that fragment into part-spores at an early stage within the ascus. Most of these taxa would be included in the genus *Melanopsammella sensu stricto*, if generic separation were required (see Réblová & Winka, 2000). The uniting characters are conidiogenesis with multiple conidiogenous loci and fragmenting, 1-septate ascospores. Another species with sometimes fragmenting ascospores, *Chaetosphaeria preussii* W. Gams & Hol.-Jech. (anamorph *Chloridium preussii* W. Gams & Hol.-Jech.), has conidiogenesis with a

single locus and clusters with the *Gongromeriza*-group.

Although the *Chloridium*-group corresponds to the anamorph genera *Gonytrichum* and *Chloridium* section *Chloridium*, it does not comprise all species of *Chloridium* with similar conidiogenesis, e.g. the *Chloridium* anamorphs of *Chaet. crustacea*, *Chaet. fennica* and *Chaet. fusiformis*. These taxa grouped with *Cylindrotrichum* species having conidiogenesis with multiple loci and similar conidial and ascospore morphology. They are discussed below as the *Kylindria*-group.

The *Gongromeriza*-group – Fig. 3

Representative species: *Chaetosphaeria barbicineta* (Ellis & Everh.) M.E. Barr, *Chaet. bramleyi*, *Chaet. callimorpha*, *Chaet. chalaroides* Hol.-Jech., *Chaet. cupulifera*, *Chaet. cubensis* Hol.-Jech., *Chaet. dilabens* Réblová & W. Gams, *Chaet. hebetiseta* Réblová & W. Gams, *Chaet. innumera*, *Chaet. lentomita*, *Chaet. myriocarpa*, *Chaet. novaezelandiae* S. Hughes, *Chaet. preussii*, *Chaet. pygmaea*.

Anamorph genera: *Gongromeriza* Preuss, *Linnaea* 24: 106, 1851 [= *Chloridium* section *Gongromeriza* (Preuss) W. Gams & Hol.-Jech.]; *Rhinotrichum* Corda section *Psilobotrys* Sacc., *Michelia* 1: 87, 1877 [= *Chloridium* section *Psilobotrys* (Sacc.) W. Gams & Hol.-Jech.]; *Dictyochaeta sensu stricto* Speg., *Physis*, *Buenos Aires* 7: 18, 1923.

Conidia generally short-ellipsoidal, rarely fusiform to clavate, wedge-shaped or reniform, hyaline or pale brown, non-septate, without setulae. Conidiogenous cells mono- or polyphialides, integrated, terminal or intercalary, never in a lateral position on the conidiophore; collarettes narrow and short or flaring, vase- or funnel-shaped. Conidiogenesis on a single conidiogenous locus within the collarette.

The *Chaetosphaeria* teleomorphs typically have ellipsoidal to fusiform, 1–3-septate, hyaline and non-fragmenting ascospores or ascospores that fragment into part-spores; ascospores generally do not exceed 20 µm in length.

Other anamorph genera, *Catenularia* and *Chalara pro parte*, and their teleomorphs, show affinity with the *Gongromeriza*-group. Their teleomorphs are listed below.

Although this group seems to be homogeneous, some small discrepancies are evident in the literature. Hughes & Kendrick (1968), in their account of species of *Codinaea sensu lato*, illustrated an apex of the conidiogenous cell of the *Dictyochaeta* anamorph of *Chaetosphaeria callimorpha* (1968: 341, Fig. 13) and *Codinaea setosa* S. Hughes & W.B. Kendr. (1968: 359, Fig. 28) as producing conidia on multiple conidiogenous loci. However, other illustrations in that paper show only single openings. The culture of the *Dictyochaeta* anamorph of *Chaet. callimorpha* preserved in CBS (CBS 525.88) was examined and only conidium formation from a single conidiogenous locus was observed.

The *Kylindria*-group – Fig. 4

Representative species: *Chaetosphaeria abietis*, *Chaet. acutata*, *Chaet. crustacea*, *Chaet. decastyla*, *Chaet. fennica*, and *Chaet. fusiformis*.

Anamorph genera: *Cylindrotrichum* Bonord. *pro parte*, *Handb. allg. Mykol.*, p. 88, 1851 [excluding the type species, *Cylindrotrichum oligospermum* (Corda) Bonord.]; *Kylindria* DiCosmo, Berch & W.B. Kendr., *Mycologia* 75: 970, 1983; *Xenokylindria* DiCosmo, Berch & W.B. Kendrick, *Mycologia* 75: 971, 1983; *Chloridium* section *Chloridium pro parte* [without the type species].

Conidia long-ellipsoidal to cylindrical, clavate, hyaline or brown, septate or non-septate, without setulae. Conidiogenous cells mono- or polyphialides, never in a lateral position on the conidiophore, integrated, terminal or intercalary; collarettes flaring, usually shallow. Conidiogenesis on multiple conidiogenous loci within the collarette, the apex of the conidiogenous cell sometimes proliferating conspicuously above the primary collarette, e.g. in anamorphs of *Chaet. acutata*, *Chaet. decastyla* and *Chaet. fennica*.

The *Chaetosphaeria* teleomorphs have long-fusiform to cylindrical, 3–6-septate, hyaline, non-fragmenting ascospores, generally up to 46 µm long.

The genus *Cylindrotrichum* appears polyphyletic because the type species, *Cyl. oligospermum* (teleom. *Chaetosphaeria tulasneorum* Réblová & W. Gams), clustered separately in phylogenetic studies from other described *Cylindrotrichum* species (Réblová & Winka, 2000). Therefore, the character of conidium septation, currently used to distinguish *Cylindrotrichum* from *Chloridium*, did not prove to have a diagnostic value at the generic level, whereas whether the conidia are formed on multiple loci or on a single conidiogenous locus was more significant. Therefore, it seems appropriate to extend the genus *Chloridium* with the taxa formerly placed in *Cylindrotrichum*, while retaining only *Cyl. oligospermum* in this genus. The genus *Cacumisporium* seems to be a similar case. It has exactly the same characteristics of conidiogenesis on multiple conidiogenous loci with the collarette; in addition, conidia become bicolorous after liberation from the conidiogenous cells. In common with the feature of conidial septation, pigmentation also did not prove to have diagnostic value at the generic level (Réblová & Winka, 2000). Thus, *Cacumisporium* should be included in *Chloridium*. For the moment no formal combinations are proposed for reasons discussed below.

In order to choose the correct name for this group of taxa, three names were considered. *Cacumisporium* would have priority to name this group, but no species were included in the phylogenetic analysis. Two names, *Kylindria* and *Xenokylindria*, are available, with the same priority, which were originally confined to species separated from *Cylindrotrichum* (DiCosmo *et al.*, 1983). I chose the name *Kylindria*.

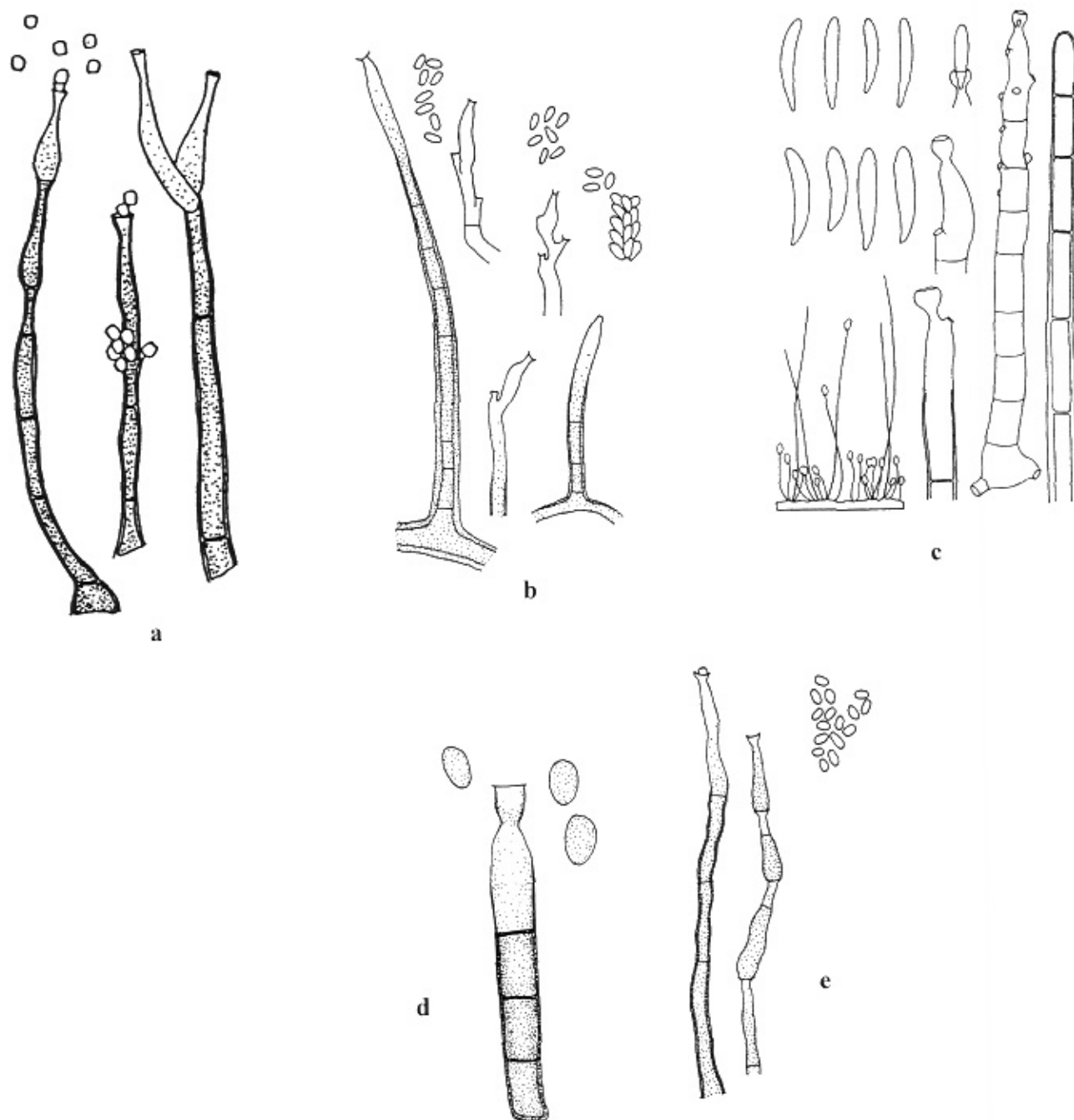
The *Gongromeriza*-group

Fig 3. a–e. The *Gongromeriza*-group. Habit sketch of selected members of the group. a. *Chaetosphaeria myriocarpa* (anamorph = *Chloridium clavaeforme*); b. *Chaetosphaeria innumera* [anamorph = *Chloridium botryoideum* (Corda) S. Hughes]; c. *Chaetosphaeriacallimorpha* (anamorph = *Dictyochaetasp.*); d. *Chaetosphaeriadilabens* (anamorph = *Chloridium* sp.); e. *Chaetosphaeria preussii* (anamorph = *Chloridium preussii*), [a, b, e after Gams & Holubová-Jechová (1976); c after Hughes & Kendrick (1968); d after Réblová & Gams (2000)].

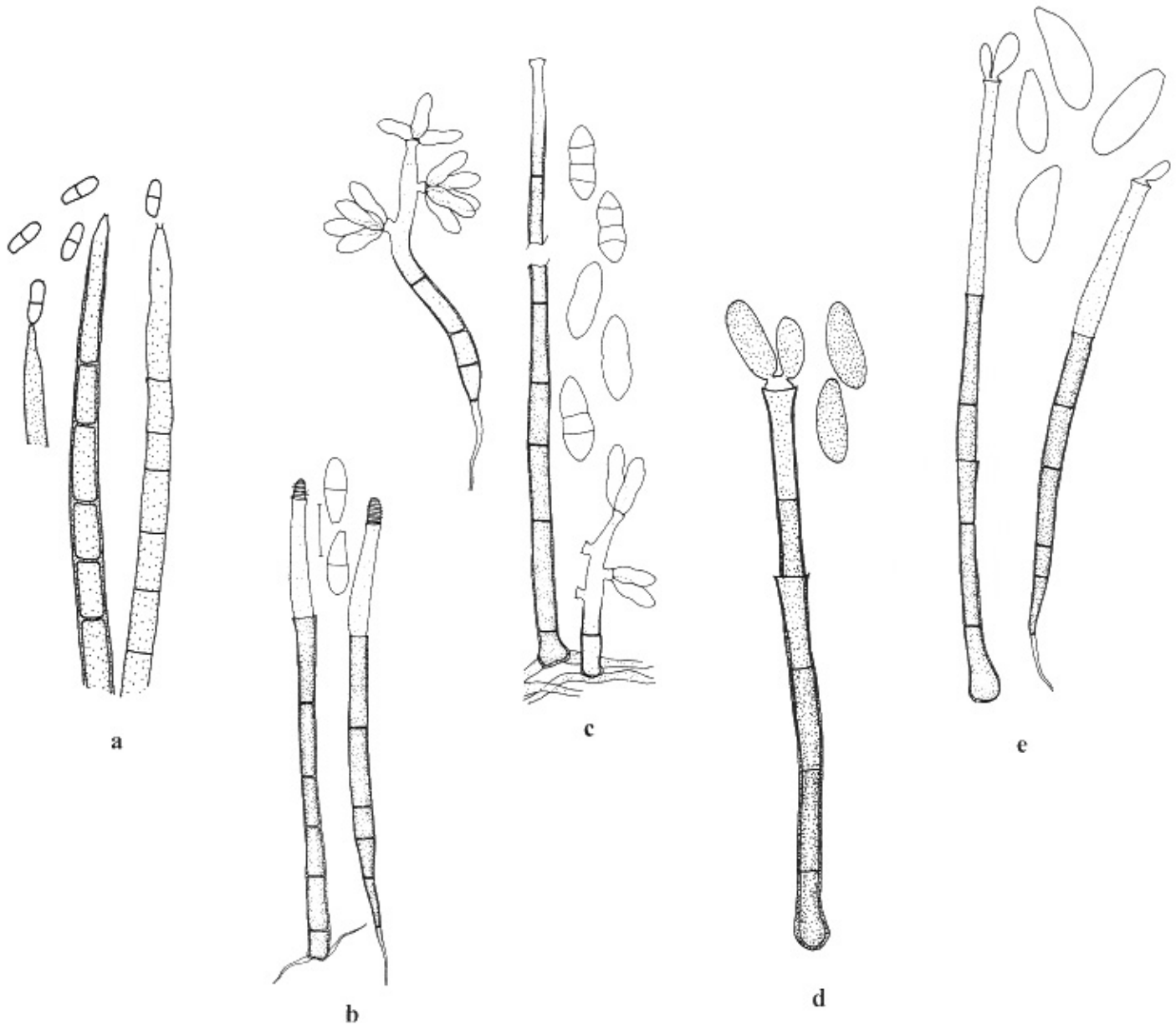
The *Kylindria*-group

Fig 4. a–e. The *Kylindria*-group. Habit sketch of members of the group. a. *Chaetosphaeria abietis* [anamorph = *Cylindrotrichum zignoellae* (Höhn.) W. Gams & Hol.-Jech.]; b. *Chaetosphaeria acutata* (anamorph = *Cylindrotrichum* sp.); c. *Chaetosphaeria fusiformis* (anamorph = *Chloridium cylindrosporum* W. Gams & Hol.-Jech.); d. *Chaetosphaeria fennica* (anamorph = *Chloridium* sp.); e. *Chaetosphaeria crustacea* (anamorph = *Cylindrotrichum-Chloridium* sp.), [a after Gams & Holubová-Jechová (1976); b–e after Réblová & Gams (1999)].

KEY TO ANAMORPH GENERA ASSOCIATED WITH *CHAETOSPHAERIA*

1. Phialides borne laterally on the conidiophore, in whorls, singly or on short branches, sometimes integrated in the conidiophore, terminal or intercalary; collarete inconspicuous or strongly recurved in the upper part or cup-shaped; conidiophores unbranched or branched; conidia often with setulae 2
1. Phialides exclusively integrated in the conidiophore, terminal or intercalary; collarete more or less pronounced; conidiophores unbranched or seldom simply branched; conidia always non-setulose 5

2. Conidia forming on a single conidiogenous locus within the collarette 3
2. Conidia forming on multiple conidiogenous loci within the collarette, hyaline, short-ellipsoidal, non-setulose, forming singly or in slimy heads; phialides in whorls or single; conidiophores unbranched or seldom branched, terminal cell sometimes a monophialide *Gonytrichum*
3. Phialides borne exclusively laterally; collarette inconspicuous or strongly recurved in the uppermost part 4
3. Phialides integrated in the conidiophore, terminal or intercalary, rarely lateral; collarette cup-shaped; conidiophores unbranched, often accompanied by setae; conidia hyaline, fusiform, falcate, non-septate or septate, with fine setulae at each end, forming slimy heads *Codinaea sensu stricto*
4. Phialides borne singly, on 1–3 supporting cells or on short branches on the conidiophore, apex of the phialide usually strongly recurved; conidiophores often terminating in a sterile whip-like elongation; conidia hyaline, oblong, fusiform, symmetrical or asymmetrical, with or without setulae, non-septate or 3-septate, forming slimy heads *Menispora*
4. Phialides borne in whorls along the main axis of the conidiophore or its branches; conidiophores branched or unbranched, apical cell sterile or developing into a monophialide; conidia hyaline, falcate, gently or strongly curved, non-septate, forming singly *Zanclospora*
5. Conidia formed on a single conidiogenous locus within the collarette 6
5. Conidia formed on multiple conidiogenous loci within the collarette, apex of the conidiogenous cell sometimes proliferating percurrently above the primary collarette 9
6. Collarette long, tubular; conidia hyaline, wedge-shaped or cylindrical, non-septate or septate, forming singly or in chains *Chalara*
6. Collarette narrow and short or flaring, vase- or funnel-shaped 7
7. Conidiophores associated with capitate hyphae, proliferating percurrently; conidia dark brown, rounded-obconical, truncate at the basal scar, rounded or flattened at the apex, forming chains *Catenularia*
7. Conidiophores not associated with capitate hyphae, proliferating percurrently or sympodially ... 8
8. Conidia generally short-ellipsoidal, rarely fusiform to clavate, wedge-shaped or reniform, hyaline or pale brown, non-septate, forming slimy heads or chains *Chloridium pro parte*
8. Conidia fusiform, symmetrical or asymmetrical, hyaline, non-septate, forming slimy heads *Dictyochoaeta sensu stricto*
9. Conidia bicolorous, middle cells pale brown, end-cells hyaline, fusiform, forming slimy heads; conidiophores proliferating percurrently *Cacumisporium*
9. Conidia hyaline or light pigmented; conidiophores proliferating percurrently or sympodially ... 10
10. Conidia non-septate, short-ellipsoidal to long-ellipsoidal or cylindrical, forming complex cirrhi or slimy heads *Chloridium pro parte*
10. Conidia septate, long-ellipsoidal to cylindrical or clavate, forming dry or slimy heads *Cylindrotrichum pro parte*

KEY TO SPECIES OF *CHAETOSPHAERIA*

This key is mainly based on anamorphic features. Delayed formation of ascospore septa is typical of *Chaetosphaeria* and has been observed in many species. For example, *Chaet. callimorpha* and *Chaet. montana* initially have 1-septate ascospores, but mature ascospores have two additional septa. In *Chaet. crustacea*, 3-septate ascospores are usually observed within the asci. Ascospores released from the perithecia and attached to the substratum surface or outer perithecial wall always have 4–6 septa. In case of doubt about the state of maturity of ascospores and the formation of additional septa, therefore, I recommend following both key entries for species with 1-septate and species with more than 1-septate ascospores at maturity.

The numbers after each species name indicate principal references listed after the key.

1. Ascospores 1-septate at maturity, sometimes fragmenting into part-spores 2
1. Ascospores more than 1-septate at maturity, usually 3–6-septate, sometimes fragmenting into part-spores 13

2.	Anamorph <i>Chalara</i>	3
2.	Anamorph different	4
3.	Anamorph <i>Chalara breviclavata</i> ; conidia hyaline, ellipsoidal to shortly clavate, 3.5–4.5 μm wide, 10–20 μm long; ascospores 9–17 \times 3.5–4 μm ; asci 62–83 \times 6.5–8 μm <i>Chaet. chalaroides</i> ⁸	8
3.	Anamorph <i>Chalara brevispora</i> ; conidia hyaline, wedge-shaped, 1.5–2 μm wide, ca 3 μm long; ascospores 8.5–10.5(–11.5) \times 2–2.5 μm ; asci 59–68 \times 5–6 μm	<i>Chaet. bramleyi</i> ^{3,5}
4.	Anamorph <i>Phialophora phaeophora</i> ; conidia hyaline, wedge-shaped, 2–2.5 \times 4.5–5(–6) μm ; conidiophores proliferating percurrently, collarete darker, funnel or vase-shaped; ascospores cylindrical to ellipsoidal, (5–)6–8 \times 2–2.5 μm ; asci (47–)52–58(–65) \times 4–5 μm ..	<i>Chaet. pygmaea</i> ⁴
4.	Anamorph different	5
5.	Anamorph <i>Chloridium</i>	6
5.	Anamorph different	10
6.	Conidiogenesis with a single locus within the collarete	7
6.	Anamorph <i>Chloridium virescens</i> ; conidiogenesis with multiple loci within the collarete; conidia hyaline, short-ellipsoidal, 3–4 \times 2–2.5 μm ; conidiophores proliferating percurrently, forming two distinct layers, collarete shallow; ascospores ellipsoidal, fragmenting into part-spores, 6–10 \times 2–3 μm ; asci 55–80 \times 3.5–4.5(–6) μm	<i>Chaet. vermicularioides</i> ⁵
7.	Conidia ellipsoidal	8
7.	Anamorph <i>Chloridium clavaeforme</i> ; conidia wedge-shaped, hyaline, (1.5–)2–2.5 \times 2.5–3.5 μm ; conidiophores proliferating percurrently, collarete darker, funnel or vase-shaped; ascospores ellipsoidal to cylindrical, 5–7(–8) \times 2.5–3 μm ; asci 45–60 \times 4–5 μm <i>Chaet. myriocarpa</i> ^{2,4,5}	
8.	Ascospores non-fragmenting	9
8.	Ascospores fragmenting, part-spores 2.5–3.5 \times 1.5–2 μm ; asci 45–55 \times 3.5–4 μm ; anamorph <i>Chloridium preussii</i> ; conidia short-ellipsoidal, hyaline, 1.5–2 \times 2.5–3.5 μm ; conidiophores proliferating percurrently, collarete cup-shaped	<i>Chaet. preussii</i> ⁵
9.	Anamorph <i>Chloridium pachytrachelum</i> ; conidia ellipsoidal to cylindrical, hyaline, (2–)2.5–3.5 \times (3.5–)5–7.5(–9) μm ; conidiophores proliferating percurrently, collarete cup-shaped, darker than the tip of phialides; ascospores fusiform, (10.5–)12.5–14.5(–16.5) \times 4–5 μm ; asci (86–)90–107 \times 6–8(–10.5) μm	<i>Chaet. lentomita</i> ⁵
9.	Anamorph <i>Chloridium</i> sp.; conidia ellipsoidal, slightly apiculate at the base, hyaline, 3.5–4(–5) \times 2–2.5 μm ; conidiophores proliferating percurrently, forming two distinct layers, collarete cup-shaped; ascospores cylindrical to slightly fusiform, 10.5–17.5 \times 2.5–3.5 μm ; asci 70–75 \times 6–7 μm	<i>Chaet. barbicineta</i> ¹
10.	Anamorph <i>Gonytrichum</i>	11
10.	Anamorph different	12
11.	Anamorph <i>Gonytrichum caesium</i> ; conidia short-ellipsoidal, hyaline, 1.5–2 \times 3–5 μm ; conidiophores with a conspicuous lateral branching pattern, collarete shallow; ascospores fusiform, fragmenting, part-spores 2.5–3.5(–4.5) \times 2–2.5(–3) μm ; asci (40–)67–90 \times 4–5 μm <i>Chaet. inaequalis</i> ⁵	
11.	Anamorph <i>Gonytrichum chlamydosporium</i> ; conidia short-ellipsoidal, hyaline 1.0–2 \times 3–4 μm ; conidiophores unbranched, proliferating percurrently, collarete shallow; ascospores fusiform, fragmenting, part-spores 3–4 \times 2–3 μm ; asci (45–)72–86(–90) \times 3.5–4 μm	<i>Chaet. chloroconia</i> ⁵
12.	Anamorph <i>Zanclospora brevispora</i> ; conidia falcate, 1-celled, curved, hyaline, 1.5–2 \times 5.5–8(–9.5) μm ; conidiophores unbranched; ascospores fusiform, 8–10 \times 3–4 μm ; asci 63–75 \times 5–7 μm	<i>Chaet. brevispora</i> ¹⁰
12.	Anamorph <i>Codinaea</i> sp.; conidia 2-celled, setulose, hyaline, 14–17 \times 1.5–2.5 μm ; conidiophores proliferating sympodially, phialides borne also laterally; ascospores cylindrical to fusiform, 9–12.5 \times 2.5–3.5 μm ; asci 60–80 \times 6–8 μm , with stipe 5–15 μm ...	<i>Chaet. dingleyae</i> ¹⁰
13(1).	Anamorph <i>Chloridium</i>	14
13.	Anamorph different	19
14.	Conidiogenesis with a single locus within the collarete	15
14.	Conidiogenesis with multiple loci within the collarete	17

15. Conidia hyaline 16
15. Conidia pale brown, ellipsoidal, $3-4 \times 2-2.5 \mu\text{m}$; conidiophores proliferating percurrently and sympodially, collarete funnel-shaped or campanulate; anamorph *Chloridium* sp.; ascospores 3-septate, fragmenting, part-spores $(2-)2.5-3 \times 2-2.5 \mu\text{m}$; asci $58-72 \times 5-6.5 \mu\text{m}$ *Chaet. dilabens*¹⁴
16. Anamorph *Chloridium botryoideum*; conidia ellipsoidal, hyaline, $1-1.5 \times (2.5-)3-4.5(-5) \mu\text{m}$; conidiophores proliferating sympodially, collarete narrow and short; ascospores fusiform, 3-septate, $(10-)12-16 \times 3.5-4 \mu\text{m}$; asci $65-90 \times 7-9 \mu\text{m}$ *Chaet. innumera*⁵
16. Anamorph *Chloridium-Dictyochoeta*; conidia ellipsoidal to slightly asymmetrical, hyaline, non-septate, $4-4.5(-5) \times 2-2.5 \mu\text{m}$; conidiophores simply branched, proliferating percurrently and sympodially, associated with setae; setae darker near the base, paler upwards with blunt, hyaline end-cell; collarete narrow and short; ascospores fusiform, 3-septate, $(15-)17-21(-22.5) \times 4-5(-7) \mu\text{m}$; asci $96.5-123(-126) \times 10.5-11.5 \mu\text{m}$ *Chaet. hebetiseta*¹⁴
17. Conidia hyaline 18
17. Anamorph *Chloridium* sp.; Conidia pale brown, ellipsoidal, $8.5-9.5(-10) \times 3-4.5 \mu\text{m}$; conidiophores proliferating percurrently and sympodially, collarete shallow, apex of the conidiogenous cell proliferating percurrently above the primary collarete; ascospores elongate-fusiform and tapering strongly towards the ends immediately after the middle septum, 3-septate, $(34.5-)36.5-42(-43) \times (3.5-)4(-4.5) \mu\text{m}$; asci $(126-)133-152(-168) \times (8.5-)9-10.5 \mu\text{m}$ *Chaet. fennica*¹³
18. Anamorph *Chloridium-Cylindrotrichum*; conidia cylindrical-clavate or fusiform, 1-celled, hyaline, $(11.5-)14.5-17(-21) \times 3-4.5 \mu\text{m}$; conidiophores proliferating percurrently, collarete shallow; ascospores cylindrical-fusiform, predominantly 3-septate, at maturity 4-6-septate, $(15.5-)19-26(-28) \times 3-3.5(-4) \mu\text{m}$; asci $75-105(-115) \times (8.5-)9.5-10.5 \mu\text{m}$ *Chaet. crustacea*¹³
18. Anamorph *Chloridium cylindrosporium*; conidia cylindrical with tapering and rounded or truncate ends, 0-3-septate, $10.5-13.5 \times 3.5-5 \mu\text{m}$; conidiophores proliferating sympodially, forming two layers, collarete shallow; ascospores cylindrical-fusiform, tapering towards one end, 3-septate, $(34.5-)39-53.5(-62) \times 2.5-3(-4) \mu\text{m}$; asci $(89-)99-126(-146) \times 8.5-10.5(-11.5) \mu\text{m}$ *Chaet. fusiformis*^{5,13}
19. Anamorph *Codinaea sensu stricto* 20
19. Anamorph different 22
20. Setae absent among conidiophores; conidia falcate, asymmetrical, non-septate, hyaline, setulose, $7.5-11 \times 1.6-2.5 \mu\text{m}$; conidiophores proliferating sympodially, collarete cup-shaped; ascospores fusiform, 3-septate, $15-22 \times 4-5 \mu\text{m}$; asci $70-100 \mu\text{m}$ long in the *pars sporifera*, $7-10 \mu\text{m}$ wide, stipe $8-14 \mu\text{m}$ *Chaet. talbotii*¹⁰
20. Setae generally present among conidiophores 21
21. Setae strongly pointed at their apices, always with opaque contents in the apical cells; conidia falcate, non-septate, hyaline, with short setulae, $23-29 \times 2.5-3 \mu\text{m}$; conidiophores proliferating sympodially, collarete cup-shaped; ascospores fusiform, 3-septate, $12-18 \times 4-6 \mu\text{m}$; asci $65-80 \times 7-12 \mu\text{m}$ *Chaet. pulchriseta*¹⁰
21. Setae blunt at their apices, always with paler or hyaline contents of the apical cells; conidia falcate, hyaline, non-septate, with short setulae, $22-26(-29) \times 3-4 \mu\text{m}$; conidiophores proliferating sympodially, collarete cup-shaped; ascospores fusiform, 1(-3)-septate, $(18.5-)19-25 \times 5.5-7 \mu\text{m}$; asci $100-130 \times (9.5-)10.5-12.5 \mu\text{m}$ *Chaet. montana*¹¹
22. Anamorph *Dictyochoeta sensu stricto*; conidia cylindrical to oval, asymmetrical, hyaline, non-septate, non-setulose, $10-15.5 \times 2-3 \mu\text{m}$; conidiophores proliferating sympodially, collarete cup-shaped; ascospores fusiform, 1(-3)-septate, $11-16 \times 3-4 \mu\text{m}$; asci $80-100 \times 6-8 \mu\text{m}$ *Chaet. callimorpha*²
22. Anamorph different 23
23. Anamorph cylindrotrichum-like 24
23. Anamorph different 25
24. Anamorph *Cylindrotrichum* sp.; conidia cylindrical-clavate, hyaline, 1-septate, $(11-)12.5-15.5(-16.5) \times 4-5 \mu\text{m}$; conidiophores proliferating percurrently, collarete shallow, apex of the conidiogenous cell proliferating percurrently above the primary collarete; ascospores long-

- fusiform, 3-septate, (28–)30.5–38(–44) × 3–4(–5) μm; asci (95–)121–147 × (8.5–)9.5–10.5(–11.5) μm *Chaet. acutata*¹³
24. Anamorph *Cylindrotrichum zignoëllae*; conidia cylindrical to fusiform, hyaline, non-septate, 6–12 × 2–3.5 μm; conidiophores proliferating percurrently and sympodially, collarette narrow; ascospores cylindrical-fusiform, 3-septate, 27–36.5(–41) × (2.5–)3–4 μm; asci (89–)90–120(–130) × 9.5–10.5 μm *Chaet. abietis*^{5,13}
25. Anamorph *Catenularia* 26
25. Anamorph different 28
26. Ascospore longer than 18 μm 27
26. Ascospores not exceeding 18 μm in length (12–18 × 2.5–3.5 μm), 3-septate; asci 60–80 × 4.5–7 μm; anamorph *Catenularia cubensis*; conidia rounded-obconical, truncate at the basal scar, rounded or flattened at the apex, dark brown, non-septate, 3.5–5.5 μm wide at the distal end, 1.5–2.5 μm wide at the flattened base, 5.5–9 μm long *Chaet. cubensis*⁷
27. Anamorph *Catenularia cuneiformis*; conidia rounded-obconical, truncate at the basal scar, rounded or flattened at the apex, dark brown, non-septate, (5.5–)7.5–10(–11.5) μm wide at the distal end, (2.5–)3.5–4.5(–6) μm wide at the flattened base, (9–)11–13.5(–15) μm long; ascospores fusiform, 4–5-septate, 15–28 × 4–5 μm; asci 80–120 × 9–10 μm *Chaet. cupulifera*³
27. Anamorph *Catenularia* sp., conidia rounded-obconical, truncate at the basal scar, rounded or flattened at the apex, dark brown, non-septate, 11.4–18.2 μm wide at the distal end, 3.5–5.0 μm wide at the flattened end, 12.5–17.5 μm long; ascospores fusiform, 3-septate, 20–24 × 4.5–5.5 μm; asci 80–100 × 9–11 μm *Chaet. novaezelandiae*⁹
28. Synanamorphs *Menispora* and *Phialophora* 29
28. Anamorph *Cacumisporium capitulatum*; conidia bicolorous, fusiform, 3-septate, 19–22(–24) × 6–7 μm; conidiophores proliferating percurrently, collarette shallow, apex of the conidiogenous cells proliferating percurrently above the primary collarette; ascospores cylindrical or cylindrical to fusiform, 3–5-septate, (28–)30–42(–46) × 3–4 μm; asci 68–90 μm long in the *pars sporifera*, 10.5–11.5 μm wide, stipe 30–54 μm long *Chaet. decastyla*¹³
29. Synanamorphs *Menispora glauca* and *Phialophora* sp.; conidia of *Menispora glauca* fusiform, curved, hyaline, 3-septate, with fine setulae at each end, 17–24(–27) × 3–4 μm; conidia of *Phialophora* cylindrical to oval, asymmetrical, hyaline, non-septate, 4–5 × 1.5–2 μm; ascospores fusiform, 3-septate, 21–29 × 4–5.5(–6) μm; asci (100–)115–150 × 8.5–11.5 μm *Chaet. ovoidea*^{4,6,12}
29. Synanamorphs *Menispora caesia* and *Phialophora* sp.; conidia of *Menispora caesia* cylindrical to oval, asymmetrical, hyaline, non-septate, without setulae, 15–20 × 2.5–3.5(–4) μm; conidia of *Phialophora* sp. cylindrical to oval, asymmetrical, hyaline, non-septate, (5–)6–7.5 × 1–1.5 μm; ascospores fusiform, predominantly 1-septate, later 3-septate, 19–23(–25) × 3–3.5(–4) μm; asci 90–115 × 7–8.5 μm *Chaet. pulviscula*^{2,6,12}

Principal references to modern descriptions:

- ¹ Barr (1993)
- ² Booth (1957)
- ³ Booth (1958)
- ⁴ Constantinescu *et al.* (1995)
- ⁵ Gams & Holubová-Jechová (1976)
- ⁶ Holubová-Jechová (1973b)
- ⁷ Holubová-Jechová (1982)
- ⁸ Holubová-Jechová (1984)
- ⁹ Hughes (1965)
- ¹⁰ Hughes & Kendrick (1968)
- ¹¹ Réblová (1998a)
- ¹² Réblová (1998b)
- ¹³ Réblová & Gams (1999)
- ¹⁴ Réblová & Gams (2000)

Discussion

Assessing the characters of anamorphs in the life cycle of a holomorph is a basic step in the systematics of *Chaetosphaeria*. From the phylogenetic point of view, an ideal situation would be if one teleomorph genus were associated with one anamorph genus, or with one to several synanamorph genera produced by the same fungus. Ten anamorph genera of dematiaceous hyphomycetes producing phialidic conidia have been linked to *Chaetosphaeria*. The anamorph genera were originally distinguished on a very narrow basis and seem to be variations on a theme that no longer can be considered to represent phylogenetically homogenous taxa.

The question of the taxonomic value of particular characters that might serve as a solid basis for distinguishing natural units of conidial anamorphs has been addressed several times (e.g. Gams & Holubová-Jechová, 1976; Kendrick, 1980; DiCosmo *et al.*, 1983; Cabello & Arambarri, 1989; Holubová-Jechová, 1990), each study giving different weight to individual morphological characters. In the present analysis, the uniting characters of the anamorphs of *Chaetosphaeria* were observed to be (i) mononematous, macronematous, erect, dark brown pigmented conidiophores, and (ii) phialides that are mostly integrated, terminal or intercalary or sometimes borne in a lateral position. The main differentiating characters of anamorphs belonging to each of the four groups distinguished in *Chaetosphaeria* above are (i) structure of the phialides, (ii) presence or absence of lateral phialides on the conidiophore, (iii) shape of conidia, and (iv) presence or absence of setulae. Certain combinations of these features correlate with particular morphological types of ascospores. Sympodially or percurrently proliferating conidiophores correspond to poly- and monophialides, respectively. Pigmentation of conidia appears to be taxonomically misleading and phylogenetically less significant at the genus level, possibly useful in distinguishing species.

Chaetosphaeria has a long history of taxonomic problems. While the characters of perithecia, ascospores and asci are very uniform, they are often insufficient for correct identification. The great species diversity in *Chaetosphaeria* is manifested in the associated anamorphs. Distinction of closely related species is impossible on the basis of ascospore, ascus and perithecium morphology only, e.g. *Chaet. myriocarpa* and *Chaet. pygmaea*, *Chaet. chloroconia* and *Chaet. vermicularioides*, *Chaet. barbicincta* and *Chaet. lentomita*, *Chaet. callimorpha*, *Chaet. montana* and *Chaet. pulchriseta*, etc. Thus, *Chaetosphaeria* seems to represent an example where evolutionary

change is manifested most visibly in the morphology of the conidiophores, conidiogenous cells and conidia rather than of the perithecia, asci and ascospores.

Our phylogenetic analysis using LSU rDNA data set of 25 representative taxa from eight of eleven anamorph genera showed that the genus *Chaetosphaeria* is not monophyletic as circumscribed currently (Réblová & Winka, 2000). It should be pointed out that this phylogenetic discussion is based on a gene tree rather than a species tree, and that it is still based on a rather limited selection of species. *Chaetosphaeria aterrima* (Fuckel) Réblová and *Chaet. tulasneorum* Réblová & W. Gams and two related asexual taxa, *Custingophora olivacea* Stolk, Hennebert & Klopotek and *Cylindrotrichum hennebertii* W. Gams & Hol.-Jech., did not cluster with other species of *Chaetosphaeria*. At the moment, 30 species of *Chaetosphaeria* and ten anamorph genera are accepted. The known links to teleomorphs of seven of them are exclusively with the *Chaetosphaeriaceae*, mostly with *Chaetosphaeria*. The genera *Chalara*, *Cylindrotrichum* and *Phialophora*, as presently used, are polyphyletic.

The type species of *Cylindrotrichum*, the *Cyl. oligospermum* anamorph of *Chaet. tulasneorum*, and its non-setose asexual counterpart, *Cyl. hennebertii*, grouped within the *Hypocreales/Microascales* clade (Réblová & Winka, 2000), separate from the remaining species of *Cylindrotrichum*. I know of only one herbarium specimen containing both the *Chaetosphaeria* and *Cyl. oligospermum* morphs (Réblová & Gams, 1999). This species will require further examination and taxonomic treatment. These two species differ from other *Cylindrotrichum* species by their narrowly cylindrical, 1-septate conidia. Similar conidia are found in *Chaetopsis* Grev., which is regarded as a separate genus with polyblastic conidiogenesis and a predominantly lateral branching pattern of the conidiophores. The relationship of *Chaetopsis* to *Cyl. oligospermum* was discussed by Kendrick (1980) and DiCosmo *et al.* (1983). The proposal made in the latter paper to separate *Cyl. oligospermum* and *Cyl. hennebertii* from other species placed in *Cylindrotrichum* at that time seems warranted. Samuels (1985) suggested that the results of the numerical analysis performed by DiCosmo *et al.* (1983) were misleading. In his study of four species of *Chaetopsina* Rambelli associated with perithecia of *Nectria* Fr., Samuels (1985) concluded that none of the characters given great or even moderate weight (conidium shape and presence of mono- or polyphialides) by DiCosmo *et al.* (1983) were highly significant. He discovered another rather subtle character (pigmentation of the setose conidiophores) that united *Chaetopsina* anamorphs of *Nectria*, without the need to classify them in more than one genus. Samuels' decision was confirmed by our study (Réblová & Winka, 2000),

although a rather limited sample of species was employed in the molecular analysis. Furthermore, none of the characters emphasized by DiCosmo *et al.* (1983) proved to be significant at the generic level.

The subsequent discussion concerns only the species of *Chaetosphaeria sensu stricto* corresponding to the *Chaetosphaeriaceae*. *Chalara* is morphologically simple but phylogenetically a very heterogeneous taxon and has been linked to teleomorphs belonging to different groups of ascomycetes. Paulin & Harrington (this volume) review the phylogeny of chalara-like anamorphs. I will focus only on those *Chalara* and *Cylindrotrichum* species in the monophyletic *Chaetosphaeriaceae* that form two morphologically homogeneous groups of taxa. The *Chalara* species that have been linked to *Chaetosphaeria bramleyi* (Booth, 1958; Gams & Holubová-Jechová, 1976), *Chaet. chalaroides* (Holubová-Jechová, 1984) and the monotypic genus *Ascochalara* Réblová (Réblová, 1999e) share very similar appearance of conidiophores, conidia and conidiogenous cells. Apart from the deep tubular collarete in *Chalara*, these species most strongly resemble *Chloridium*, for instance the *Chloridium claviforme* (Preuss) W. Gams & Hol.-Jech. anamorph of *Chaet. myriocarpa* and the *Phialophora phaeophora* anamorph of *Chaet. pygmaea* (*Phialophora phaeophora* represents a miniature *Chloridium*; Gams, this volume). Both *Chl. claviforme* and *Ph. phaeophora* have a tendency to form similar wedge-shaped conidia and flaring or funnel-shaped collarettes somewhat deeper than those of other *Chloridium* species.

Similarly, the species of *Cylindrotrichum* auct. belonging to *Chaetosphaeria* show a similar degree of variability. Three *Cylindrotrichum* species with multiple conidiogenous loci that have been linked to *Chaetosphaeria*, viz. *Chaet. abietis*, *Chaet. acutata*, and *Chaet. crustacea*, show remarkable similarity with two other species of *Chloridium* having the same conidial ontogeny, the anamorphs of *Chaet. fennica* and *Chaet. fusiformis*. However, their conidiogenesis from multiple conidiogenous loci would place them in section *Chloridium*. Here, they are designated the *Kylindria*-group. The main difference separating these genera is conidial septation; non-septate conidia in *Chloridium* and septate in *Cylindrotrichum*. However, this character does not have phylogenetic value at the generic level, but rather diagnostic value in distinguishing species (Réblová & Winka, 2000).

The *Chloridium virescens* (Pers.) W. Gams & Hol.-Jech. anamorph of *Chaetosphaeria vermicularioides* did not cluster with other species of *Chloridium* of the *Gongromeriza*-group, but was nested with high bootstrap support among species of *Gonytrichum* (as the *Chloridium*-group) sharing the same morphological characteristics of conidia, conidium ontogeny and ascospore mor-

phology. *Gonytrichum* is characterized by conidiophores having lateral phialides in whorls or formed singly along the main axis, and a specific branching pattern of conidiophores recognized particularly in *Gonytrichum caesium* C.G. Nees & F. Nees. Nevertheless, the lateral phialides often disappear during cultivation, usually after a few transfers on artificial media, leaving conidiophores identical to those of species of *Chloridium* section *Chloridium*. The associated teleomorphs correspond in part to *Melanopsammella*. In order to keep *Melanopsammella* as a separate, though closely related taxon to *Chaetosphaeria*, a narrower definition of the generic concept would be required. Because *Chloridium virescens* is otherwise consistent in morphology of conidiophores and conidia with other *Chloridium* species of the *Gongromeriza*-group and in the structure of a phialide with species of the *Kylindria*-group, I do not believe that these three groups represent distinct genera. The differences manifested in the structure of their phialides, single locus (*Gongromeriza*-group) vs. multiple loci (*Chloridium*-group and *Kylindria*-group), are too small. However, serious problems would arise if all groups of chaetosphaeriaceous anamorphs were subsumed in a single genus, because members of the *Menispora*-group differ so widely from the others, and might represent extremes within the same pattern of development that is found in other anamorphs of *Chaetosphaeria*.

The *Menispora*-group was recognized as a sister to the *Chloridium*-group within one large clade (Réblová & Winka, 2000). It contains asexual species of *Codinaea sensu stricto*, *Codinaeopsis*, *Menispora* and two other sexual species classified in *Striatosphaeria* and *Chaetosphaeria*. As in the *Chloridium*-group, lateral phialides do not occur regularly; but they are typical of most species of *Menispora*, *Codinaeopsis* and partly *Dictyochaeta sensu lato*. The main characters that separate the *Menispora*-group from the *Chloridium*-group are the structure of the phialide and the shape of the conidia: large, oblong, often curved, usually provided with setulae, formed from a single conidiogenous locus in the *Menispora*-group vs. small, short-ellipsoidal, non-setulose conidia formed from multiple conidiogenous loci in the *Chloridium*-group. However, the conidia of *Codinaeopsis*, *Codinaea sensu stricto* and *Menispora* resemble those of *Chloridium* and *Cylindrotrichum* species of the *Kylindria*-group, with the exception that setulose conidia and lateral phialides never appear.

Codinaea Maire (1937) has often been considered a synonym (Gamundí *et al.*, 1977) of *Dictyochaeta* Speg. (Spegazzini, 1923). The genus is based on *Codinaea aristata* Maire, whose holotype is considered lost (Hughes & Kendrick, 1968). According to the illustration, the fungus has long, brown and multiseptate setae, shorter conidiophores with monopialides producing

falcate, hyaline, 1-celled and setulose conidia. *Dictyochoaeta fuegiana* Speg., the type of *Dictyochoaeta*, was described with long, brown, multiseptate setae that may end in a polyphialide and are accompanied by shorter conidiophores ending in a mono- or polyphialide, producing clavate, 1-celled, non-setulose conidia. Despite the similar characters of these two genera, the presence of setulose conidia distinguishes them. Hughes & Kendrick (1968) preferred to use the name *Codinaea*; after examining type material of *D. fuegiana* they regarded its systematic position as uncertain. Later, Gamundí *et al.* (1977) recollected and redescribed *D. fuegiana* and adopted Spegazzini's name, making *Codinaea* a synonym. When Gamundí *et al.* (1977) merged both genera, followed by other authors (e.g. Kirk, 1982; Holubová-Jechová, 1984), they did not attribute much significance to the presence or absence of setulae at the generic level but used it rather as a solid feature for distinguishing species.

Since the description of both *Codinaea* and *Dictyochoaeta*, more than 80 species have been described (Kuthubutheen & Nawawi, 1991). Réblová & Winka (2000) analysed several strains of species falling in *Dictyochoaeta sensu stricto* and *Codinaea sensu stricto* using large subunit rDNA sequences: the *Dictyochoaeta* anamorph of *Chaetosphaeria callimorpha* (Mont.) Sacc. on one hand and *Dictyochoaeta simplex* (S. Hughes & W.B. Kendr.) Hol.-Jech. and *D. fertilis* (S. Hughes & W.B. Kendr.) Hol.-Jech. on the other. On the basis of the LSU rDNA sequence data, species corresponding to *Codinaea sensu stricto* (the *Menispora*-group) separated clearly from species that match the circumscription of *Dictyochoaeta sensu stricto* (the *Gongromeriza*-group). Moreover, species of *Dictyochoaeta sensu stricto* grouped with several sexual and asexual species currently recognized as *Chloridium* section *Gongromeriza* and section *Psilobotrys* (Gams & Holubová, 1976). The uniting characters are conidiogenesis from a single locus within the collarette and non-setulose conidia. Several species of *Chloridium*, including *Chloridium smithiae* (Sinclair & Eicker, 1985), *Chl. codinaeoides* Pirozynski (Pirozynski, 1972) and the *Chloridium*-*Dictyochoaeta* anamorph of *Chaetosphaeria hebetiseta* Réblová & W. Gams (Réblová & Gams, 2000), occupy an intermediate position between the two sections of *Chloridium* as well as between *Chloridium* and *Dictyochoaeta sensu stricto*, providing difficulties in their classification at the generic level. However, the distinction of *Codinaea* and *Dictyochoaeta* seems quite important, though both genera show only slight differences from the taxa mentioned above. The existence of intermediate or extralimital species that share features partly of *Menispora*, *Chloridium*, *Codinaea*, *Cylindrotrichum*, *Dictyochoaeta* and *Gonytrichum* led to the description of other intermediate genera,

including *Codinaeopsis* Morgan-Jones and *Dictyochoaetopsis* Arambarri & Cabello. For these reasons, though it seems appropriate to separate *Codinaea* from *Dictyochoaeta*, *Codinaea* should be confined to species with setulose conidia and be included in *Menispora* as a synonym. *Dictyochoaeta* comprises species with non-setulose conidia and can be merged with *Chloridium* (*Gongromeriza*). On the basis of molecular data, it is no longer justified to separate *Chloridium* species into these two sections, as the species with sympodially and percurrently proliferating conidiophores in combination with flaring and narrow collarettes, respectively, did not clearly separate from each other. The relationship of *Dictyochoaeta sensu stricto* with *Chloridium* (*Gongromeriza*), and *Codinaea sensu stricto* with *Codinaeopsis*, *Dictyochoaetopsis* and *Menispora*, requires further investigation. The type species of both genera, *C. aristata* and *D. fuegiana*, have not yet been studied with molecular methods.

The distinction of *Codinaea sensu stricto* and *Menispora*, although they are retained as separate genera, now seems hardly justified. The main difference between the two genera is in the morphology of the conidiogenous locus and structure of conidiophores. In *Menispora* species, the lower part of the conidiophores is fertile. The lateral phialides are borne singly or at times on short branches on the conidiophore. The uppermost part of the phialide is strongly recurved through a full 180°, having a beak-like appearance and ending in a very narrow and short collarette. The extended upper part of the conidiophore is sterile, sinuous and whip-like. Species recognized as *Codinaea sensu stricto* have shorter, usually sympodially branched conidiophores with several lateral phialidic openings giving the conidiophores a geniculate appearance, or seldom only with one terminal phialidic opening. Conidiophores are often accompanied by setae that may end in a mono- or polyphialide. Phialides have flaring collarettes and conidia are setulose. However, several species recognized as *Menispora* have exactly the same characteristics as *Codinaea sensu stricto*, with one exception, their narrow, recurved uppermost part of the conidiogenous cell, e.g. *Menispora britannica* (M.B. Ellis) P.M. Kirk (Kirk, 1985), *M. gamundiae* Arambarri & Cabello (Arambarri & Cabello, 1995) and *M. fuegiana* Arambarri & Godeas (Arambarri & Godeas, 1994). In these species, the long, erect conidiophores with one to several phialidic openings are associated with sterile, sinuous setae. Their inclusion in *Menispora* required an expansion of the generic concept to species with integrated phialides. However, they might be related to species of the *Gongromeriza*-group.

The *Dictyochoaeta sensu lato* and *Menispora* species that possess single, laterally borne phialides on the conidiophore and flaring collarettes were recently re-

classified in the new genus *Dictyochoetopsis* (Arambarri & Cabello, 1990). This group includes, for example, *Dictyochoeta antillana* Castañeda, *D. menisporoides* Hol.-Jech., the *Codinaea* anamorph of *Chaet. dingleyae*, *Codinaea elegantissima* Lunghini, *C. filamentosa* Onofri, *Menispora glauco-nigra* Cooke & Ellis and *Menispora apicalis* Berk. & M.A. Curtis. For *Menispora* and *Dictyochoetopsis*, it is not unusual that species with both setulose conidia and conidia without setulae occur together within one genus. Species of these genera with non-setulose conidia always have lateral phialides.

Codinaeopsis Morgan-Jones (1976) is a monotypic genus described for a marginal species, *Codinaea gonytrichoides* Shearer & Crane. The phialides have flaring collarettes and are borne in whorls along the main axis of a conidiophore, thus representing the branching pattern described for *Gonytrichum* species. However, in strains of *Gonytrichum*, lateral phialides borne in regular whorls or singly on the conidiophore can be accommodated without a need of generic distinction. The positioning of dematiaceous hyphomycete genus *Codinaeopsis* in the *Menispora*-group indicates that its link to *Chaetosphaeria* is highly probable.

The phylogenetic relationships among the anamorphs of *Chaetosphaeria* are very close, and a similar gradation and patterns of characters of conidiophores and phialides and conidium ontogeny occur in both major clades distinguished in the phylogenetic analyses (Réblová & Winka, 2000). *Chaetosphaeria* appears to be a monophyletic taxon. There are several possible solutions to the question of the large number of anamorph genera. We can retain all ten, morphologically distinct but evolutionarily closely related anamorph genera, including *Cylindrotrichum pro parte* (i.e. *Kylindria*) but exclude *Cyl. oligospermum*, *Cyl. hennebertii* and *Custingophora*, which are not monophyletic with the *Chaetosphaeriaceae*. However, because all anamorphs differ predominantly in the structure of the phialides (which is sometimes difficult to observe) and slightly in conidial characters, in combination with the irregular occurrence of lateral phialides on the conidiophores, it is questionable whether these characters alone are sufficient for the delimitation of genera. They can be useful in combination with other characteristics of relevant anamorphs and teleomorphs. Because the only known links are to *Chaetosphaeria*, it might be reasonable to: (i) keep *Chaetosphaeria* as a single genus that would consist of several infrageneric taxa in accordance with grouping in the phylogenetic analysis, and amalgamate all anamorphs within a single anamorph genus corresponding to *Chaetosphaeria*, or (ii) to separate

the four natural groups of taxa recognized in *Chaetosphaeria*, corresponding to the four subclades in the phylogenetic analyses, which can be regarded as single genera. We should also consider several other dematiaceous hyphomycetes that were not included in the analysis and that share similar characteristics of conidiophores, position and structure of phialides and morphology of conidia with anamorphs of *Chaetosphaeria*, for instance *Chalarodes* McKenzie, *Cryptophiale* Pirozynski, *Menisporopsis* S. Hughes, *Menidochium* Castañeda, *Phaeostalagmus* W. Gams, *Thozetella* O. Kuntze or *Venustusynnema* Castañeda & W.B. Kendr. They may be related to the chaetosphaeriaceous anamorphs, or their links to *Chaetosphaeria* might be discovered later.

At the moment, it seems most appropriate to retain one genus, *Chaetosphaeria*, including *Melanopsammella* as its heterotypic generic synonym, and divide it into four natural groups of taxa as described above. Each group represents a certain pattern of variation. The distinction among these groups is a step towards the recognition of *Chaetosphaeria* as one or four closely related genera.

Conclusions

From the study of *Chaetosphaeria* and its anamorphs, it is obvious that the diagnostic characters displayed by anamorphs are of major taxonomic relevance. It is important to study morphological and ontogenetic characters, particularly those of conidiogenous cells and conidia, because they help to illuminate the phylogenetic relationships and systematics of the teleomorph genus *Chaetosphaeria*. I assume that the anamorph genera associated with *Chaetosphaeria* do not represent well-separated and delimited taxa, but rather a long, continuous lineage of one genus with a great deal of variation.

Acknowledgments

The Curators and Directors of FH and PRM herbaria are acknowledged for loaning herbarium material. I thank Prof. Dr Walter Gams for insightful discussion on *Chaetosphaeria* and its anamorph genera. This research was supported by the Foundation of the Academy of Sciences (C 6005910), Czech Republic.

Literature cited

- ARAMBARRI, A.M. & CABELLO, M.N., 1990 — Consideration about *Dictyochoeta*, *Codinaeopsis* and a new genus: *Dictyochoetopsis*. — *Mycotaxon* 37: 11–14.
 ARAMBARRI, A.M. & CABELLO, M.N., 1995 — *Menispora gamundiae* sp. nov., a new hyphomycete from Argenti-

- na (Buenos Aires province). — *Mycol. Res.* **99**: 377–378.
- ARAMBARRI, A.M. & GODEAS, A.M., 1994 — *Menispora fuegiana* sp. nov., a new hyphomycete from Tierra del Fuego (Argentina). — *Mycotaxon* **52**: 95–98.
- BARR, M.E., 1990 — Prodrum to non-lichenized, pyrenomycetous members of class Hymenoascmycetes. — *Mycotaxon* **39**: 43–184.
- BARR, M.E., 1993 — Redisposition of some taxa described by J. B. Ellis. — *Mycotaxon* **46**: 45–76.
- BARR, M.E. & CRANE, J.L., 1979 — Another conidial state for a species of *Chaetosphaeria*. — *Canad. J. Bot.* **57**: 835–837.
- BOOTH, C., 1957 — Studies on pyrenomyces I. and II. — *Mycol. Pap.* **68**: 1–27.
- BOOTH, C., 1958 — The genera *Chaetosphaeria* and *Thaxteria* in Britain. — *Naturalist* **1958**: 83–90.
- CABELLO, M.N. & ARAMBARRI, A.M., 1988 — Considerations about the validity of the genus *Cylindrotrichum* Bonorden. — *Mycotaxon* **31**: 435–438.
- CABELLO, M.N. & ARAMBARRI, A.M., 1989 — A numerical taxonomy study of some phialidic genera of Hyphomycetes: cluster analysis. — *Mycotaxon* **34**: 679–696.
- CLEMENTS, F.E. & SHEAR, C.L., 1931 — The genera of fungi. — New York, 496 pp.
- CONSTANTINESCU, O., HOLM, K. & HOLM, L., 1995 — Teleomorph-anamorph connections in Ascomycetes: the anamorphs of three species of *Chaetosphaeria*. — *Mycol. Res.* **99**: 585–592.
- CURZI, M., 1926 — Una moria di giovani piante pero e un nuovo genere di Pyrenomycetidae. — *Atti Ist. Bot. R. Univ. Pavia, Ser. 3*, **3**: 73–90.
- DICOSMO, F., BERCH, S. & KENDRICK, W.B., 1983 — *Cylindrotrichum*, *Chaetopsis*, and two new genera of hyphomycetes, *Kylindria* and *Xenokylindria*. — *Mycologia* **75**: 949–973.
- ELLIS, J.B. & EVERHART, B.M., 1892 — The North American Pyrenomyces. — Newfield, New Jersey.
- ELLIS, J.B. & EVERHART, B.M., 1893 — New species of fungi from various localities. — *Proc. Acad. Nat. Sci. Philadelphia* **1893**: 440–466.
- FERNÁNDEZ, F.A., LUTZONI, F.M. & HUHDORF, S.M., 1999 — Teleomorph-anamorph connections: the new pyrenomycetous genus *Carpoligna* and its *Pleurothecium* anamorph. — *Mycologia* **91**: 251–262.
- FISHER, P.J. & PETRINI, O., 1983 — Two new pyrenomyces from submerged wood. — *Trans. Brit. Mycol. Soc.* **81**: 396–398.
- FUCKEL, L., 1870 — *Symbolae Mycologicae*. — *Jahrb. Nassau. Vereins Naturk.* **23–24**: 1–459.
- FUCKEL, L., 1872 — *Symbolae Mycologicae*. Nachtrag 1. — *Jahrb. Nassau. Vereins Naturk.* **25–26**: 287–346.
- GAMS, W. & HOLUBOVÁ-JECHOVÁ, V., 1976 — *Chloridium* and some other dematiaceous hyphomycetes growing on decaying wood. — *Stud. Mycol.* **13**: 1–99.
- GAMUNDI, I.J., ARAMBARRI, A.M. & GIAIOTTI, A., 1977 — Micoflora de la hojarasca de *Nothofagus dombeyi*. — *Darwiniana* **21**: 81–114.
- HINO, I., 1932 — Genus *Miyoshiella* to be included in genus *Chaetosphaeria*. — *Bull. Miyazaki Coll. Agr. For.* **4**: 187–192.
- HINO, I., 1961 — *Icones fungorum bambusicolorum Japonicorum*. — The Fuji Bamboo Garden, Yamaguti.
- HOLUBOVÁ-JECHOVÁ, V., 1973a — Lignicolous hyphomycetes from Czechoslovakia. 3. *Sporoschisma*, *Sporoschismopsis* and *Catenularia*. — *Folia Geobot. Phytotax.* **8**: 209–218.
- HOLUBOVÁ-JECHOVÁ, V., 1973b — Lignicolous hyphomycetes from Czechoslovakia 4. *Menispora*. — *Folia Geobot. Phytotax.* **8**: 317–336.
- HOLUBOVÁ-JECHOVÁ, V., 1982 — New or interesting phialidic hyphomycetes from Cuba. — *Mycotaxon* **15**: 277–292.
- HOLUBOVÁ-JECHOVÁ, V., 1984 — Lignicolous hyphomycetes from Czechoslovakia 7. *Chalara*, *Exochalara*, *Fusichalara* and *Dictyoachaeta*. — *Folia Geobot. Phytotax.* **19**: 387–438.
- HOLUBOVÁ-JECHOVÁ, V., 1990 — Problems in the taxonomy of the dematiaceous hyphomycetes. — *Stud. Mycol.* **32**: 41–48.
- HUGHES, S.J., 1965 — New Zealand fungi 3. *Catenularia* Grove. — *New Zealand J. Bot.* **3**: 136–150.
- HUGHES, S.J. & KENDRICK, W.B., 1963 — Microfungi IX. *Menispora*. — *Canad. J. Bot.* **41**: 693–718.
- HUGHES, S.J. & KENDRICK, W.B., 1968 — New Zealand fungi 12. *Menispora*, *Codinaea*, *Menisporopsis*. — *New Zealand J. Bot.* **6**: 323–375.
- KALANI, I.K., 1964 — *Chaetosphaeria poonensis* sp. nov. from India. — *Sydowia* **17**: 121–123.
- KARSTEN, P., 1866 — *Enumeratio Fungorum et Myxomycetum in Lapponia orientali aestate 1861 lectorum*. — *Notiser Sällsk. Fauna Fl. Fenn. Förh.* **8**: 19–224.
- KAUR, I.K., 1991 — Two new species of Pyrenomyces. — *Indian J. Mycol. Pl. Pathol.* **21**: 257–259.
- KENDRICK, W.B., 1980 — The generic concept in Hyphomycetes – a reappraisal. — *Mycotaxon* **11**: 339–364.
- KIRK, P.M., 1982 — New or interesting microfungi IV. Dematiaceous hyphomycetes from Devon. — *Trans. Brit. Mycol. Soc.* **78**: 55–74.
- KIRK, P.M., 1985 — New or interesting microfungi XIV. Dematiaceous hyphomycetes from Mt. Kenya. — *Mycotaxon* **23**: 305–352.
- KOHLMEYER, J., 1963 — Fungi marini novi vel critici. — *Nova Hedwigia* **6**: 297–329.
- KUTHUBUTEEN, A.J. & NAWAWI, A., 1991 — Key to *Dictyoachaeta* and *Codinaea* species. — *Mycol. Res.* **95**: 1224–1229.
- MAIRE, R., 1937 — *Fungi Catalaunici, Series altera. Contribution à l'étude de la Flore Mycologique de la Catalogne*. — *Publ. Inst. Bot. Barcelona* **3**: 1–128.
- MAUBLANC, A. & RANGEL, E., 1915 — Alguns fungos do Brasil novos ou mal conhecidos. — *Bol. Agr. São Paulo* **16**: 310–328.
- MORGAN-JONES, G., 1976 — Notes on Hyphomycetes X. *Codinaeopsis* gen. nov. — *Mycotaxon* **4**: 166–170.

- MÜLLER, E. & ARX, J.A. VON, 1962 — Die Gattungen der didymosporen Pyrenomyceten. — Beitr. Krypt.-Fl. Schweiz **11**(2): 1–922.
- MÜLLER, E. & BOOTH, C., 1972 — Generic position of *Sphaeria phaeostroma*. — Trans. Brit. Mycol. Soc. **58**: 73–77.
- MÜLLER, E., HARR, J., & SULMONT, P., 1968 — Deux Ascomycètes dont le stade conidien présente des conidies phaeophragmiées endogenes. — Rev. Mycol. **33**: 369–378.
- MUSSAT, E., 1901 — Synonymia generum, specierum subspecierumque in Vol. 1–14 descriptorum. — Sylloge Fungorum omnium hucusque cognitorum digessit P.A. Saccardo **15**: 1–455.
- NISSL, G. VON, 1876 — Notizen über neue und kritische Pyrenomyceten. — Verh. Naturf. Ver. Brünn **14**: 165–218.
- PETRAK, F., 1925 — Mykologische Notizen VIII. Nos. 401–501. — Ann. Mycol. **23**: 1–143.
- PIROZYNSKI, K.A., 1972 — Microfungi of Tanzania. I. Miscellaneous fungi on oil Palm. II. New hyphomycetes. — Mycol. Pap. **129**: 1–64.
- RÉBLOVÁ, M., 1997 — Revision and reclassification of some *Chaetosphaeria* species. — Czech Mycol. **50**: 73–83.
- RÉBLOVÁ, M., 1998a — A new *Chaetosphaeria* with a *Dictyochoaeta* anamorph. — Czech Mycol. **50**: 151–159.
- RÉBLOVÁ, M., 1998b — Revision of three *Melanomma* species described by L. Fuckel. — Czech Mycol. **50**: 161–179.
- RÉBLOVÁ, M., 1999a — Studies in *Chaetosphaeria sensu lato* I. The genera *Chaetosphaerella* and *Tengiomyces* gen. nov. of the *Helminthosphaeriaceae*. — Mycotaxon **70**: 387–420.
- RÉBLOVÁ, M., 1999b — Studies in *Chaetosphaeria sensu lato* II. *Coniobrevicolla* gen. et sp. nov. — Mycotaxon **70**: 421–429.
- RÉBLOVÁ, M., 1999c — Studies in *Chaetosphaeria sensu lato* III. The genera *Umbrinosphaeria* gen. nov. and *Miyoshiella* with *Sporidesmium* anamorph. — Mycotaxon **71**: 13–43.
- RÉBLOVÁ, M., 1999d — Studies in *Chaetosphaeria sensu lato* IV. *Crassochoaeta* gen. nov., a new lignicolous genus of the *Trichosphaeriaceae*. — Mycotaxon **71**: 45–67.
- RÉBLOVÁ, M., 1999e — Teleomorph–anamorph connections in Ascomycetes 2. *Ascochalara* gen. et spec. nov. and its chalara-like anamorph. — Sydowia **51**: 210–222.
- RÉBLOVÁ, M., BARR, M.E. & SAMUELS, G.J., 1999 — *Chaetosphaeriaceae*, a new family for *Chaetosphaeria* and its relatives. — Sydowia **51**: 49–70.
- RÉBLOVÁ, M. & GAMS, W., 1999 — Teleomorph–anamorph connections in Ascomycetes. 1. *Cylindrotrichum* and *Cacumisporium* anamorphs of *Chaetosphaeria*. — Czech Mycol. **51**: 1–40.
- RÉBLOVÁ, M. & GAMS, W. 2000 — Life-history of Ascomycetes: Two new species of *Chaetosphaeria* with *Chloridium* and *Chloridium-Dictyochoaeta* anamorphs. — Mycoscience **41** (in press).
- RÉBLOVÁ, M. & WINKA, K., 2000 — Phylogeny of *Chaetosphaeria* and its anamorphs based on morphological and molecular data. — Mycologia **92** (in press)
- SACCARDO, P.A., 1878 — Fungi Veneti novi vel critici. Serie 3. — Michelia **1**: 446–452.
- SACCARDO, P.A., 1883 — Sylloge Fungorum omnium hucusque cognitorum. vol. 2: 1–813. Pavia.
- SACCARDO, P.A., 1886 — Sylloge Fungorum omnium hucusque cognitorum. vol. 4: 1–807. Pavia.
- SAMUELS, G.J., 1997 — Four species of *Nectria* and their *Chaetopsina* anamorphs. — Mycotaxon **22**: 13–32.
- SAMUELS, G.J. & BARR, M.E., 1997 — Notes on and additions to the *Niessliaceae* (*Hypocreales*). — Canad. J. Bot. **75**: 2165–2176.
- SAMUELS, G.J. & MÜLLER, E., 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.
- SINCLAIR, R. & EICKER, A., 1985 — A new species of *Chloridium* from South Africa. — Trans. Brit. Mycol. Soc. **84**: 566–568.
- SIVANESAN, A. & CHANG, H.S., 1995 — *Pseudofusicophilialis lignicola* gen. et sp. nov. and *Chaetosphaeria capitata* sp. nov. from wood in Taiwan. — Mycol. Res. **99**: 711–716.
- SIVANESAN, A. & CHANG, H.S., 1997 — *Chaetosphaeria ampulliformis* sp. nov. associated with a *Hemicorynespora* anamorph, and a key to *Hemicorynespora* species. — Mycol. Res. **101**: 845–848.
- SPEGAZZINI, C., 1923 — Algunos hongos de Tierra del Fuego. — Physis, Buenos Aires **7**: 7–23.
- TENG, S. C., 1996 — Fungi of China. — Mycotaxon, Ithaca, NY.
- TULASNE, L.R. & TULASNE, C., 1863 — Selecta Fungorum Carpologia, Vol. 2. — Paris.