

***Phialophora* and some similar morphologically little-differentiated anamorphs of divergent ascomycetes**

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Abstract: *Phialophora* is a little-differentiated genus of more or less pigmented, phialidic hyphomycetes. With the addition of numerous species, it has become highly polyphyletic, comprising anamorphs of discomycetes, pyrenomycetes and loculoascomycetes. The core of the genus consists of anamorphs of *Capronia* in the *Herpotrichiellaceae*, *Chaetothyriales*. Some taxa have already been segregated from *Phialophora* into genera such as *Lecythophora* (*Coniochaetaceae*) and *Phaeoacremonium* (*Magnaporthaceae*?). Ascomycete orders in which phialophora-like fungi have been placed are reviewed, and some further segregation is proposed. For the common anamorphs of the discomycete family *Dermateaceae*, the old generic name *Cadophora* is available and should be used for *Ph. fastigiata* and related taxa (one new combination). For anamorphs of *Gaeumannomyces* and *Magnaporthe* (*Magnaporthaceae*), a new genus, *Harpophora*, is proposed with four new combinations. Criteria that allow a correlation with the suggested broad-scale subdivision are outlined.

Key words: *Cadophora*, *Capronia*, *Gaeumannomyces*, *Harpophora*, *Lecythophora*, *Magnaporthe*, *Phaeoacremonium*, teleomorph connections.

Introduction

Like *Acremonium* Link and *Verticillium* Nees among the hyaline phialidic hyphomycetes, *Phialophora* Medlar is a model of a poorly defined, little differentiated and highly polyphyletic genus of more or less pigmented hyphomycetes that requires disentangling. Some species are very common saprobes in soil, wood pulp and other plant material, others are more specialized plant pathogens; human pathogenicity is known for a few species. Whilst it is still extremely difficult to differentiate species among these anamorphs, it seems possible to distinguish and name a few groups of higher ranks that can be correlated with teleomorph orders or families. Some first steps in this direction are proposed here.

The most comprehensive monograph of *Phialophora* so far produced is that by Schol-Schwarz (1970). The genus was vaguely characterized by more or less pigmented hyphae and conidiophores, solitary or aggregated, flask-shaped phialides, usually with a flaring collarete. Several additions and clarifications of species were published subsequently, e.g.

by Cole & Kendrick (1973) and Sivasithamparam (1975). Gams & Holubová-Jechová (1976) described a new, obviously also heterogeneous section, *Catenulatae* W. Gams, based on the anamorph of *Lasiosphaeria hirsuta* (Fr.) Ces. & De Not. This section was characterized by often catenate conidia with distinctly truncate conidial bases; it included several species of varying pigmentation. A key to some phialophora-like genera in the broadest sense was given by Crous *et al.* (1996).

A first step towards excluding defined groups of taxa from *Phialophora sensu* Schol-Schwarz was made by Gams & McGinnis (1983), who recognized *Lecythophora* Nannfeldt (Fig. 2 d) for anamorphs of *Coniochaeta* (Sacc.) Cooke [in Schol-Schwarz the *Ph. hoffmannii*-group + *Ph. lignicola* (Nannf.) Goidānich].

Coryne Nees, anamorph of the discomycete genus *Ascocoryne* J.W. Groves & D.E. Wilson (1967), was included in *Phialophora* by Schol-Schwarz (1970) but can easily be distinguished, as discussed below.

Phaeoacremonium W. Gams *et al.* (Fig. 2 f) was introduced by Crous *et al.* (1996) for species similar to *Phialophora parasitica* Ajello *et al.*, colonizers of vascular systems in woody plants and from medical origins, with slender, aculeate phialides and non-flaring collarettes.

Several similar fungi were not included in *Phialophora* previously, but should be considered here:

Phialocephala W.B. Kendrick (1961) is characterized by dark conidiophore stipes and densely penicillate conidiophores bearing conidia in slimy masses.

Cladorrhinum Sacc. & Marchal (Fig. 2 b) was reintroduced by Von Arx & Gams (1967) for phialophora-like anamorphs with almost exclusively intercalary phialides with widely flaring collarettes, formed in a reticulate system of aerial hyphae.

Exophiala J.W. Carmichael is now clearly defined for black-yeast anamorphs of *Capronia* Sacc., with imperceptibly annellate, narrow conidiogenous openings (de Hoog, 1977; Masclaux *et al.*, 1995; and many subsequent publications). *Wangiella* McGinnis (1977) was introduced for a similar, closely related fungus that has conidiogenous cells with multiple annellidic openings, as well as separately developing phialides.

Pseudogliomastix W. Gams (Fig. 3 a) was introduced by Gams & Boekhout (1985) for the anamorph of *Wallrothiella subiculosa* Höhnelt, which was formerly classified in *Gliomastix* Guég. It is characterized by pigmented, branched conidiophores and somewhat darker conidia, the walls of which are pigmented throughout and not only pigment-incrustated, as they are in some species of *Acremonium* section *Gliomastix*.

Redelimitation and reclassification of phialophora-like anamorphs

In this section, the various components of *Phialophora* are distributed over the respective orders and families of ascomycetes, with some necessary renaming. In cases where the anamorphs are rarely encountered in culture separate from the teleomorph, little need is felt for formal anamorph binomials or separate anamorph genera.

LEOTIALES

Helotiaceae

Species of *Ascocoryne* J.W. Groves & D.E. Wilson 1967 have anamorphs now classified in *Coryne* (Fig. 1 f), with hyaline, more or less penicillate conidiophores and phialides that lack any sign of visible collarette. They have a strong tendency to form sporodochium-like or gelatinous conidiomata *in vivo* and

in vitro (Fig. 1 f; Roll-Hansen & Roll-Hansen, 1979; Seifert, 1989). *Claussenomyces* Kirschst. is normally connected with synnematus anamorphs in *Dendrostilbella* Höhn. (Seifert, 1985) but some species form anamorphs *in vitro* that are indistinguishable from *Coryne* (G. Marson, unpublished).

Dermateaceae

The commonest saprobic species (-aggregates) classified in *Phialophora* are *Ph. fastigiata* (Lagerb. & Melin) Conant (Fig. 1 a) and *Ph. malorum* (Kidd & Beaumont) McColloch (Fig. 1 b, c). Le Gal & Mangenot (1960, 1961) demonstrated their relationship with discomycete teleomorphs in *Mollisia* (Fr.) P. Karst., *Pyrenopeziza* Fuckel and related genera. Greenleaf & Korf (1980) isolated a *Phialophora* that is similar to *Ph. fastigiata* (Lagerb. & Melin) Conant from *Mollisia dextrinophila* Korf (Fig. 1 d). Other recent ascospore isolates of such fungi did not produce phialophora-like anamorphs (M.M. Nauta, pers. comm.). While the vegetative hyphae in these species are more or less pigmented, the phialides are pale to hyaline, particularly the collarettes. For these species, the genus *Cadophora* Conant is available, which certainly now warrants recognition. The correct binomials should therefore be used as follows:

Cadophora fastigiata Lagerb. & Melin

Cadophora melinii Nannf.

Cadophora repens Davidson

Cadophora malorum (Kidd & Beaum.) W. Gams, *comb. nov.* = *Sporotrichum malorum* Kidd & Beaum., Trans. Brit. Mycol. Soc. 10: 111. 1974 = *Phialophora malorum* (Kidd & Beaum.) McColloch, Mycologia 36: 589. 1944. The synonyms listed by Schol-Schwarz (1970) under this name still require critical revision.

Other binomials available in *Cadophora* are not adopted at this time, pending a more thorough study on their identity.

Anamorphs of the closely related genus *Tapesia* (Pers.) Fuckel (= *Mollisia* (Fr.) P. Karst, *nom. cons.*) were placed by Aebi (1972) in the similar genus *Cystodendron* Bubák (Fig. 1 g), characterized by dark, densely penicillate and more or less sporodochial conidiophores and phialides with pronounced tubular collarettes.

Pseudopezizula tracheiphila (Müll.-Thurg.) Korf & Zhuang was associated with the anamorph *Phialophora tracheiphila* (Sacc. & D. Sacc.) Korf (Korf *et al.*, 1986). The vascular pathogen causing brown stem rot in soya beans, *Phialophora gregata* (Allington & Chamberlain) W. Gams (Fig. 1 e; Chen *et al.*, 1996; Yamamoto *et al.*, 1992), also has discomycete affinities according to 18S and 28S rDNA sequences (Paulin

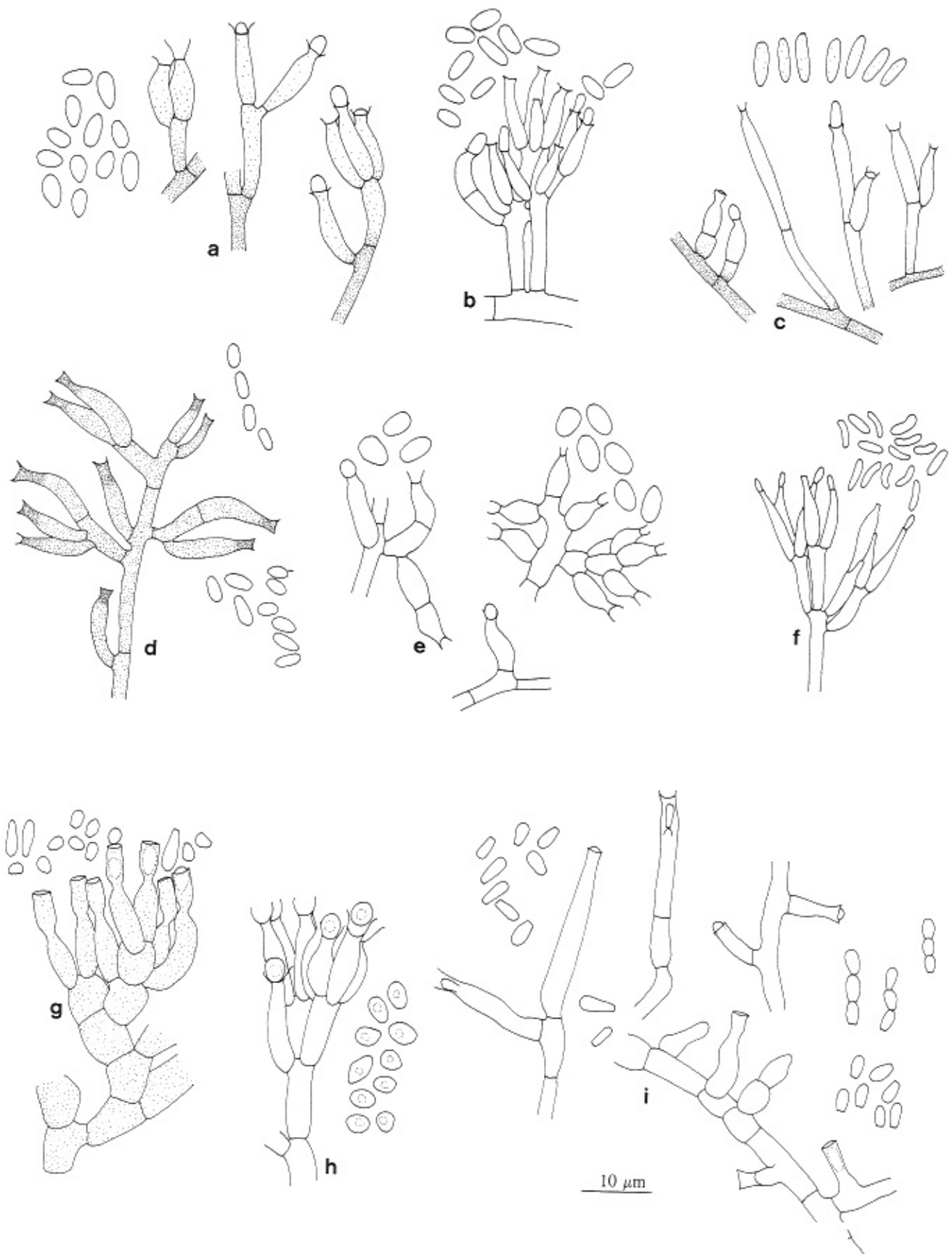


Fig. 1. Phialophora-like anamorphs of discomycetes. a. *Cadophora fastigiata*, CBS 226.30. b. and c. *Cadophora malorum*, CBS 260.32 and 258.89. d. Anamorph of *Mollisia dextrinospora*, CBS 401.78. e. *Phialophora gregata*, CBS 184.70. f. *Coryne* anamorph of *Ascocoryne sarcoides*, CBS 247.80. g. *Cystodendron dryophilum*, from type of *Tubercularia dryophila* in Herb. B. h. *Myrioconium* sp., CBS 465.71. i. Anamorph of *Cistella hymeniophila*, CBS 886.73 and herb. H.A. 4378 in CBS.

& Harrington, this volume). The generic classification of the anamorphs of these species awaits reconsideration.

Hyaloscyphaceae

Raschle (1977) illustrated several phialophora-like anamorphs of *Hyalopeziza* Fuckel, *Urceolella* Boud., and *Unguicularia* Höhn. species, without a detailed analysis. The connection of *Ph. rhodogena* (Mangenot) W. Gams from section *Catenulatae* (Fig. 1 i) with the teleomorph *Cistella hymeniophila* (P. Karst.) Korf was established by Helfer (1991). This species, like *Ph. brachyconia* W. Gams, *Ph. hyalina* W. Gams, and *Ph. brevicollaris* W. Gams, differs from the remaining members of the section by its hyaline hyphae and phialides. A separate generic classification may be envisaged.

Sclerotiniaceae

The common microconidial forms of many *Sclerotiniaceae* classified in *Myrioconium* Syd. (Fig. 1 h) have generally hyaline structures with densely, irregularly penicillate conidiophores, phialides with a pronounced collarette and slimy, subglobose conidia. A similar, not necessarily congeneric fungus, has been classified in *Phialophora* as *Ph. alba* van Beyma.

CALICIALES

Mycocaliciaceae

Mycocalicium schefflerae Samuels & D.E. Buchanan (1983) was shown to have a lecythophora-like palely pigmented anamorph with broad hyphae and many intercalary phialides.

SORDARIALES

Sordariaceae

Podospora austrohemisphaerica Lundqvist *et al.* (1999) was described as having densely penicillate conidiophores and phialides with a widely flaring collarette, resembling *Ph. cyclaminis* van Beyma; conidia are globose, individually hyaline but brownish in mass. In other species of the genus, the phialides are shorter and broadly flask-shaped, all producing guttulate conidia (Bell & Mahoney, 1995). According to Lundqvist *et al.* (l.c.), twenty species of *Podospora* Ces. have so far been linked with phialophora-like anamorphs, others with *Cladorrhinum*. It is noteworthy to observe that these conidia do not germinate *in vitro* and apparently have spermatial functions, suggesting little need for a formal anamorph name.

Wallrothiella subiculosa Höhn., [anam. *Pseudogliomastix protea* (Sacc.) W. Gams & Boekhout (1985) (Fig. 3 a)], seems to occupy a basal position in the *Sordariales*, but its family classification is still

uncertain (Réblová & Winka, 2000); an affinity to the *Niessliaceae* has been assumed, but, according to 28S rDNA sequences, the genus falls outside the *Hypocreales* (Rehner & Samuels, 1995). According to conidiophore and conidial pigmentation, *Phialophora geniculata* van Emden 1975 (Fig. 3 b), a species common in tropical alkaline soils (Nagai *et al.*, 1995) (syn. *Ph. taiwanensis* Matsushima 1983), is very close to the anamorph of *W. subiculosa* and may be congeneric.

Batistiaceae

Batistia annulipes (Mont.) Cif. was connected with the synnematosous anamorph genus *Acrostroma* Seifert in cultural work by Samuels & Rodrigues (1989). This fungus is a synnematosous counterpart of *Phialophora* section *Catenulatae*.

Lasiosphaeriaceae

Lasiosphaeria hirsuta (Fr. : Fr.) Ces. & De Not., *L. hispida* (Tode : Fr.) Fuckel (Fig. 2 a) and *L. ovina* (Fr. : Fr.) Ces. & De Not. of *Phialophora* section *Catenulatae* have pigmented mycelium and phialophora-like conidiophores with mostly catenate conidia. The teleomorphs of *Cladorrhinum* (Fig. 2 b) are found in *Apiosordaria* von Arx & W. Gams and *Cercophora* Fuckel in this family (Mouchacca & Gams, 1993). An anamorph more typical of *Phialophora* with conidial heads is seen in the similar *Eosphaeria uliginosa* (Fr.) Höhn. (Petrini *et al.*, 1984). *Barrina polyspora* Ramaley (1997), with its polysporous asci, might belong to this family as well. Its anamorph resembles the lecythophora-like anamorph of *Munkovalsaria rubra* Aptroot *et al.* in the *Dacampiaceae*. Because cultures of these anamorphs are probably rarely encountered separately from their teleomorphs, no nomenclatural formalization is envisioned at this time.

Chaetosphaeriaceae

This family was introduced for *Chaetosphaeria* Tul. & C. Tul. and related genera by Réblová *et al.* (1999) and comprises mainly anamorphs in *Chloridium* Link, *Dictyochoaeta* Speg., *Menispora* Pers., *Kylindria* DiCosmo *et al.* and *Cacumisporium* Preuss (see Réblová, this volume). *Phialophora phaeophora* W. Gams (section *Catenulatae*) (Fig. 2 c) is the anamorph of *Chaetosphaeria pygmaea* (P. Karst.) O. Const. (Constantinescu *et al.*, 1995). This species could be interpreted as a miniature *Chloridium*.

Coniochaetaceae

Lecythophora Nannf. (Fig. 2 d) has been repeatedly correlated with teleomorphs in *Coniochaeta* (e.g. Checa

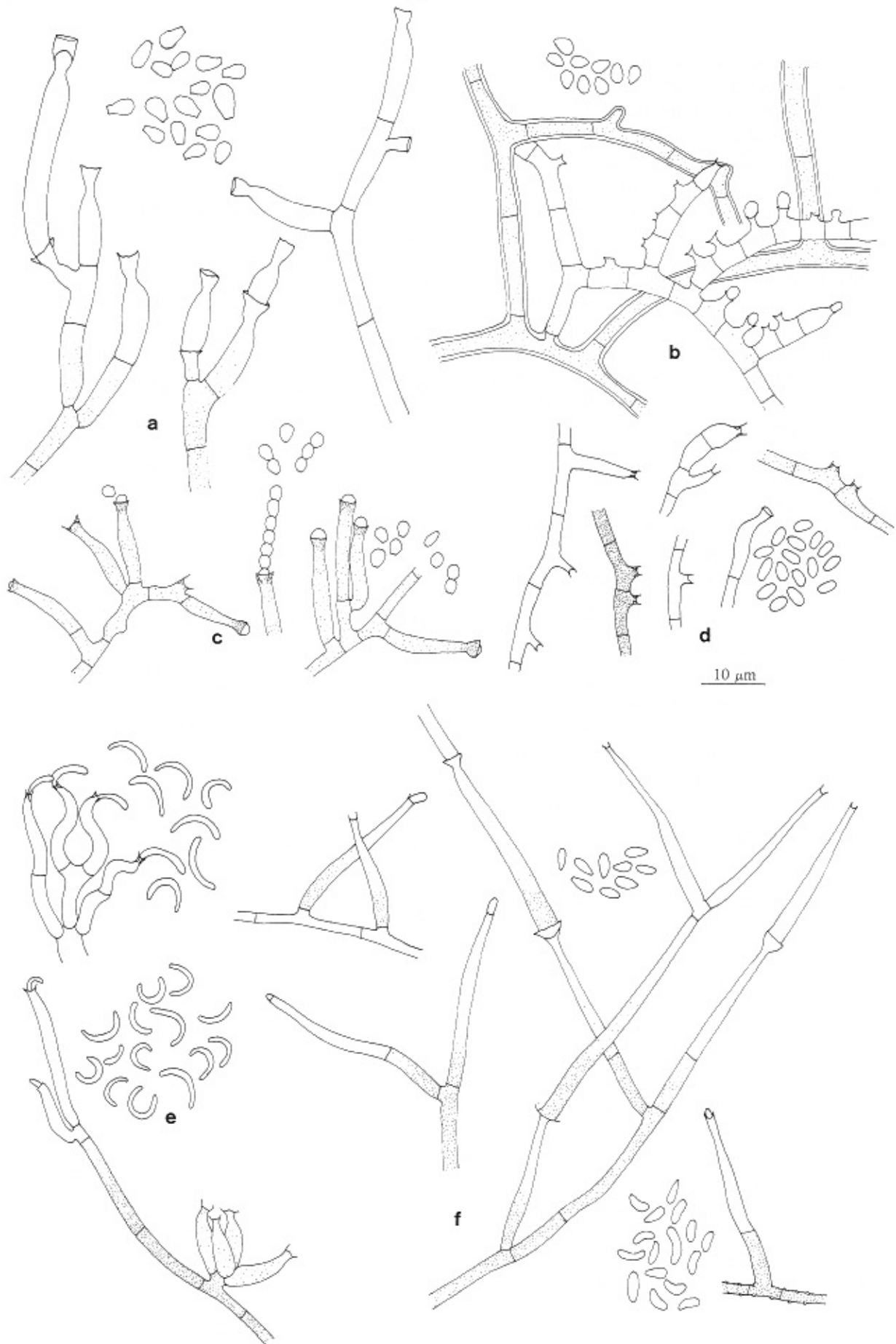


Fig. 2. Phialophora-like anamorphs of pyrenomycetes. **a.** Anamorph of *Lasiochaeria hispida*, CBS 955.72. **b.** *Cladorrhinum samala*, type specimen, IMI 113129. **c.** *Phialophora phaeophora* anamorph of *Chaetosphaeria pygmaea*, CBS 699.74. **d.** *Lecytophora lignicola*, CBS 267.33 **e.** *Harpophora radicola*, CBS 296.53 and 350.77. **f.** *Phaeoacremonium parasiticum*, CBS 984.73.

Checa *et al.*, 1988; Romero *et al.*, 1999). The genus is characterized and differentiated from *Phialophora* by more or less hyaline undifferentiated fertile hyphae, with mostly intercalary phialides, with very short lateral necks but mostly visible periclinal wall thickenings below the hardly flaring collarettes. The different anamorphs of distinct *Coniochaeta* species have not yet been differentiated in culture.

Helminthosphaeriaceae

Veramycina elegans Subram. is a phialocephala-like synanamorph of *Oedemium minus* (Link) S. Hughes, anamorph of *Chaetosphaerella phaeostroma* (Durieu & Mont.) E. Müll. & C. Booth in the *Helminthosphaeriaceae* (Réblová, 1999), but this fungus does not grow in culture.

DIAPORTHALES

Magnaporthaceae

A distinct group of species formerly included in *Phialophora* comprises the anamorphs of *Gaeumannomyces* von Arx & D.L. Olivier and *Magnaporthe* R.A. Krause & R.K. Webster, which have mostly sickle-shaped phialoconidia (Fig. 2 e). The colonies are fast-growing and often have darker and broader 'runner hyphae' (see also Cunningham, 1981). In several species, narrower and strongly curved conidia were found to be non-germinable spermatia, while broader, less curved conidia germinated readily *in vitro* (Wong & Walker, 1975). The habit of the fast-growing, thin colonies is a valuable criterion for recognizing this group (Deacon, 1973, 1974; Landschoot & Jackson, 1989; Scott & Deacon, 1983; Walker, 1980, 1981; Wong & Walker, 1975). The introduction of a new genus for this group is appropriate because the anamorphs are morphologically sufficiently distinct. Only a few anamorph species have so far formally been named in this complex, besides the well-known plant-pathogenic teleomorphs. A further addition is the closely related *Cephalosporium maydis* Samra *et al.*, for which so far no adequate generic classification has been available (Bryan *et al.*, 1995; Ward & Bateman, 1999). According to ITS sequences, *Phialophora radiculicola* Cain (Fig. 2 e) is a central species in this complex, well suited to serve as type of the new anamorph genus *Harpophora*. *Cephalosporium maydis*, together with *Magnaporthe poae* Landschoot & Jackson and *Gaeumannomyces incrustans* Landschoot & Jackson are genetically somewhat more distant (Ward & Bateman, 1999).

HARPOPHORA W. Gams, *gen. nov.*

Genus hyphomycetum, anamorphoses Magnaporthacearum complectens. Coloniae celeriter crescentes, plus minusve

olivaceo-brunneae, hyphis latioribus radiantibus. Phialides *Phialophorae* similes, plus minusve pigmentatae, collare divergens ferentes. Conidia cylindrica, valde curvata, fere hyalina. Species typica *Harpophora radiculicola* (Cain) W. Gams.

A genus of hyphomycetes comprising phialidic anamorphs of the *Magnaporthaceae*. Colonies growing rapidly, more or less olivaceous-brown, typically showing some broader radiating 'runner hyphae' and narrower lateral hyphae. Phialides resembling those of *Phialophora*, more or less pigmented, with a conspicuous divergent collarette. Conidia borne in slimy heads, cylindrical with strong curvature, hyaline, sometimes not germinable *in vitro*. Type species *Harpophora radiculicola* (Cain) W. Gams.

Etym.: Greek *harpos* = sickle, in reference to the conidial shape, *pherein* = to bear and alluding to the similarity with *Phialophora*.

Harpophora radiculicola (Cain) W. Gams, *comb. nov.* (Fig. 2 e).

= *Phialophora radiculicola* Cain, *Canad. J. Bot.* 30: 340. 1952.

Harpophora maydis (Samra *et al.*) W. Gams, *comb. nov.*

= *Cephalosporium maydis* Samra, Sabet & Hingorani, *Phytopathology* 53: 404. 1963.

Harpophora graminicola (Deacon) W. Gams, *comb. nov.*

= *Phialophora radiculicola* var. *graminicola* Deacon, *Trans. Brit. Mycol. Soc.* 63: 322. 1974 = *Phialophora graminicola* (Deacon) John Walker, *Mycotaxon* 11: 90. 1980.

Harpophora zeicola (Deacon & D.B. Scott) W. Gams, *comb. nov.*

= *Phialophora zeicola* Deacon & D.B. Scott, *Trans. Brit. Mycol. Soc.* 81: 256. 1983.

Phaeoacremonium Crous *et al.* (1996) (Fig. 2 f) is characterized by pigmented conidiophores that gradually become paler in the upper part, slender, aculeate phialides with hardly flaring collarettes, and hyaline, mostly allantoid conidia. Yan *et al.* (1995) already demonstrated that the type species, formerly classified as *Ph. parasitica* Ajello *et al.*, was unrelated to other species of *Phialophora* using ITS rDNA sequences. Its affinity with the *Magnaporthaceae* was shown by Dupont *et al.* (1998). One equally common colonizer of woody vascular bundles in grapevine, the causal agent of Petri grapevine decline called *Phaeoacremonium chlamydosporum* W. Gams *et al.*, falls outside this complex. It has been transferred to a separate genus, *Phaeomoniella* Crous & W. Gams in the *Chaetothyriales* (Fig. 4 c; Crous & Gams, 2000). This fungus is also morphologically distinguished by very darkly pigmented conidiophore stipes, which contrast sharply with the pale phialides and never curved conidia.

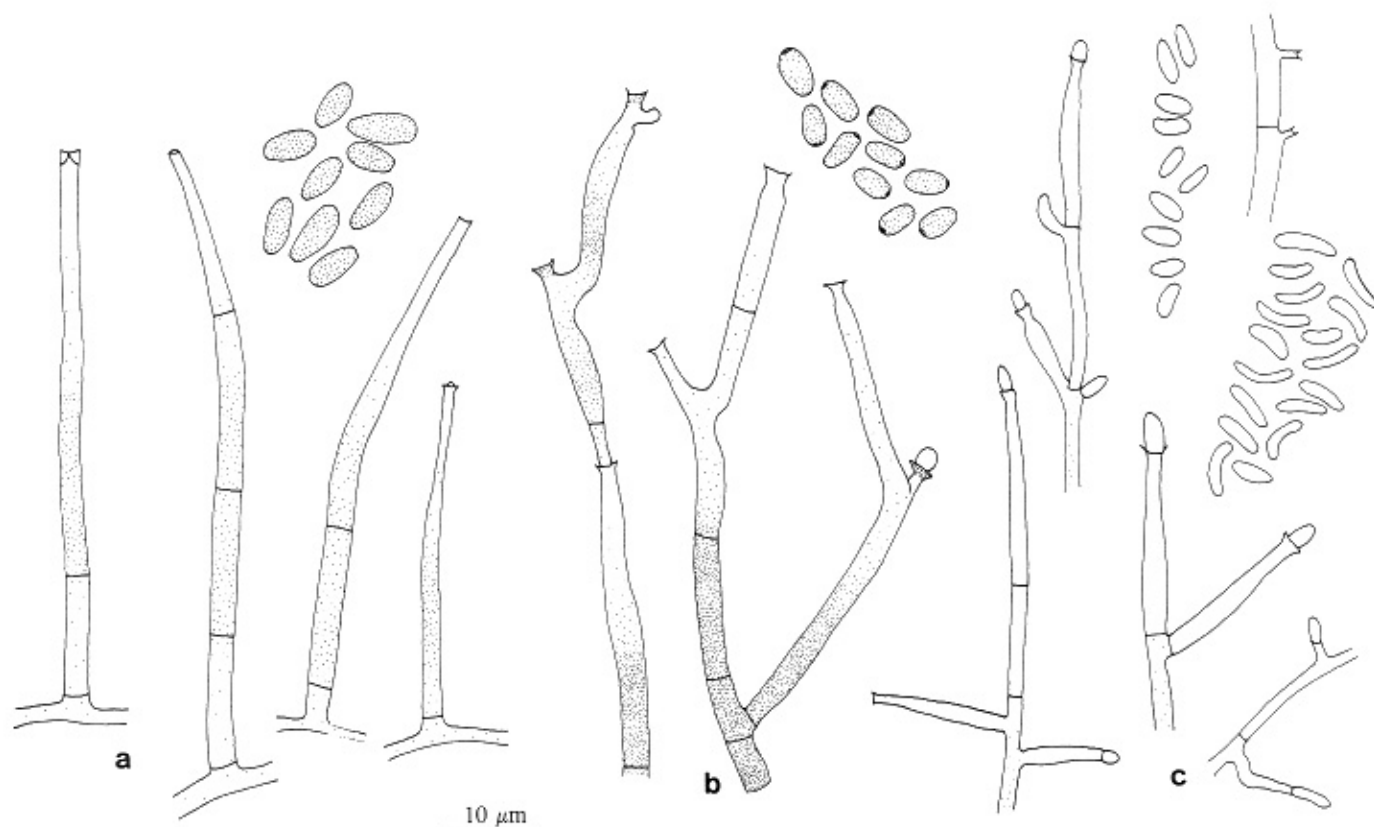


Fig. 3. Phialophora-like anamorphs of uncertain affinity. a. *Pseudogliomastix* anamorph of *Wallrothiella subiculosa*, CBS 656.94. b. *Phialophora geniculata*, CBS 673.83. c. *Margarinomyces bubakii*, CBS 269.33.

OPHIOSTOMATALES

Ophiostomataceae

While most anamorphs in this family have polyblastic conidiogenesis, a few species of *Ophiostoma* have *Phialocephala* anamorphs. A similar genus, *Sporendocladia* G. Arn. ex Nag Raj & W.B. Kendrick was delimited by Wingfield *et al.* (1987) because of 'ring wall building' in the development of basally truncate, catenate conidia. A phylogenetic analysis of this group is still missing.

HYPOCREALES

Clavicipitaceae

The classification of the tolypocladium-like *Phialophora endoparasitica* Barron & Szijarto (1982) and *Ph. tribrachiata* Barron & Szijarto (1984) in the *Clavicipitaceae* is still speculative, lacking teleomorph or DNA sequence evidence. These species parasitize rotifers and form hyaline colonies. In any case, they are unrelated to other species of *Phialophora*.

Acremonium, a genus with *Hypocreales* affinities, need not be further considered in this context, except

for *A. atrogriseum* (Panasenko) W. Gams, which was recently again described as a new species, *Phialophora intermedia* Iwatsu *et al.* (1988). The correct classification of this fungus with slightly swollen phialides and somewhat pigmented mycelium has not yet been resolved.

Ceratostomataceae (*Melanosporaceae*), family of uncertain affinity (*Hypocreales* or *Sordariales?*, Rehner & Samuels, 1995).

The genus *Proteophiala* Ciferri (1957) (and not the sometimes cited genus *Harziella* Cost. & Matr., an illegitimate homonym, introduced for a very distinct hypocrealean mycoparasite growing on *Lepista nuda*) is best suited to accommodate the short-lived phialidic anamorphs of many *Ceratostomataceae*: Species of *Melanospora* Corda, *Microthecium* Corda (Hawksworth & Udagawa, 1977), *Persiciospora* P.F. Cannon & D. Hawksw., *Sphaerodes* Clem. (Horie *et al.*, 1986), *Pteridiosperma* Penz. & Sacc. (Udagawa & Muroi, 1981), and synanamorphs of *Harzia* Cost., *Olpitrichum* G.F. Atk. and *Papulaspora* Preuss. This genus is distinguished by its completely hyaline hyphae, conidiophores and conidia, and the flask-

shaped phialides borne on apically more or less inflated conidiophores.

SPATHULOSPORALES (order of uncertain affinity)
In *Hispidocarpomyces galaxauricola* Nakagiri (*Hispidocarpomycetaceae*), Nakagiri (1993) found penicillate spermatophores with very long tubular collarettes, and in *Retrostium amphiroae* Nakagiri & Tad. Ito (1997) (*Spathulosporaceae*) the collarettes were somewhat shorter and more phialophora-like.

DOTHIDEALES

Dothideaceae

The tree root-inhabiting and poorly sporulating species, *Phialophora finlandica* C.J.K. Wang & Wilcox and *Phialocephala fortinii* C.J.K. Wang & Wilcox (sterile mycelium known as *Mycelium radices atrovirens* Melin) (Wang & Wilcox, 1985; Harney *et al.*, 1997), are related to *Hortaea* Nishim. & Miyaji in the *Dothideales* (Rogers *et al.*, 1999). Other species of *Phialocephala* have teleomorphs in *Ophiostoma* (see above).

Dacampiaceae

Munkovalsaria rubra Aptroot *et al.* (Aptroot, 1995) is associated with a lecythophora-like anamorph with relatively broad hyphae. No binomial anamorph name is needed for this very characteristic fungus, which has the unique odour of *m*-cresol in culture.

Unclassified family

Tirisporella beccariana (Ces.) E.B.G. Jones *et al.* (1996) has very broad hyphae and a phialophora-like anamorph with cup-shaped collarettes and elongate dacryoid conidia, otherwise resembling *Ph. olivacea* W. Gams in section *Catenulatae*.

CHAETOTHYRIALES

Herpotrichiellaceae

Molecular studies by Yan *et al.* (1995), Untereiner & Naveau (1999), de Hoog *et al.* (1999) and others have shown that the type species of *Phialophora*, *Ph. verrucosa* Medlar, and its closest relative, *Ph. americana* (Nannf.) S. Hughes (Fig. 4 a), belong to the *Herpotrichiellaceae*, *Chaetothyriales*. The latter species was connected to the teleomorph *Capronia semimmersa* (Candoussau & Sulmont) Untereiner & Naveau (Untereiner & Naveau, 1999). These species are commonly found on decayed wood and both can cause chromoblastomycosis and other diseases in humans, as reviewed by de Hoog *et al.* (1999). Morphologically, they are characterized by short, lageniform, darkly pigmented phialides, with distinct, usually even darker, flaring collarettes (Fig. 5, left column).

This combination of morphological features distinguishes these and two newly described taxa (de Hoog *et al.*, 1999) from all others classified in the genus. Other *Capronia* teleomorphs with *Phialophora* connections are *Capronia acutisetata* Samuels, *C. epimyces* M.E. Barr and *C. dactylotricha* Untereiner *et al.* (Untereiner, 1995; Untereiner *et al.*, 1995; Untereiner, this volume); the latter two also have *Exophiala* synanamorphs with percurrent proliferation. This is the group of *Phialophora* species that comprises most of the medically relevant members and it will continue to form the core of a naturally delimited genus *Phialophora*.

Exophiala is a monophyletic though highly diversified group, also connected to teleomorphs in *Capronia* (Uijthof, 1996; Uijthof *et al.*, 1997; Untereiner & Naveau, 1999; Rogers *et al.*, 1999); it is characterized by dark conidiogenous cells with inconspicuous annellidic elongation (Fig. 5, top left). Structures appearing similar to polyphialides in *E. dermatitidis* have the same annellidic mechanism, though extremely condensed, seen when using SEM, as well as the occasional occurrence of phialides with balloon-shaped collarettes. McKemy *et al.* (1999) still recognized the genus *Wangiella* McGinnis (1977) for this species and *E. heteromorpha* because of the additional presence of phialides, but in both species conidiogenous cells with percurrent elongation (though inconspicuous) predominate. Haase *et al.* (1999), using SSU rDNA sequencing, found that *E. dermatitidis*, *E. heteromorpha* and *E. mansonii* form a weakly separated subclade within the *Herpotrichiellaceae*, for which no clear-cut phenetic criterion is available. Therefore, it seems preferable to retain all these closely related taxa in one genus, *Exophiala*.

Cladophialophora Borelli (1980) is intimately related with the other *Herpotrichiellaceae* (Masclaux *et al.*, 1995; Gerrits van den Ende & de Hoog, 1999). It is distinguished by the production of a synanamorph with chains of cladosporium-like, hardly seceding blastoconidia, as well as phialophora-like conidia.

UNCLASSIFIED

Margarinomyces: Van Beyma (1943) recognized *Margarinomyces* Laxa as distinct from *Phialophora*, because the phialides of its species commonly lack flaring collarettes. Schol-Schwarz (1970) merged the two genera, because in the type species, *M. bubakii* Laxa (Fig. 3 c), collarettes can sometimes be observed. A feature generally overlooked in this fungus is the 'acropleurogenous' pattern of branching; i.e., a prostrate fertile hypha ends with a phialidic opening, then, tracing it backwards, one or several intercalary phialides follow with lateral necks, before further back discrete, lateral phialophora-type phialides with a basal

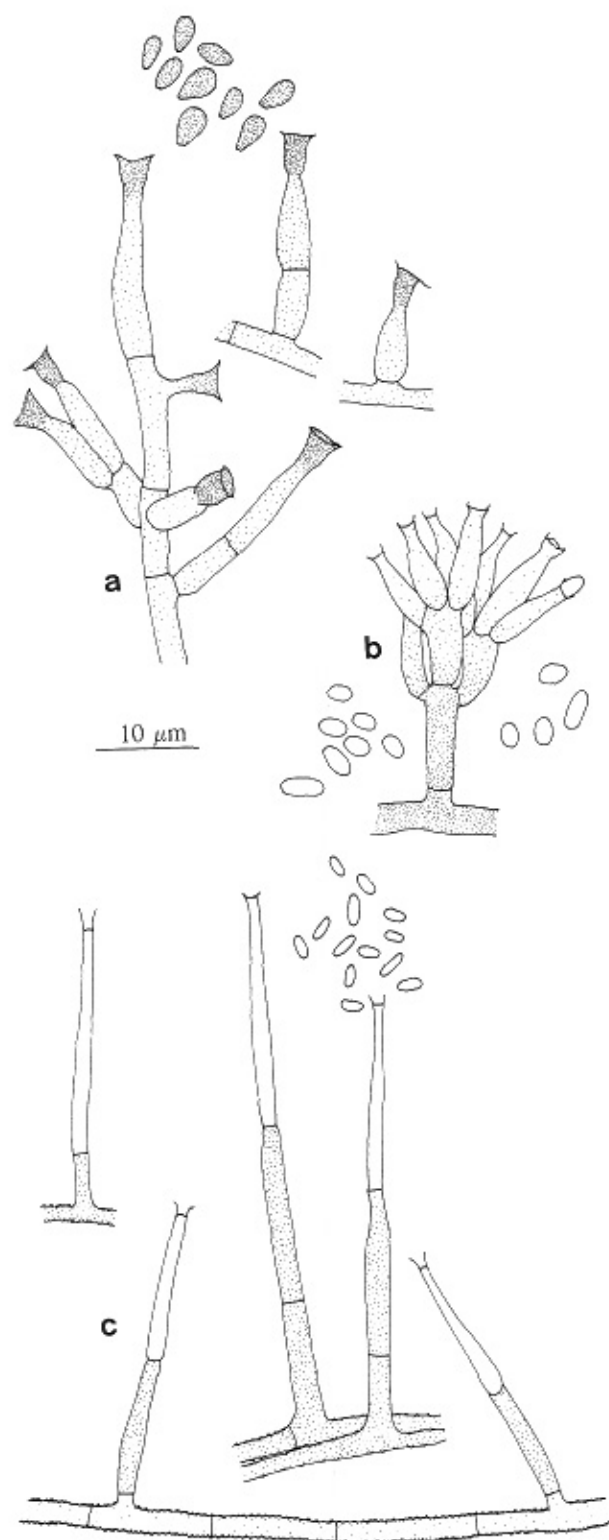


Fig. 4. Phialophora-like anamorphs of loculoascomycetes. a. *Phialophora americana*, CBS 281.35. b. *Phialophora?* *finlandica*, CBS 166.90. c. *Phaeomoniella chlamydospora*, CBS 239.74.

septum are formed. This feature is unusual in this complex and seems to warrant the recognition of a

redefined genus *Margarinomyces*. This pattern is also observed in the hyaline counterpart, *Phialemonium* W. Gams & McGinnis (1983). But the affinity of these two anamorph genera among the ascomycetes has not yet been elucidated.

The species *Phialophora richardsiae* (Nannf.) Conant and *Ph. mustea* Neerg. are characterized by their dimorphic conidia (darkly pigmented and hyaline) and saucer-shaped collarettes. The former species has been sequenced by Yan *et al.* (1995) and found to occupy a distant position from other *Phialophora* species, but no conclusion about its phylogenetic affinities was made.

The causal agent of carnation wilt, *Ph. cinerescens* (Wollenw.) van Beyma, has densely penicillate hyaline phialides with pronounced vase-shaped collarettes and somewhat pigmented conidia. It may also have a remote relationship.

Not all species described by Schol-Schwarz (1970) and subsequent authors in *Phialophora* can be reclassified, at present, and this survey is admittedly incomplete. To revise the enormous amount of material available will require major efforts. At the moment, a broad genus *Phialophora sensu lato* continues to have its value as a kind of dustbin for poorly classified fungi or simply as a morphological term. Less differentiated phialophora-like synanamorphs commonly occurring as synanamorphs of other hyphomycete genera are not treated here.

Criteria for distinction of anamorph groups

Conidiogenesis is phialidic in all these fungi, with conidia being blown out in basipetal succession from a single conidiogenous locus within a collarette, with pronounced periclinal wall thickening resulting from successive conidium formation.

The most suitable criteria for further subdivision are found in the pigmentation of the mycelium and the fertile hyphae. In species of *Phialophora sensu stricto*, all structures are darkly pigmented. In *Cadophora* and *Harpophora* species, old hyphae are dark, younger parts near-hyaline, with conidiophores and phialides being intermediate. Colonies of *Harpophora* species grow faster and have sickle-shaped conidia.

In addition, colony habit and growth rate are valuable in recognizing members of the *Chaetothyriales*. Their colonies are very dark olivaceous, compact, black-yeast-like, and slow-growing. The strongest contrast occurs with the *Harpophora* anamorphs of *Gaeumannomyces* species, which have less pigmented and fast-growing colonies, while other groups are intermediate.

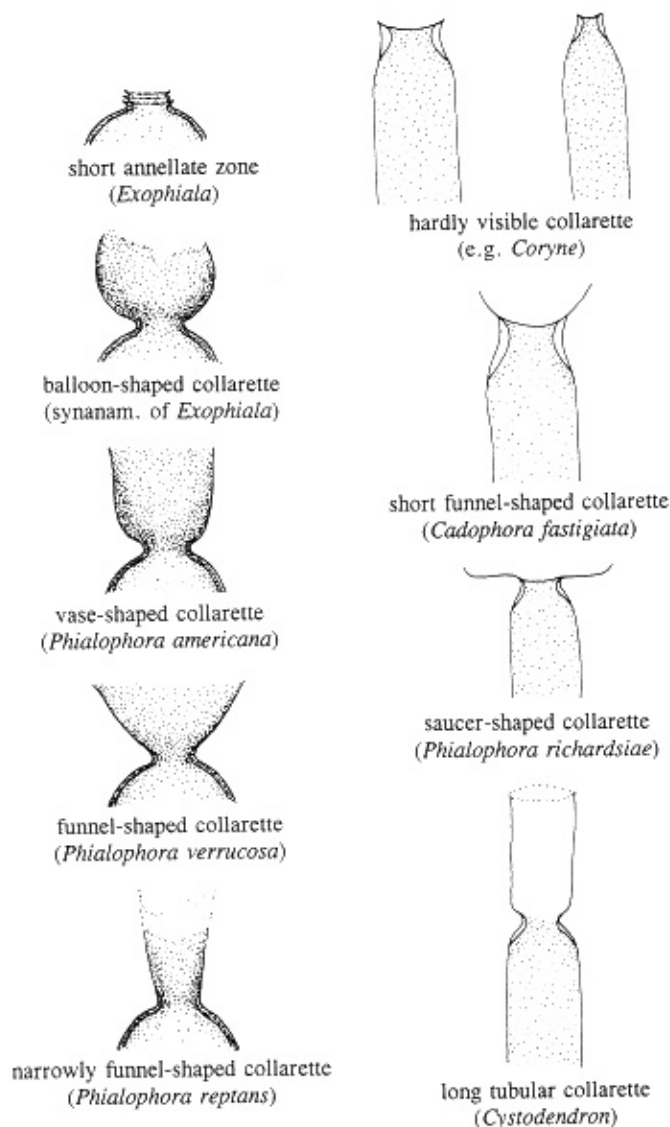


Fig. 5. Shapes of phialides in phialophora-like taxa (left column after de Hoog *et al.*, 1999).

Phialide shape: Short flask-shaped phialides or intercalary phialides with sessile collarettes are characteristic of species of *Phialophora sensu stricto*. In most other taxa discussed, the phialides are more or less cylindrical.

Intercalary phialides: In most taxa of *Phialophora sensu lato*, intercalary phialides with lateral collarettes occur occasionally as well as the dominant terminal phialides. In species of *Lecythophora* and *Cladorrhinum*, intercalary phialides predominate, whereas terminal or lateral discrete phialides comprise a minority. An acropleurogenous pattern is characteristic of discrete groups of anamorphs: behind a terminal phialide follows a series of intercalary cells with

subterminal lateral phialidic necks, before discrete lateral phialides are formed further back. This is particularly characteristic of *Margarinomyces bubakii* in the pigmented and *Phialemonium* species in the non-pigmented phialophora-like hyphomycetes.

Shape of the collarette (Fig. 5): In species of *Phialophora sensu stricto*, de Hoog *et al.* (1999) distinguished four shapes of collarettes, which all are somewhat constricted at the phialide tip (Fig. 5, left column). In addition, the extremes of either saucer-shaped or perfectly tubular collarettes occur, as well as less differentiated shapes (Fig. 5, right column). In *Margarinomyces* and *Coryne* species, flaring collarettes are usually absent.

Conidial shape and pigmentation: In most phialophora-like taxa, conidia are elongate. But (sub-)globose to dacryoid conidia occur in *Ph. cyclaminis*, *Ph. richardsiae*, *Myrioconium* spp., *Cladorrhinum* spp., and anamorphs of *Podospora* spp., *Tirisporella beccariana*, etc. In addition to the species of *Phialophora sensu stricto*, the occurrence of pigmented conidia is a valuable feature in identifying *Ph. cinerescens*. Dimorphic, strongly pigmented and hyaline, conidia are characteristic of the still unclassified species *Ph. richardsiae* and *Ph. mustea* Neergaard.

Conidial germinability may be a further criterion. In *Cladorrhinum foecundissimum* Sacc. & Marchal, conidia do not germinate, but in some other species of the genus they do. For the anamorphs of *Podospora*, Lundqvist *et al.* (1999) stated that conidia have a spermatial function, as they do in the members of the *Spathulosporales* listed. In *Harpophora* species, germinable conidia are observed next to non-germinable spermatia, apparently not sharply morphologically delimited (Wong & Walker, 1975).

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