**Mycosphaerella** is polyphyletic

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**Abstract**: Mycosphaerella, one of the largest genera of ascomycetes, encompasses several thousand species and has anamorphs residing in more than 30 form genera. Although previous phylogenetic studies based on the ITS DNA locus supported the monophyly of the genus, DNA sequence data derived from the LSU gene distinguish several clades and families in what has hitherto been considered to represent the Mycosphaerellaceae. Several important leaf spotting and extremotolerant species need to be disposed to the genus Teratosphaeria, for which a new family, the Teratosphaeriaceae, is introduced. Other distinct clades represent the Schizothyriaceae, Davidiellaceae, Capnodiaceae, and the Mycosphaerellaceae. Within the two major clades, namely Teratosphaeriaceae and Mycosphaerellaceae, most anamorph genera are polyphyletic, and new anamorph concepts need to be derived to cope with dual nomenclature within the Mycosphaerellaceae complex.

**Taxonomic novelties**: Batcheloromyces eucalypti (Alcorn) Crous & U. Braun, comb. nov., Catenulosorma Crous & U. Braun, gen. nov., Catenulosorma abietis (Butlin & Pahli) Crous & U. Braun, comb. nov., Catenulosorma chromoblastomycosum Crous & U. Braun, sp. nov., Catenulosorma elgneri (Joanne E. Taylor & Crous) Crous & U. Braun, comb. nov., Catenulosorma excentricum (B. Sutton & Ganap.) Crous & U. Braun, comb. nov., Catenulosorma germanicum Crous & U. Braun, sp. nov., Catenulosorma macowanii (Sacc.) Crous & U. Braun, comb. nov., Catenulosorma microsporum (Joanne E. Taylor & Crous) Crous & U. Braun, comb. nov., Catenulosorma proteusrum (Crous & M.E. Palm) Crous & U. Braun, comb. nov., Penidiella cream & U. Braun, gen. nov., Penidiella colombiana Crous & U. Braun, sp. nov., Penidiella cubensis (R.F. Castaño) Braun, Crous & U. Braun, comb. nov., Penidiella flicordophora Crous & U. Braun, sp. nov., Penidiella stromelicidae (Milio & Dunav) Crous & U. Braun, comb. nov., Penidiella venezuelensis (R.F. Castañeda) U. Braun, sp. nov., Readeriella vaalea (K.D. Hyde & Crous) Crous & U. Braun, comb. nov., Readeriella tridade (Crous & U. Braun, sp. nov., Readeriella quasicercospora (Crous & Alfenas) Crous & U. Braun, comb. nov., Readeriella gauchensis (M.-N. Cortinas & J.M. Wing) Crous & U. Braun, comb. nov., Readeriella molleri (Crous & M.J. Wing) Crous & U. Braun, comb. nov., Readeriella nubiosa (Ganap. & Corbin) Crous & U. Braun, comb. nov., Readeriella pulcherrima (Gadgil & M. Dick) Crous & U. Braun, comb. nov., Readeriella stellensbochiana (Crous & U. Braun, comb. nov., Readeriella toledana (Crous & Bills) Crous & U. Braun, comb. nov., Readeriella zuluanesis (M.J. Wing) Crous & T.A. Cout) Crous & U. Braun, comb. nov., Teratosphaeria africana (Crous & M.J. Wing) Crous & U. Braun, comb. nov., Teratosphaeria asiatica (Crous) Crous & U. Braun, comb. nov., Teratosphaeria asociata (Crous & Cameron) Crous & U. Braun, comb. nov., Teratosphaeria bellula (Crous & M.J. Wing) Crous & U. Braun, comb. nov., Teratosphaeria cryptica (Cooke) Crous & U. Braun, comb. nov., Teratosphaeria elgneri (Crous & Alfenas) Crous & U. Braun, comb. nov., Teratosphaeria excentricum (Crous & Cameron) Crous & U. Braun, comb. nov., Teratosphaeria flabriata (Crous & Summerell) Crous & U. Braun, comb. nov., Teratosphaeria flexuosa (Crous & M.J. Wing) Crous & U. Braun, comb. nov., Teratosphaeria gamsi (Crous) Crous & U. Braun, comb. nov., Teratosphaeria jesterhokens (P.S. van Wyk, Marsas & Knox-Dav) Crous & U. Braun, comb. nov., Teratosphaeria maxii (Crous) Crous & U. Braun, comb. nov., Teratosphaeria mexicana (Crous) Crous & U. Braun, comb. nov., Teratosphaeria molleri (Crous) Crous & U. Braun, comb. nov., Teratosphaeria nubiosa (Cooke) Crous & U. Braun, comb. nov., Teratosphaeria ochra (Crous & M.J. Wing) Crous & U. Braun, comb. nov., Teratosphaeria pileiflaxis (Crous & M.J. Wing) Crous & U. Braun, comb. nov., Teratosphaeria perpendiculata (Crous & M.J. Wing) Crous & U. Braun, comb. nov., Teratosphaeria plumbulitans (Crous & Mandisal) Crous & U. Braun, comb. nov., Teratosphaeria pseudosafricana (Crous & T.A. Cout) Crous & U. Braun, comb. nov., Teratosphaeria pseudocryptica (Crous) Crous & U. Braun, comb. nov., Teratosphaeria pseudosuberosa (Crous & M.J. Wing) Crous & U. Braun, comb. nov., Teratosphaeria quasicercospora (Crous & T.A. Cout) Crous & U. Braun, comb. nov., Teratosphaeria readenelleophora (Crous & Mandisal) Crous & U. Braun, comb. nov., Teratosphaeria secundaria (Crous & Alfenas) Crous & U. Braun, comb. nov., Teratosphaeria stramenticola (Crous & Alfenas) Crous & U. Braun, comb. nov., Teratosphaeria suberosa (Crous & F.E. Ferreira, Alfenas & M.J. Wing) Crous & U. Braun, comb. nov., Teratosphaeria suttonii (Crous & M.J. Wing) Crous & U. Braun, comb. nov., Teratosphaeria toledana (Crous & Bills) Crous & U. Braun, comb. nov., Teratosphaeriaceae Crous & U. Braun, fam. nov.

**Key words**: Ascomycetes, Batcheloromyces, Colletogloeopsis, Readeriella, Teratosphaeria, Trimmatispora, DNA sequence comparisons, systematics.

**INTRODUCTION**

The genus Mycosphaerella Johanson as presently circumscribed contains close to 3000 species (Aptroot 2006), excluding its anamorphs, which represent thousands of additional species (Crous et al. 2000, 2001, 2004a, b, 2006a, b, 2007b, Crous & Braun 2003). Crous (1998) predicted that Mycosphaerella would eventually be split according to its anamorph genera, and Crous et al. (2000) recognised six sections, as originally defined by Barr (1972). This was followed by a set of papers (Crous et al. 2001, Goodwin et al. 2001), where it was concluded, based on ITS DNA sequence data, that Mycosphaerella was monophyletic. A revision of the various coelomycete and hyphomycete anamorph concepts led Crous & Braun (2003) to propose a system whereby the asexual morphs could be allocated to various form genera affiliated with Mycosphaerella holomorphs.

In a recent study that formed part of the US “Assembling the Fungal Tree of Life” project, Schoch et al. (2006) were able to show that the Mycosphaerellaceae represents a family within Capnodiaceae. Furthermore, some variation was also depicted within the family, which supported similar findings in other recent papers employing LSU sequence data, such as Hunter et al. (2006), and Batzer et al. (2007). To further elucidate the phylogenetic variation observed within the Mycosphaerellaceae in these studies, a subset of isolates was selected for the present study, representing the various species recognised as morphologically distinct from Mycosphaerella s. str.

The genus Mycosphaerella has in recent years been linked to approximately 30 anamorph genera (Crous & Braun 2003, Crous et al. 2007b). Many of these anamorph genera resulted from a reassessment of cercosporoid forms. Chupp (1954) was of the opinion that they all represented species of the genus Cercospora Fresen., although he clearly recognised differences in their morphology. In a series of papers by Deighton, as well as others such as Sutton, Braun and Crous, the genus Cercospora was delimited based on its type species, Cercospora penicillata (Ces.) Fresen., while taxa formerly included in the genus by Chupp (1954) but differing in conidiophore arrangement, conidiogenesis, pigmentation, conidiatal catenulation, septation, and scar/hilum structure were allocated to other genera. Similar studies in which the type species were recollected and subjected to DNA sequence...
| Anamorph                          | Teleomorph                                  | Accession number | Host                                      | Country     | Collector       | GenBank Accession number |
|----------------------------------|---------------------------------------------|------------------|-------------------------------------------|-------------|-----------------|--------------------------|
| Batcheloromyces eucalypti        | CBS 313.76; CPC 3632                         |                  | Eucalyptus tessellaris                    | Australia   | J.L. Alcorn     | EU019245                |
| Batcheloromyces leucadendri      | CBS 110892; CPC 1837                        |                  | Leucadendron sp.                          | South Africa| L. Swart        | EU019246                |
| Batcheloromyces proteae          | CBS 110696; CPC 1518                        |                  | Ptelea cynaroides                         | South Africa| L. Viljoen      | EU019247                |
| Capnobotrylla renispora          | CBS 214.90*; CBS 176.88; IAM 13014; JCM 6932|                  | Capnobotrys neessii                       | Japan       | J. Sugiyama     | EU019248                |
| Catenulostoma abietis            | CBS 290.90                                  |                  | Man, skin lesion                          | Netherlands | R.G.F. Wintermans| EU019249                |
| Catenulostoma castellani        | CBS 105.75*; ATCC 2478                      |                  | Man, tinea nigra                          | Venezuela   | —               | EU019250                |
| Catenulostoma chromoblastomycosum| CBS 597.97                                  |                  | Man, chromoblastomycosis                  | Zaire       | V. de Brouwere  | EU019251                |
| Catenulostoma elghense           | CBS 111030; CPC 1958                        |                  | Ptelea grandiceps                         | South Africa| J.E. Taylor     | EU019252                |
| Catenulostoma germanicum         | CBS 539.88                                  |                  | Stone                                     | Germany     | —               | EU019253                |
| Catenulostoma macowanii          | CBS 110756; CPC 1872                       |                  | Ptelea nitida                             | South Africa| J.E. Taylor     | EU019254                |
| Catenulostoma microsporum        | CBS 110890; CPC 1832; Teratosphaeria microsphaera|              | Ptelea cynaroides                         | South Africa| L. Swart        | EU019255                |
| Catenulostoma sp.                | CBS 118911; CPC 12085                      |                  | Eucalyptus sp.                            | Uruguay     | M.J. Wingfield  | EU019256                |
| Cercosporella centauricola       | CBS 120253                                  |                  | Centarea solstitialis                     | Greece      | D. Berner       | EU019257                |
| Cibisella dimorphospora          | CBS 120034; CPC 12636                       |                  | Eucalyptus nitens                         | Australia   | —               | EU019258                |
| Cibisella minutapora             | CPC 13071*                                 |                  | Eucalyptus henryi                         | Australia   | A.J. Cameron     | EU019259                |
| Cibisella nontingens             | CBS 120725*; CPC 13217                      |                  | Eucalyptus tereticornis                   | Australia   | B. Summerell     | EU019260                |
| Cladosporium bruheii             | Davidiella allitica                         | CBS 115663; ATCC 6670; CPC 5101 | CCA-treated Douglas-fire pole            | U.S.A., New York| C.J. Wang     | EU019261                |
| Cladosporium cladosporoides      | CBS 109.21; ATCC 11277; ATCC 200940; IFO 638; IMI 049625 |                  | Sooty mould on Hedera helix               | U.K.        | —               | EU019262                |
| Cladosporium sphaerospermum      | CBS 188.54; ATCC 11290; IMI 049638          |                  | —                                         | —           | —               | EU019263                |
| Cladosporium uredinicola         | ATCC 46649                                  |                  | Hyperparasite on Cronartium fusiforme f. sp. quercum | U.S.A., Alabama| —              | EU019264                |
| Coccodinium bartschi             | CBS 121703; CPC 13861–13863                 |                  | Sooty mould on unidentified tree          | Canada      | K.A. Seifert    | EU019265                |
| Dissoconium aciculare            | CBS 342.82*; CPC 1534                       |                  | Eysiphe, on Medicago lupulina             | Germany     | T. Hijwegen     | EU019266                |
| Dissoconium commune              | "Mycosphaerella" communis                   | CBS 114238*; CPC 10440 | Eucalyptus globulus                       | Spain       | J.P.M. Vazquez  | EU019267                |
| Dissoconium dekkeri              | "Mycosphaerella" lateralis                  | CBS 567.89*; CPC 1535 | Juniperus chinensis                       | Netherlands | T. Hijwegen     | EU019268                |
| Fumago spora capnodioides        | Capnodium salicinum                         | CBS 131.34       | Sooty mould on Bursaria spinosa           | Indonesia   | —               | EU019269                |
| Hortaea werneckii                | CBS 107.67*                                 |                  | Man, tinea nigra                          | Portugal    | —               | EU019270                |
| Nothothalassia dendritica        | Teratosphaeria dendritica                   | CPC 12820        | Eucalyptus nitens                         | Australia   | A.J. Cameron     | EU019271                |
| "Passalora" zambiae              | CBS 112971*; CMW 14782; CPC 1227            |                  | Eucalyptus globulus                       | Zambia      | T. Coutinho     | EU019272                |
| Pendiella columbiana             | CBS 486.80                                  |                  | Paepalanthus colombianus                  | Colombia    | W. Gams         | EU019274                |
| Anamorph          | Teleomorph          | Accession number | Host                        | Country     | Collector          | GenBank Accession number |
|-------------------|---------------------|------------------|----------------------------|-------------|--------------------|--------------------------|
| Penidiella nectandrae | CBS 734.87*; ATCC 200392; INIFAT 87/45 | Nectandra coriacea | Cuba                      | R.F. Castañeda & G. Arnold | EU019275               |
| Penidiella rigidophora | CBS 314.95* | Leaf litter of Smilax sp. | Cuba                      | R.F. Castañeda | EU019276               |
| Penidiella strumelloidea | CBS 114484*; VKM F-2534 | Carex leaf from stagnant water | Russia                  | S. Ozereskaya | EU019277               |
| Penidiella venezuelensis | CBS 106.75* | Man,-tree nigra | Venezuela                  | D. Borelli   | EU019278               |
| Phaeotheca triangularis | CBS 471.90* | Wet surface of humidifier of air conditioning | Belgium                | H. Beguin     | EU019279               |
| Phaeothecoidea eucalypti | CPC 13010 | Corymbia henryi | Australia                  | B. Summerell | EU019280               |
| Phaeothecoidea eucalypti | CPC 12918* | Eucalyptus botryoides | Australia                | B. Summerell | EU019281               |
| Pleurophoma sp. | Teratosphaeria fibrillosa | Protea nita | South Africa               | J.E. Taylor  | EU019282               |
| Pseudotaeniolina globosa | CBS 109889* | Rock | Italy                      | C. Urzi      | EU019283               |
| Ramularia pratensis var. pratensis | CPC 11294 | Rumex crispus | Korea                     | H.D. Shin    | EU019284               |
| Ramularia sp. | CBS 324.87 | On Mycosphaerella sp., leaf spot on Brassica sp. | Netherlands | —                       | EU019285               |
| Readeriella brunneotingens | CPC 13303 | Eucalyptus tereticornis | Australia                | P.W. Crous   | EU019286               |
| Readeriella destructans | CBS 111396*; CPC 1366 | Eucalyptus grandis | Indonesia                 | M.J. Wingfield | EU019287               |
| Readeriella eucalyptoides | CPC 12352 | Eucalyptus sp. | U.S.A. Hawaii              | W. Gams      | EU019288               |
| Readeriella eucalyptoides | CPC 11196 | Eucalyptus globulus | Spain                     | M.J. Wingfield | EU019289               |
| Readeriella gauchensis | CBS 120303*; CMW 17331 | Eucalyptus grandis | Uruguay                  | M.J. Wingfield | EU019290               |
| Readeriella mirabilis | CBS 116293; CPC 10596 | Eucalyptus fastigata | New Zealand               | W. Gams      | EU019291               |
| Readeriella molleriana | CPC 131164*; CMW 4940; CPC 1214 | Eucalyptus globulus | Portugal                  | M.J. Wingfield | EU019292               |
| Readeriella ovata complex | CPC 18 | Eucalyptus cladocalyx | South Africa              | P.W. Crous   | EU019293               |
| Readeriella ovata complex | CPC 111149; CPC 23 | Eucalyptus cladocalyx | South Africa              | P.W. Crous   | EU019294               |
| Readeriella stellenboschiana | CBS 116248; CPC 10886 | Eucalyptus sp. | South Africa               | P.W. Crous   | EU019295               |
| Readeriella zuluensis | CBS 120301*; CMW 17321 | Eucalyptus grandis | South Africa               | M.J. Wingfield | EU019296               |
| Septoria tritici | Mycosphaerella graminicola | Triticum aestivum | —                         | G.H.J. Kema  | EU019297               |
| Septoria tritici | CBS 100335; IPO 69001.61 | Triticum sp. | South Africa              | P.W. Crous   | EU019298               |
| Trimmatostruma betulinum | CBS 282.74 | Betula verrucosa | Netherlands               | W.M. Loerakker | EU019299               |
| Trimmatostruma salticis | CPC 13571 | Salix alba | Germany                   | U. Braun     | EU019300               |
| Trimmatostruma bellula | CBS 111700; CPC 1821 | Protea eximia | South Africa               | J.E. Taylor  | EU019301               |
| Trimmatostruma mexicana | CPC 12349 | Eucalyptus sp. | U.S.A. Hawaii              | W. Gams      | EU019302               |
| Trimmatostruma globulosa | CBS 114419; CPC 10497 | Eucalyptus globulus | New Zealand               | —                       | EU019303               |
| Trimmatostruma globulosa | CBS 116005*; CMW 3282; CPC 937 | Eucalyptus globulus | Australia                 | A. Carnegie   | EU019304               |
analysis were undertaken to characterise Mycosphaerella (Verkley et al. 2004), and anamorph genera such as Pseudocercospora Speg., Stigmina Sacc., Phaeoisariopsis Ferraris (Crous et al. 2006a), Ramulispora Mura (Crous et al. 2003), Batcheloromyces Marasas, P.S. van Wyk & Knox-Dav. (Taylor et al. 2003), Phaeolepispora Rangel and Dothistroma Hulbary (Crous et al. 2000, 2001, Barnes et al. 2004).

To assess the phylogeny of the species selected for the present study, DNA sequences were generated of the 28S rRNA (LSU) gene. In a further attempt to address monophyletic groups within this complex, these data were integrated with their morphological characteristics. To further resolve pleomorphism among the species studied, isolates were examined on a range of cultural media to induce possible synanamorphs.

MATERIALS AND METHODS

Isolates

Chosen isolates represent various species previously observed to be morphologically distinct from Mycosphaerella s. str. (Crous 1998, Crous et al. 2004a, b, 2006a, b, 2007b). In a few cases, specifically Teratosphaeria fibrillosa Syd. & P. Syd. and Coccodinium bartschii A. Massal., fresh material had to be collected from South Africa and Canada, respectively. Excised tissue pieces bearing ascomata were soaked in water for approximately 2 h, after which they were placed in the bottom of Petri dish lids, with the top half of the dish containing 2% malt extract agar (Gams et al. 2007).

Ascospore germination patterns were examined after 24 h, and single-ascospore and conidial cultures established as described by Crous (1998). Colonies were sub-cultured onto synthetic nutrient-poor agar (SNA), potato-dextrose agar (PDA), oatmeal agar (OA), MEA (Gams et al. 2007), and incubated at 25 °C under continuous near-ultraviolet light to promote sporulation.

DNA phylogeny

Fungal colonies were established on agar plates, and genomic DNA was isolated following the CTAB-based protocol described in Gams et al. (2007). The primers V9G (de Hoog & Gerrits van den Ende 1998) and LR5 (Vilgalys & Hester 1990) were used to amplify part of the nuclear rDNA operon spanning the 3' end of the 18S rRNA gene (SSU), the first internal transcribed spacer (ITS), the 5.8S rRNA gene, the second ITS region (ITS2) and the 5' end of the 28S rRNA gene (LSU). The primers ITS4 (White et al. 1990), LR0R (Rehner & Samuels 1994), LR3R (www.biology.duke.edu/fungi/mycolab/primers.htm), and LR6 (Moncalvo et al. 1993), were used as internal sequence primers to ensure good quality sequences over the entire length of the amplicon. The ITS1, ITS2 and 5.8S rRNA gene (ITS) were only sequenced for isolates of which these data were not available. The ITS data were not included in the analyses but deposited in GenBank where applicable. The PCR conditions, sequence alignment and subsequent phylogenetic analysis using parsimony, distance and Bayesian analyses followed the methods of Crous et al. (2006c). Gaps longer than 10 bases were coded as single events for the phylogenetic analyses; the remaining gaps were treated as new character states. Sequence data were deposited in GenBank (Table 1) and alignments in TreeBASE (www.treebase.org).

Taxonomy

Wherever possible, 30 measurements (× 1 000 magnification)
RESULTS

DNA phylogeny

Amplification products of approximately 1 700 bases were obtained for the isolates listed in Table 1. The LSU region of the sequences was used to obtain additional sequences from GenBank which were added to the alignment. The manually adjusted alignment contained 97 sequences (including the two outgroup sequences) and 844 characters including alignment gaps. Of the 844 characters used in the phylogenetic analysis, 308 were parsimony-informative, 105 were variable and parsimony-uninformative, and 431 were constant.

The parsimony analysis of the LSU region yielded 1 135 equally most parsimonious trees (TL = 1 502 steps; CI = 0.446; RI = 0.787; RC = 0.351), one of which is shown in Fig. 1. Three orders are represented by the ingroup isolates, namely Chaetothyriales (100 % bootstrap support), Helotiales (100 % bootstrap support) and Capnodiaceae (100 % bootstrap support). These are discussed in detail in the Taxonomy and Discussion sections. A new collection of Coccodinium bartsi A. Massal clusters (100 % bootstrap support) with members of the Herpotrichiellaceae (Chaetothyriales), whereas the type species of the genus Trimmatostroma Corda, namely T. salcis Corda, as well as T. betulinum (Corda) S. Hughes, are allied (99 % bootstrap support) with the Dermataceae (Helotiales). The Capnodiaceae encompasses members of the Capnodiales, Trichosphaeriales, Davidiellaceae, Schizothyriaceae and taxa traditionally placed in the Mycosphaerellaceae, which is divided here into the Teratosphaeriaceae, (65 % bootstrap support), and the Mycosphaerellaceae (76 % bootstrap support), which contains several subclades. Also included in the Capnodiaceae are Devriesia staurophora (W.B. Kendr.), Seifert & N.L. Nick., Staninwardia suttonii Crous & Summerell and Capnobotryella renispora Sugiy. as sister taxa to Teratosphaeriaceae s. str. Neighbor-joining analysis using three substitution models on the sequence data yielded trees supporting the same topologies, but differed from the parsimony tree presented with regard to the order of the families and orders at the deeper nodes, e.g., the Helotiales and Chaetothyriales are swapped around, as are the Capnodiaceae and the Trichosphaeriales / Davidiellaceae (data not shown). Using neighbour-joining analyses, the Mycosphaerellaceae s. str. clade obtained 71 %, 70 % and 70 % bootstrap support respectively with the uncorrected “p”, Kimura 2-parameter and HKY85 substitution models wheresae the Teratosphaeriaceae clade obtained 74 %, 79 % and 78 % bootstrap support respectively with the same models. The Schizothyriaceae clade appeared basal in the Capnodiaceae, irrespective of which substitution model was used.

Bayesian analysis was conducted on the same aligned LSU dataset using a general time-reversible (GTR) substitution model with inverse gamma rates and dirichlet base frequencies. The Markov Chain Monte Carlo (MCMC) analysis of 4 chains started from a random tree topology and lasted 23 881 500 generations. Trees were saved each 100 generations, resulting in 238 850 saved trees. Burn-in was set at 22 000 000 generations after which the likelihood values were stationary, leaving 18 815 trees from which the consensus tree (Fig. 2) and posterior probabilities (PP’s) were calculated. The average standard deviation of split frequencies was 0.011508 at the end of the run. The same overall topology as that observed using parsimony was obtained, with the exception of the inclusion of Staninwardia suttonii in the Mycosphaerellaceae (PP value of 0.74) and not in the Teratosphaeriaceae. The Mycosphaerellaceae s. str. clade, as well as the Teratosphaeriaceae clade, obtained a PP value of 1.00.

Taxonomy

Based on the dataset generated in this study, several well-supported genera could be distinguished in the Mycosphaerella complex (Figs 1–2), for which we have identified morphological characters. These genera, and a selection of their species, are treated below.

Key to Mycosphaerella, and Mycosphaerella-like genera treated

1. Ascomata thyrothecial; anamorph Zygosporium ................................................................. Schizothyrium
2. Ascomata pseudothecial .............................................................................................................. 2
3. Ascomata frequently linked by superficial stroma; hamathelial tissue, ascospore sheath, multi-layered endotunica, prominent periphysoids, and ascospores turning brown in asci frequently observed ......................................................... Teratosphaeria
4. Conidiophores solitary, pale brown, giving rise to primary and secondary, actively discharged conidia; anamorph Dissoconium ...........................................................................................................teleomorph Mycosphaeraella-like
5. Conidiomata variable from solitary conidiophores to sporodochia, fascicles to pycnidia, but conidia not actively discharged ................................................................. Mycosphaerella s. str.
Fig. 1. One of 1135 equally most parsimonious trees obtained from a heuristic search with 100 random taxon additions of the LSU alignment using PAUP v. 4.0b10. The scale bar shows 10 changes, and bootstrap support values from 100 replicates are shown at the nodes. Thickened lines indicate the strict consensus branches and ex-type sequences are printed in bold face. The tree was rooted to two sequences obtained from GenBank (Athelia epiphylla AY586633 and Paullicorticium ansatum AY586693).
Fig. 2. Consensus phylogram (50% majority rule) of 18,815 trees resulting from a Bayesian analysis of the LSU sequence alignment using MrBayes v. 3.2. Bayesian posterior probabilities are indicated at the nodes. Ex-type sequences are printed in bold face. The tree was rooted to two sequences obtained from GenBank (Athelia epiphylla AY586633 and Paullicorticium ansatum AY586693).
Treatment of phylogenetic clades

**Davidiellaceae clade**

*Davidiella* Crous & U. Braun, Mycol. Progr. 2: 8. 2003.

Type species: *Davidiella tassiana* (De Not.) Crous & U. Braun, Mycol. Progr. 2: 8. 2003.

Basionym: *Sphaerella tassiana* De Not., Sferiacei Italici 1: 87. 1863.

Description: Schubert et al. (2007 – this volume).

Anamorph: Cladosporium Link, Ges. Naturf. Freunde Berlin Mag. Neuesten Entdeck. Gesammten Naturk. 7: 37. 1816.

Type species: Cladosporium herbarum (Pers. : Fr.) Link, Ges. Naturf. Freunde Berlin Mag. Neuesten Entdeck. Gesammten Naturk. 7: 37. 1816.

Basionym: Dematium herbarum Pers., Ann. Bot. (Usteri), Stück: Neuesten Entdeck. Gesammten Naturk. 7: 37. 1816.

Notes: The genus *Davidiella* (Davidiellaceae) was recently introduced for teleomorphs of *Cladosprium s. str.* (Braun et al. 2003). The genus *Cladosprium* is well-established, and contains around 772 names (Dugan 2003). The genus *Cladosprium* has 33 names (www.MycoBank.org), of which only around five species have acknowledged *Cladosprium* states.

**Teratosphaeriaceae clade**

*Teratosphaeria* Syd. & P. Syd., Ann. Mycol. 10: 39. 1912.

Type species: *Teratosphaeria fibrillosa* Syd. & P. Syd., Ann. Mycol. 10: 40. 1912. Fig. 3.

Description: Crous et al. (2004a; figs 182–185).

Notes: Although similar in morphology, the genus *Teratosphaeria* was separated from *Mycosphaerella* based on its ascomatal arrangement, and periphysate ostioles (Müller & Oehrens 1982). It was later synonymised under *Mycosphaerella* by Taylor et al. (2003), who showed that the type species clustered within *Mycosphaerella* based on ITS DNA sequence data. The LSU sequence data generated in the present study, has clearly shown that *Mycosphaerella* is polyphyletic, thus contradicting earlier reports of monophyly by Crous et al. (2000) and Goodwin et al. (2001), which were based on ITS data.

A re-examination of *T. fibrillosa*, the type species of *Teratosphaeria*, revealed several morphological features that characterise the majority of the taxa clustering in the clade, though several characters have been lost in some of the small-spored species. These characters are discussed below:

1. *Teratosphaeria fibrillosa* has a superficial stroma linking ascomata together, almost appearing like a spider’s web on the leaf surface. Although this feature is not seen in other taxa in this clade, some species, such as *M. suberosa* Crous, F.A. Ferreira, Alfenas & M.J. Wingf. and *M. pseudosuberosa* Crous & M.J. Wingf. have a superficial stroma, into which the ascomata are inbedded (Crous 1998, Crous et al. 2006b).

2. Ascospores of *Teratosphaeria* become brown and verruculose while still in their asci. This feature is commonly observed in species such as *M. jonkershoekensis* P.S. van Wyk, Marasas & Knox-Dav., *M. alstairii* Crous, *M. mexicana* Crous, *M. maxii* Crous and *M. excentricum* Crous & Carnegie (Crous 1998, Crous & Groenewald 2006a, b, Crous et al. 2007b).

3. A few ascomata of *T. fibrillosa* were found to have some pseudoparaphysoidal remnants (cells to distinguish pseudoparaphyses), though they mostly disappear with age. This feature is rather uncommon, though pseudoparaphyses were observed in ascomata of *M. eucalypti* (Wakef.) Hansf.

4. Ascospores of *Teratosphaeria* were found to be covered in a mucous sheath, which is commonly observed in other taxa in this clade, such as *M. bellula* Crous & M.J. Wingf., *M. pseudocryptica* Crous, *M. suberosa*, *M. pseudosuberosa*, *M. associata* Crous & Carnegie, *M. dendritica* Crous & Summerell and *M. fimbriata* Crous & Summerell (Crous et al. 2004b, 2006b, 2007b). Re-examination of fresh collections also revealed ascospores of *M. cryptica* (Cooke) Hansf. and *M. nubilosa* (Cooke) Hansf. to have a weakly definable sheath. Germinating ascospores of species in this clade all exhibit a prominent mucoid sheath.

5. Ascii of *T. fibrillosa* were observed to have a multi-layered endotunica, which, although not common, can be seen in species such as *M. excentrica*, *M. maxii*, *M. alstairii*, *M. pseudosuberosa*, *M. fimbriata* (Crous et al. 2006b, 2007b, Crous & Groenewald 2006a, b), and also *M. nubilosa*.

6. Finally, ascomata of *T. fibrillosa* and *T. proteae-areboreae* P.S. van Wyk, Marasas & Knox-Dav. have well-developed ostioral periphyses, which are also present in species such as *M. suberosa*, *M. pseudosuberosa*, *M. maxii* and *T. microspora* Joanne E. Taylor & Crous (Crous 1998, Crous et al. 2004a, b, 2006b). Morphologically thus, the *Teratosphaeria* clade is distinguishable from *Mycosphaerella s. str.*, though these differences are less pronounced in some of the smaller-spored species. Based on these distinct morphological features, as well as its phylogenetic position within the *Capnodiales*, a new family is herewith proposed to accommodate species of *Teratosphaeria*:

**Teratosphaeriaceae** Crous & U. Braun, fam. nov. MycoBank MB504464.

Ascomata pseudothecial, superficiales vel imersa, saepe in stromate ex cellulis brunneis pseudoparenchymatis disposta, globulares, unicellularis, papillatis, apice ostiolato, peripheritate, saepe cum periphysoidibus: tunica multistratata, ex cellulis brunneis angularibus composta, strato interiore ex cellulis applanatis hyalinis; saepe cum pseudoparaphysibus subcylindricis, ramosis, septatis, anastomosibus. Asci fasciculati, octospori, bitunicati, saepe cum endotunica multistratosa. Ascospores ellipsoideae-fusiformes vel obovoideae, -septatae, hyalinae, deinde palpide brunnaeae et verruculoseae, saepe mucosae.

Ascomata pseudothecial, superficially to immersed, frequently situated in a stroma of brown pseudoparenchymatal cells, globose, unicellular, papillate, ostiolate, canal periphysate, with periphysoids frequently present; wall consisting of several layers of brown texture angularis; inner layer of flattened, hyaline cells. *Pseudoparaphyses* frequently present, subcylindrical, branched, septate, anastomosing. *Asci* fasciculate, 8-spored, bitunicate, frequently with multi-layered endotunica. *Ascospores* ellipsoid-fusoid to obovoid, 1-septate, hyaline, but becoming pale brown and verruculose, frequently covered in mucoid sheath.

*Teratosphaeria africana* (Crous & M.J. Wingf.) Crous & U. Braun, comb. nov. MycoBank MB504466.
Fig. 3. Teratosphaeria fibrillosa (epitype material). A. Leaf spots. B. Subepidermal ascomata linked by means of stromatic tissue. C. Paraphyses among asci. D. Periphysoids. E. Ascospores becoming brown in asci. F–G. Multi-layered endotunica. H–K. Ascospores, becoming brown and verruculose. L–M. Germinating ascospores. Scale bars = 10 µm.

**Basionym**: Mycosphaerella africana Crous & M.J. Wingf., Mycologia 88: 450. 1996.

**Teratosphaeria associata** (Crous & Carnegie) Crous & U. Braun, **comb. nov.** MycoBank MB504467.
Basionym: Mycosphaerella associata Crous & Carnegie, Fungal Diversity 26: 159. 2007.

**Teratosphaeria alicantii** (Crous) Crous & U. Braun, **comb. nov.** MycoBank MB504468.
Basionym: Mycosphaerella alicantii Crous, in Crous & Groenewald, Fungal Planet, No. 4. 2006.
Anamorph: Batcheloromyces sp.
Teratosphaeria bellula (Crous & M.J. Wingf.) Crous & U. Braun, **comb. nov.** MycoBank MB504469.

Basionym: Mycosphaerella bellula Crous & M.J. Wingf., Mycotaxon 46: 20. 1993.

Teratosphaeria cryptica (Cooke) Crous & U. Braun, **comb. nov.** MycoBank MB504470.

Basionym: Sphaeria cryptica Cooke, Grevillea 20: 5. 1891.

≡ Mycosphaerella cryptica (Cooke) Hansf., Proc. Linn. Soc. New South Wales 81: 35. 1956.

Anamorph: **Readerella nubilosa** (Ganap. & Corbin) Crous & U. Braun, **comb. nov.** MycoBank MB504471.

Basionym: Colletogloeum nubilum Cooke, Trans. Brit. Mycol. Soc. 72: 237. 1979.

≡ Colletogloeopsis nubilum (Ganap. & Corbin) Crous & M.J. Wingf., Canad. J. Bot. 75: 668. 1997.

Teratosphaeria dendritica (Crous & Summerell) Crous & U. Braun, **comb. nov.** MycoBank MB504472.

Basionym: Mycosphaerella dendritica Crous & Summerell, Fungal Diversity 26: 161. 2007.

Anamorph: **Nothostrasseria dendritica** (Hansf.) Nag Raj, Canad. J. Bot. 61: 25. 1983.

Basionym: Spilomyces dendriticus Hansf., Proc. Linn. Soc. New South Wales 81: 32. 1956.

Teratosphaeria excentrica (Crous & Carnegie) Crous & U. Braun, **comb. nov.** MycoBank MB504473.

Basionym: Mycosphaerella excentrica Crous & Carnegie, Fungal Diversity 26: 164. 2007.

Anamorph: **Catenulostrama excentricum** (B. Sutton & Ganap.) Crous & U. Braun, **comb. nov.** MycoBank MB504475.

Basionym: Trimmatostroma excentricum B. Sutton & Ganap., New Zealand J. Bot. 16: 529. 1978.

Teratosphaeria fibrillosa Syd. & P. Syd., Ann. Mycol. 10: 40. 1912.

≡ Mycosphaerella fibrillosa (Syd. & P. Syd.) Joanne E. Taylor & Crous, Mycol. Res. 107: 657. 2003.

Specimens examined: **South Africa**, Western Cape Province, Bains Kloof near Wellington, on living leaves of Protea grandiflora, 26 Feb. 1911; E.M. Dodge, holotype PREM: Stellenbosch, Jonkershoek valley, 53°30' 44.4" 7° E18° 56' 50.6", 1 Apr. 2007, on leaves of Protea sp., P.W. Crous & L. Mostert, **epitype designated here** CBS H-19913, culture ex-epitype CBS 121707 = CPC 13960.

Teratosphaeria fimbriata (Crous & Summerell) Crous & U. Braun, **comb. nov.** MycoBank MB504476.

Basionym: Mycosphaerella fimbriata Crous & Summerell, Fungal Diversity 26: 166. 2007.

Teratosphaeria flexuosa (Crous & M.J. Wingf.) Crous & U. Braun, **comb. nov.** MycoBank MB504477.

Basionym: Mycosphaerella flexuosa Crous & M.J. Wingf., Mycol. Mem. 21: 58. 1998.

Teratosphaeria gamsii (Crous) Crous & U. Braun, **comb. nov.** MycoBank MB504478.

Basionym: Mycosphaerella gamsii Crous, Stud. Mycol. 55: 113. 2006.

Teratosphaeria jonkershoekensis (P.S. van Wyk, Marasas & Knox-Dav.) Crous & U. Braun, **comb. nov.** MycoBank MB504479.

Basionym: Mycosphaerella jonkershoekensis P.S. van Wyk, Marasas & Knox-Dav., J. S. African Bot. 41: 234. 1975.

Teratosphaeria maxii (Crous) Crous & U. Braun, **comb. nov.** MycoBank MB504480.

Basionym: Mycosphaerella maxii Crous, in Crous & Groenewald, Fungal Planet No. 6. 2006.

Teratosphaeria mexicana (Crous) Crous & U. Braun, **comb. nov.** MycoBank MB504481.

Basionym: Mycosphaerella mexicana Crous, Mycol. Mem. 21: 81. 1998.

Teratosphaeria microspora Joanne E. Taylor & Crous, Mycol. Res. 104: 631. 2000.

≡ Mycosphaerella microspora (Joanne E. Taylor & Crous) Joanne E. Taylor & Crous, Mycol. Res. 107: 657. 2003.

Anamorph: **Catenulostrama microsporum** (Joanne E. Taylor & Crous) Crous & U. Braun, **comb. nov.** MycoBank MB504482.

Basionym: Trimmatostroma microsporum Joanne E. Taylor & Crous, Mycol. Res. 104: 631. 2000.

Teratosphaeria molleriana (Thüm.) Crous & U. Braun, **comb. nov.** MycoBank MB504483.

Basionym: Sphaeria molleriana Thüm., Revista Inst. Sci. Lit. Coimbra 28: 31. 1881.

≡ Mycosphaerella molleriana (Thüm) Lindau, Nat. Pflanzenfam. 1: 424. 1897.

≡ Mycosphaerella vespa Carnegie & Keane, Mycol. Res. 102: 1275. 1998.

≡ Mycosphaerella ambipylla A. Maxwell, Mycol. Res. 107: 354. 2003.

Anamorph: **Readerella molleriana** (Crous & M.J. Wingf.) Crous & U. Braun, **comb. nov.** MycoBank MB504484.

Basionym: Colletogloeopsis molleriana Crous & M.J. Wingf., Canad. J. Bot. 75: 670. 1997.

Teratosphaeria nubilosa (Cooke) Crous & U. Braun, **comb. nov.** MycoBank MB504485.

Basionym: Sphaeria nubilosa Cooke, Grevillea 19: 61. 1892.

≡ Mycosphaerella nubilosa (Cooke) Hansf., Proc. Linn. Soc. New South Wales 81: 36. 1956.

≡ Mycosphaerella juvenis Crous & M.J. Wingf., Mycologia 88: 453. 1996.

Teratosphaeria ohnowa (Crous & M.J. Wingf.) Crous & U. Braun, **comb. nov.** MycoBank MB504486.

Basionym: Mycosphaerella ohnowa Crous & M.J. Wingf., Stud. Mycol. 50: 206. 2004.

Teratosphaeria parkiiaffinis (Crous & M.J. Wingf.) Crous & U. Braun, **comb. nov.** MycoBank MB504487.

Basionym: Mycosphaerella parkiiaffinis Crous & M.J. Wingf., Fungal Diversity 26: 168. 2007.

Teratosphaeria parva (R.F. Park & Keane) Crous & U. Braun, **comb. nov.** MycoBank MB504488.

Basionym: Mycosphaerella parva R.F. Park & Keane, Trans. Brit. Mycol. Soc. 79: 99. 1982.

≡ Mycosphaerella grandis Carnegie & Keane, Mycol. Res. 96: 414. 1994.

Teratosphaeria perpendicularis (Crous & M.J. Wingf.) Crous & U. Braun, **comb. nov.** MycoBank MB504489.

Basionym: Mycosphaerella perpendicularis Crous & M.J. Wingf., Stud. Mycol. 55: 113. 2006.

Teratosphaeria pluritubularis (Crous & Mansilla) Crous & U. Braun, **comb. nov.** MycoBank MB504490.

Basionym: Mycosphaerella pluritubularis Crous & Mansilla, Stud. Mycol. 55: 114. 2006.
**Teratosphaeria pseudoafricana** (Crous & T.A. Cout.) Crous & U. Braun, **comb. nov.** MycoBank MB504491. 
Basionym: *Mycosphaerella pseudoafricana* Crous & T.A. Cout., Stud. Mycol. 55: 115. 2006.

**Teratosphaeria pseudocryptica** (Crous) Crous & U. Braun, **comb. nov.** MycoBank MB504492. 
Basionym: *Mycosphaerella pseudocryptica* Crous, Stud. Mycol. 55: 116. 2006. 
Anamorph: **Readeriella** sp.

**Teratosphaeria pseudosuberosa** (Crous & M.J. Wingf.) Crous & U. Braun, **comb. nov.** MycoBank MB504493. 
Basionym: *Mycosphaerella pseudosuberosa* Crous & M.J. Wingf., Stud. Mycol. 55: 118. 2006. 
Anamorph: **Catenulostroma** sp.

**Teratosphaeria quasicercospora** (Crous & T.A. Cout.) Crous & U. Braun, **comb. nov.** MycoBank MB504494. 
Basionym: *Mycosphaerella quasicercospora* Crous & T.A. Cout., Stud. Mycol. 55: 119. 2006.

**Teratosphaeria readeriellophora** (Crous & Mansilla) Crous & U. Braun, **comb. nov.** MycoBank MB504495. 
Basionym: *Mycosphaerella readeriellophora* Crous & Mansilla, Stud. Mycol. 50: 207. 2004. 
Anamorph: **Readeriella readeriellophora** Crous & Mansilla, Stud. Mycol. 50: 207. 2004. Fig. 18.

**Teratosphaeria secundaria** (Crous & Alfenas) Crous & U. Braun, **comb. nov.** MycoBank MB504496. 
Basionym: *Mycosphaerella secundaria* Crous & Alfenas, Stud. Mycol. 55: 122. 2006.

**Teratosphaeria stramenticola** (Crous & Alfenas) Crous & U. Braun, **comb. nov.** MycoBank MB504497. 
Basionym: *Mycosphaerella stramenticola* Crous & Alfenas, Stud. Mycol. 55: 123. 2006.

**Teratosphaeria suberosa** (Crous, F.A. Ferreira, Alfenas & M.J. Wingf.) Crous & U. Braun, **comb. nov.** MycoBank MB504498. 
Basionym: *Mycosphaerella suberosa* Crous, F.A. Ferreira, Alfenas & M.J. Wingf., Mycologia 85: 707. 1993.

**Teratosphaeria suttonii** (Crous & M.J. Wingf.) Crous & U. Braun, **comb. nov.** MycoBank MB504499. 
Basionym: *Mycosphaerella suttonii* Crous & M.J. Wingf. (suttoniae), Canad. J. Bot. 75: 783. 1997. 
Anamorph: **Readeriella epicoccoides** (Cooke & Massée) Crous & U. Braun, **comb. nov.** MycoBank MB504500. 
Basionym: *Cercospora epicoccoides* Cooke & Massée apud Cooke, Grevillea 19: 91. 1891.

**Teratosphaeria toledana** (Crous & Bills) Crous & U. Braun, **comb. nov.** MycoBank MB504501. 
Basionym: *Mycosphaerella toledana* Crous & Bills, Stud. Mycol. 50: 208. 2004. 
Anamorph: **Readeriella toledana** (Crous & Bills) Crous & U. Braun, **comb. nov.** MycoBank MB504502. 
Basionym: *Phaeophleospora toledana* Crous & Bills, Stud. Mycol. 50: 208. 2004.

**Key to treated anamorph genera of Teratosphaeria (Teratosphaeriaceae)**

1. Hyphae submerged to superficial, disarticulating into arthroconidia ................................................................. 2
2. Hyphae not disarticulating into arthroconidia ........................................................................................................... 3

2. Mature, brown hyphae disarticulating into thick-walled, spherical, smooth to verruculose 0(–2) transversely septate, brown conidia .............................................................................................................. **Pseudotaeniolina** (= *Friedmanniomycetes*)

2. Hyphae superficial, brown to green-brown, smooth, disarticulating to form pale brown, cylindrical, 0–3-septate conidia with subtruncate ends, frequently with a **Readeriella** synanamorph .............................................................................. **Cibiessia**

3. Hyphal ends forming endoconidia; hyphae pale to medium brown, verruculose, end cells dividing into several brown, verruculose, thick-walled, ellipsoid to obovoid endoconidia ................................................................. **Phaeothecoidea**

3. Endoconidia absent .................................................................................................................................................. **4**

4. Conidiogenous cells integrated in hyphae; well-developed conidiomata or long, solitary, macronematous, terminally penicillate conidiophores absent .................................................................................. 5
4. Conidiomata well-developed or with long, solitary, terminally penicillate conidiophores .................................................. 7

5. Conidia in chains, holoblastic, pseudocladosporium-like in morphology, but scars and hila not excessively thickened, nor refractive, producing chlamydospores in culture; species are mostly heat resistant ................................................................. **Devresia**
5. Conidia solitary on indistinct to well defined phialides on hyphae ........................................................................ 6

6. Conidiogenous cells integrated in the distal ends of hyphae; conidia thick-walled, brown, smooth, 1-septate ............................................................................................................................... **Capnobotryella**
6. Conidiophores short and frequently reduced to conidiogenous cells that proliferate percurrently via wide necks, giving rise to hyaline, 0–(2)-septate, broadly ellipsoidal conidia .................................................. Hortaea

7. Conidia brown, with hyaline basal appendages; conidiomata pynidial, conidiogenous cells phialidic, but also percurrent, subhyaline .......................................................... Nothostrasseria

7. Conidia brown, but basal appendages lacking, amero- to scolecospores .................................................. 8

8. Conidiomata pynidial to acervular ............................................................................................................... 9

8. Conidiomata not enclosed by host tissue, fasciculate to sporodochial or solitary, hyphomycetous .................................................. 10

9. Conidia solitary, dry, without mucilaginous sheath .................................................................................. Readeriella

9. Conidia catenulate, with persistent mucilaginous sheath ........................................................................ Staninwardia

10. Conidiophores usually solitary, rarely densely fasciculate to synnematos (in vivo), penicillate, with a branched, apical conidiogenous apparatus giving rise to ramoconidia and branched chains of secondary conidia; scars not to slightly thickened and darkened-refractive ........................................................................................................ Penidiella

10. Conidiophores not penicillate, without a branched conidiogenous apparatus, in vivo fasciculate to sporodochial ........................................................................................................ 11

11. Biotrophic; fruiting composed of sporodochia and radiating layers of hyphae arising from the stromata, conidiophores arising from superficial sporodochia and radiating hyphae, conidiogenous cells unilocular, with conspicuous anellations, conidia solitary or in fragile disarticulating chains, aseptate or transversely 1–3-septate, usually with distinct frills, secession rhexolytic .................. Batcheloromyces

11. Biotrophic, leaf-inhabiting, with distinct, subepidermal to erumpent, well-developed sporodochia, or saxicolous, saprobic, sometimes causing opportunistic human infections; radiating layers of hyphae arising from sporodochia; conidiogenous cells without annellations; conidia in true simple or branched basipetal chains, transversely 1- to pluriseptate or with longitudinal and oblique septa (dictyosporous), occasionally disactoseptate ........................................................................ Catenulostroma

To explain the arguments behind the selection and synonymies of some of these anamorphic genera, they are briefly discussed below:

**Acidomyces** Baker et al., Appl. Environ. Microbiol. 70: 6270. 2004. (nom. invál.)

Type species: *Acidomyces richmondensis* Baker et al., Appl. Environ. Microbiol. 70: 6270. 2004. (nom. invál.)

Notes: The genus presently clusters among isolates in the *Teratosphaeria* clade based on sequences deposited in GenBank. *Acidomyces* lacks a Latin description and holotype specimen, and is thus invalidly described. The genus, which was distinguished from other taxa based on its DNA phylogeny (*Dothideomycetes*), forms filamentous hyphae with disarticulating cells. It is unclear how it differs from *Friedmanniomyces* Onofri and *Pseudotaeniolina* J.L. Crane & Schonk.

**Batcheloromyces** Marasas, P.S. van Wyk & Knox-Dav., J. S. African Bot. 41: 1975.

Type species: *Batcheloromyces proteae* Marasas, P.S. van Wyk & Knox-Dav., J. S. African Bot. 41: 43. 1975.

Description: Crous et al. (2004a; figs 4–26).

Notes: *Batcheloromyces* is presently circumscribed as a genus that forms emergent hyphae, giving rise to superficial sporodochial plates, forming brown, verrucose, erect conidiophores that proliferate holoblastically, with ragged percurrent proliferations that become visible with age. Conidia are produced singly or in fragile, disarticulating chains, are brown, thick-walled, 0–3 transversely euseptate (though at times they appear as distoseptate). The genus *Batcheloromyces* has in recent years been confused with *Stigmata* (Sutton & Pascoe 1989) on the basis that some collections showed conidiophores to give rise to solitary conidia only, though conidial catenulation was clearly illustrated by Taylor et al. (1999). In culture colonies tend to sporulate in a slimy mass (on OA), though a synanamorph can be seen (in *B. leucadendri*, Fig. 4) to sporulate via holoblastic conidogenesis on hyphal tips of the aerial mycelium, forming elongate-globose to ellipsoidal, muriformly septate, thick-walled conidia, that occur in clusters.

The finding that *Stigmata s. str.* [based on *S. platani* (Fuckel) Sacc., the type species] is a generic synonym of *Pseudocercospora* Sp. (Crous et al. 2006a), and that the type species of *Trimmastostroma* (*T. salicus*, Fig. 5) belongs to the *Helotiales* (Fig. 1), raises the question of where to place stigmina- and trimmastostrum-like anamorphs that reside in the *Teratosphaeria* clade. Although the stigmata-like species can be accommodated in *Batcheloromyces* (see Sutton & Pascoe 1989), a new genus is required for *Teratosphaeria* anamorphs that have a trimmastostrum-like morphology. The recognition of *Batcheloromyces* and the introduction of a new anamorph genus for trimmastostrum-like anamorphs of *Teratosphaeria* are also morphologically justified. *Batcheloromyces* is easily distinguishable from *Stigmata s. str.* by its special structure of the fruiting body, composed of sporodochia and radiating layers of hyphae arising from the sporodochia and the conidia often formed in delicate disarticulating chains. Trimmastostrum-like anamorphs of *Teratosphaeria* are morphologically also sufficiently distinct from *Trimmastostroma s. str.* (see notes under *Catenulostroma* Crous & U. Braun) as well as *Batcheloromyces* (see key above).

**Batcheloromyces eucalypti** (Alcom) Crous & U. Braun, comb. nov. MycoBank MB804503. Basionym: *Stigmata eucalypti* Alcom, Trans. Brit. Mycol. Soc. 60: 151. 1973.

**Capnobotryella** Sugiy., in Sugiyama, *Pleomorphic Fungi: The Diversity and its Taxonomic Implications* (Tokyo): 148. 1987.

Type species: *Capnobotryella renispora* Sugiy., in Sugiyama, *Pleomorphic Fungi: The Diversity and its Taxonomic Implications* (Tokyo): 148. 1987.

Description: Sugiyama & Amano (1987, figs 7.5–7.8).
Notes: The genus forms brown, septate, thick-walled hyphae, with ellipsoidal, 0–1-septate conidia forming directly on the hyphae, via minute phialides. Hambleton et al. (2003) also noted the occurrence of endoconidiation.

**Catenulostroma** Crous & U. Braun, gen. nov. MycoBank MB504474.

*Etymology:* Named after its catenulate conidia, and stromata giving rise to sporodochia.

Hyphomycetes. Differt a Trimmatostromate habitu phytoparasitico, maculis formantibus, conidiophoris saepe fasciculatis, per stoma emergentibus vel habitu saxiphilo-saprophyticus, interdum sejunctis ex mycosibus humanis.
Habit plant pathogenic, leaf-spotting or saxicolous-saprobic, occasionally isolated from opportunistic human mycoses. Mycelium internal and external; hyphae dark brown, septate, branched. Conidiomata in vivo vary from acervuli to sporodochia or fascicles of conidiophores arising from well-developed or reduced, pseudoparenchymatal stromata. Setae and hypophodia absent. Conidiophores arising from hyphae or stromata, solitary, fasciculate to sporodochial, in biotrophic, plant pathogenic species emerging through stoma, little differentiated, semimacromeromatus, branched or not, continuous to septate, brown, smooth to verruculose. Conidigenous cells integrated, terminal or conidiophores reduced to conidigenous cells, holoblastic-thalloblastic, meristematic, unilocular, delimitation of conidium by a single septum with retrogressive delimitation of next conidium giving an unconnected chain of conidia, brown, smooth to verruculose, conidiogenous scars (conidiogenous loci) inconspicuous, truncate, neither thickened nor darkened. Conidia solitary or usually forming simple to branched basipetal chains of transversely to muriformly eu- or distoseptate, 1– to multiseptate, brown, smooth, verruculose to verrucose conidia, conidial secession schizolytic.

Type species: Catenulostroma protearum (Crous & M.E. Palm) Crous & U. Braun, comb. nov.

Description: Crous & Palm (1999), Crous et al. (2004a; figs 364–365).

Notes: Catenulostroma contains several plant pathogenic species previously placed in Trimmatostroma, a morphologically similar but, based on its type species, phylogenetically distinct genus belonging to Helotiales (Fig. 1). Trimmatostroma s. str. is well-distinguished from most Catenulostroma species by being saprobic, living on twigs and branches of woody plants, or occasionally isolated from leaf litter, i.e., they are not associated with leaf spots. The conidiomata of Trimmatostroma species are subepidermal, acervular-sporodochial with a well defined wall of textura angularis, little differentiated, macromeromatus conidiophores giving rise to long chains of conidia that disarticulate at the surface to form a grey-black to brown powdery mass. The generic affinity of other species assigned to Trimmatostroma, e.g. those having a lichenicolous habit, is unresolved.

Trimmatostroma abietis Butin & Pehl (Butin et al. 1996) clusters together with the plant pathogenic Catenulostroma species, but differs from these species in having a more complex ecology. Trimmatostroma abietis is usually foliicolous on living or necrotic conifer needles on which characteristic acervuli to sporodochia with densely arranged, fasciculate fertile hyphae are formed, comparable to the fasciculate conidiomata of the plant pathogenic species of Catenulostroma (Butin et al. 1996: 205, fig. 1). Although not discussed by Butin et al. (1996), T. abietis needs to be compared to T. abietina Doherty, which was originally described from Abies balsamea needles collected in Guelph, Canada (Doherty 1900). Morphologically the two species appear to be synonymous, except for reference to muriformly septate conidia, which is a feature not seen in vivo in the type of T. abietis. Furthermore, as this is clearly a species complex, this matter can only be resolved once fresh Canadian material has been collected to serve as epitype for T. abietina.

Isolates from stone, agreeing with T. abietis in cultural, morphological and physiological characteristics, have frequently been found (Wollenzien et al. 1995, Butin et al. 1996, Gorbushina et al. 1996, Kogej et al. 2006, Krumbein et al. 1996). Furthermore, isolates from humans (ex skin lesions and ex chronic osteomyelitis of human patients) and Ilex leaves are known (Butin et al. 1996). De Hoog et al. (1999) included strains of T. abietis from stone, man and Ilex leaves in molecular sequence analyses and demonstrated their genetical identity based on 5.8S rDNA and ITS2 data, but strains from conifer needles were not included. Furthermore, we consider T. abietis, as presently defined, to represent a species complex, with Dutch isolates from Pinus again appearing distinct from German Abies isolates, suggesting that different conifer genera could harbour different Catenulostroma species. Isolates from stone form stromatic, durable microcolonies, which are able to grow under extreme xerophilic environmental conditions. Cultural growth resembles that of other meristematic black yeasts (Butin et al. 1996, Kogej et al. 2006). Another fungus isolated from stone in Germany is in vitro morphologically close to C. abietis, but differs in forming conidia with oblique septa. Furthermore, a human pathogenic isolate from Africa clusters together with other Catenulostroma species. The habit and origin of this human pathogenic fungus in nature and its potential morphology on “natural” substrates, which typically deviates strongly from the growth in vitro, are still unknown. However, C. abietis, usually growing as a foliicolous and saxicolous fungus, has already shown the potential ability of Catenulostroma species to cause opportunistic human infections.

Key to Catenulostroma species

1. Conidia formed in basipetal chains, smooth, 4-celled, consisting of two basal cells with truncate lateral sides, each giving rise to a secondary globose apical cell, that can extend and develop additional septa, appearing as two lateral arms ................. C. excentricum
   1. Conidia variable in shape, but without two basal cells giving rise to two lateral arms .......................................................... 2

2. Conidia smooth or almost so, at most very faintly rough-walled; usually foliicolous on conifer needles or saxicolous, forming stromatic, xerophilic durable microcolonies on stone, occasionally causing opportunistic human infections ......................................................... 3

2. Conidia distinctly verruculose to verrucose; plant pathogenic, forming leaf spots ................................................................. 5

3. Conidia (8–)20–35(–60) × 4–5(–7) µm, 1–10-septate ................................................................. C. chromoblastomycosum

3. Conidia much shorter, 8–20 µm long, 0–5-septate ................................................................. 4

4. Conidia 0–5 times transversely septate, mostly two-celled; usually foliicolous on conifer needles or saxicolous .................. C. abietis

4. Conidia 2–4 times transversely septate and often with 1–2 oblique septa; isolated from stone ............................................. C. germanicum

5. Conidia rather broad, usually wider than 10 µm ........................................................................ 6
5. Conidia narrower, width below 10 µm ................................................................. 7

6. Conidia distoseptate, rather long, (12–)25–35(–45) × (7–)10–15(–25) µm; conidiomata large, up to 250 µm diam, on Protea anceps ......................................................... C. protearum

6. Conidia euseptate, shorter, (9–)6–20(–36) × (0–)4–8(–27) µm; sporodochia 90–100 × 40–80 µm; on Protea grandiceps ................................................. C. elginense

7. Conidia 1- to multiseptate, (10–)15–17(–23) × (5–)6.5–7(–9) µm; on various Proteaceae ......................................................... C. macowanii

7. Conidia in vivo predominantly 1-septate, (8–)13–15(–21) × (3.5–)5.5–6(–8) µm; on Protea cynaroides ............................................................................. C. microsporum (Teratosphaeria microspora)

Catenulostroma abietis (Butin & Pehl) Crous & U. Braun, comb. nov. MycoBank MB504504. Basionym: Trimmatostroma abietis Butin & Pehl, Antonie van Leeuwenhoek 69: 204. 1996.

Notes: Catenulostroma abietis needs to be compared to Trimmatostroma abietina Doherty (Abies balsamea needles Canada), which is either an older name for this species, or a closely related taxon. Presently T. abietina is not known from culture, and needs to be recollected.

Catenulostroma chromoblastomycosum Crous & U. Braun, sp. nov. MycoBank MB504505. Fig. 6.

Etymology: Named after the disease symptoms observed due to opportunistic human infection.

Differt a C. abieti et C. germanico conidiis longioribus, (8–)20–35(–60) × 4–5(–7) µm, 1–10-septatis.

Description based on cultures sporulating on WA supplemented with sterile pine needles. Mycelium consisting of branched, septate, smooth to finely verruculose, medium to dark brown, thick-walled, 3–4 µm wide hyphae. Conidiomata brown, superficial,
sporodochial, up to 350 µm diam. Conidiophores reduced to inconspicuous conidiogenous loci on hyphae, 2–4 µm wide, neither darkened nor thickened or refractive. Conidia occurring in branched chains, that tend to remain attached to each other, subcylindrical with subtruncate ends, straight to slightly curved, (8–)20–35(–60) × 4–5(–7) µm, 1–10-septate, medium brown, smooth to finely verruculose.

Cultural characteristics: Colonies on PDA erumpent, spreading, slow growing, with sparse to moderate aerial mycelium and smooth, irregular, submerged margins; greenish black (surface).

Specimen examined: Zaire, Pawa, isolated from man with chromoblastomycosis, Mar. 1997, V. de Brouwere, holotype CBS H-9935, culture ex-type CBS 597.97.

Notes: Catenulostroma chromoblastomycosum was originally identified as an isolate of Stenella araguata Syd. The latter fungus is morphologically distinct, however, having much shorter and narrower conidia, formed in acropetal chains, as well as quite different conidiogenous loci and conidial hila which are small, thickened and darkened.

Catenulostroma elginense (Joanne E. Taylor & Crous) Crous & U. Braun, comb. nov. MycoBank MB504506. Basionym: Trimmatostroma elginense Joanne E. Taylor & Crous, Mycol. Res. 104: 633. 2000.

Catenulostroma excentricum, see Teratosphaeria excentrica.

Catenulostroma germanicum Crous & U. Braun, sp. nov. MycoBank MB504507. Fig. 7.

Etymology: Named after the geographic location of its type strain in Germany.

Differt a C. abieti conidiis –2 oblique septatis.

Mycelium consisting of branched, septate, smooth, pale to medium brown, 2–4 µm wide hyphae, giving rise to conidial chains. Conidiophores integrated, subcylindrical, branched or not, septate, little differentiated, micronematous, 3–5 µm wide, 3- to multiseptate, medium brown, thick-walled; conidiogenous cells integrated, terminal, inconspicuous, unilocular, conidiogenous loci...
inconspicuous. Conidia in simple or branched basipetal chains, subcylindrical, straight to flexuous, (8–)10–15–(20) × 4–5–(6) µm, 2–4 transversely septate or with 1–2 oblique septa, medium to dark brown, thick-walled, smooth.

Cultural characteristics: Colonies on OA erumpent, spreading, with even, smooth margins and sparse to moderate aerial mycelium; olivaceous-grey, with iron-grey margins (surface). Colonies reaching 12 mm diam after 1 mo at 25 °C in the dark; colonies fertile.

Specimen examined: Germany (former West-Germany), isolated from stone, Oct. 1988, J. Kuroczkin, holotype CBS H-19936, culture ex-type CBS 539.88.

Notes: Catenulostroma germanicum was originally deposited as Taeniolina scripta (P. Karst.) P.M. Kirk. It is clearly distinct, however, as the latter fungus forms intricate, branched, brown conidia (Kirk 1981), unlike those of C. germanicum. Phylogenetically C. germanicum forms part of the C. abietis species complex.

Catenulostroma macowanii (Sacc.) Crous & U. Braun, comb. nov. MycoBank MB504508.

Basionym: Coniothecium macowanii Sacc., Syll. Fung. 4: 512. 1886.

Catenulostroma protearum (Crous & M.E. Palm) Crous & U. Braun, comb. nov. MycoBank MB504509.

Basionym: Trimmatostroma protearum Crous & M.E. Palm, Mycol. Res. 103: 1303. 1999.

Cibiessia Crous, Fungal Diversity 26: 151. 2007.

Type species: Cibiessia dimorphospora Crous & C. Mohammed, Fungal Diversity 26: 151. 2007.

Description: Crous et al. (2007b; figs 3–5).

Notes: The genus Cibiessia was introduced to accommodate species with chains of disarticulating conidia (arthroconidia). Some species have been shown to have a Readeriella synanamorph.

Devriesia Seifert & N.L. Nick., Can. J. Bot. 82: 919. 2004.

Type species: Devriesia staurophora (W.B. Kendr.) Seifert & N.L. Nick., Canad. J. Bot. 82: 919. 2004.

Description: Seifert et al. (2004; figs 2–42).

Notes: The genus is characterised by producing chains of pale brown, subcylindrical to fusiform, 0–1-septate conidia with somewhat thickened, darkened hilum, forming chlamydoconidia in culture, and being heat resistant. Morphologically they resemble taxa placed in Pseudocladosporium U. Braun (= Fuscidium Bonord.: Venturiaceae), though phylogenetically Devriesia is not allied to this family.

Hortaea Nishim. & Miyaji, Jap. J. Med. Mycol. 26: 145. 1984.

Type species: Hortaea werneckii (Horta) Nishim. & Miyaji, Jap. J. Med. Mycol. 26: 145. 1984.

Description: de Hoog et al. (2000, illust. p. 721).
system, consisting of a single terminal conidiogenous cell giving rise to several ramoconidia that form secondary ramoconidia, etc., or the branched apparatus is composed of several terminal and sometimes lateral conidiogenous cells giving rise to sequences of ramoconidia (conidiogenous cells and ramoconidia are often barely distinguishable, with conidiogenous cells disarticulating, becoming ramoconidia). The branched apparatus may be loose to dense, metula-like. The conidiogenous cells have only few, usually 1–3 (–4), terminal or subterminal subdenticulate loci, and ramoconidia are prominent and numerous, giving rise to branched chains of secondary conidia with flat-tipped hila. Some species of *Penidiella* with compact, metula-like branched apices are morphologically close to *Metulocladosporiella* Crous, Schroers, J.Z. Groenew., U. Braun & K. Schub. (Crous et al. 2006d). This genus encompasses two species of banana diseases belonging to *Herpotrichiellaceae* (Chaetothyriales), characterised by having conidiophore bases with rhizoid hyphal appendages and abundant micromatous conidiophores. *Penidiella* species with less pronounced penicillate apices, e.g. *P. strumelloidea* (Milko & Dunaev Crous & U. Braun, are comparable with species of the genus *Pleurothecopsis* B. Sutton (see Ellis 1976). The latter genus is distinct in having unbranched, often percurrently proliferating conidiophores, lacking ramoconidia and colourless conidia formed in simple chains.

*Cladosporium helicosporum* R.F. Castañeda & W.B. Kendr. (Castañeda et al. 1997) is another penidiella-like fungus with terminally branched conidiophores, subdenticulate conidiogenous loci and conidia in long acropetal chains, but its affinity to *Penidiella* has still to be proven.

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**Key to *Penidiella* species**

1. Conidiophores in *vivo* in well-developed, dense fascicles and distinct synnemata arising from a basal stroma; on fallen leaves of *Ficus* sp., Cuba .......................................................... *P. cubensis* 2

2. Conidiophores with a terminal conidiogenous cell, often somewhat swollen, giving rise to several ramoconidia (on one level) that form chains of straight to distinctly curved conidia; isolated from leaf of *Carex* sp., Russia ................................................................. *P. strumelloidea*

3. Mycelium verruculose; long filiform conidiophores ending with a subdenticulate cell giving rise to sets of penicillate conidiogenous cells or ramoconidia which are barely distinguishable and turn into each other; ramoconidia and conidia consistently narrow, (1.5–)2(–2.5) µm wide, and aseptate, ramoconidia sometimes heterochromous; on living leaves of *Nectandra coriacea*, Cuba ...................... *P. nectandrae*

4. Hyphae, conidiophores and conidia frequently distinctly constricted at the septa; penicillate apex of the conidiophores sparingly developed, branches more or less divergent; isolated from leaf litter of *Smilax* sp., Cuba .......................................................... *P. rigidophora*

5. Hyphae and conidia without distinct constrictions at the septa; penicillate apex of the conidiophores usually well-developed, with abundant branchings ................................. *P. venezuelensis*

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**Penidiella columbiana** Crous & U. Braun, sp. nov. MycoBank MB504510. Figs 8–9.

_Etymology:_ Named after its country of origin, Colombia.

_Mycelium ex hyphis ramosis, septatis, levibus, pallide brunneis, 2–3 µm latis compositum. Conidiophora ex hyphis superficialibus oriunda, penicillata, erecta, brunnea, crassisunicata, minute verruculosa, ad 800 µm longa, ad basim 7–9 µm lata, ad apicem pluriramosa, vel velutina. Conidia vel ellipsoidea, 0–-septata, pallide brunnea, vel tanacea, vel crouS.

_Mycelium consisting of branched, septate, smooth, pale brown, 2–3 µm wide hyphae. Conidiophores arising from superficial mycelium, terminally penicillate, erect, brown, wall up to 1 µm wide, almost smooth to finely verruculose, up to 800 µm tall, 7–9 µm wide at the base; conidiogenous region consisting of a series of branches composed of true branchlets, conidiogenous cells and ramoconidia, branched portion usually rather compact, even metula-like, but also looser, with divergent branches; primary branches (–2), subcylindrical, 1–7-septate, 50–120 × 4–6 µm; secondary branches (–2), subcylindrical, 1–5-septate, 40–60 × 4–6 µm; tertiary and additional branches 1–4-septate, 10–30 × 3–5 µm; ramoconidia consisting of branched, septate, smooth, pale brown, 2–3 µm wide hyphae. Conidiophores arising from superficial mycelium, terminally penicillate, erect, brown, wall up to 1 µm wide, almost smooth to finely verruculose, up to 800 µm tall, 7–9 µm wide at the base; conidiogenous region consisting of a series of branches composed of true branchlets, conidiogenous cells and ramoconidia, branches often percurrently proliferating, not distinctly nodulose, penicillate apex loose to often more compact, tight, metula-like; conidia longer, 7–25 × 2–5 µm; micromatous conidiophores lacking; isolated from dead leaf of *Paepalanthus colombianus*, Colombia .......................... _P. colombiana_
medium brown, smooth, wall ≤ 1 µm wide, ellipsoidal to oblclavate or obovoid, with 1–3 apical hila, 10–25 × 3–5 µm, ramoconidia with broadly truncate base, not or barely attenuated, up to 4 µm wide, or at least somewhat attenuated at the base, hila 1.5–3 µm wide. Conidia subcylindrical to ellipsoidal, 0(–1)-septate, pale brown, in chains of up to 10, 7–15 × 2–3 µm, hila truncate, unthickened, barely to somewhat darkened, 1–2 µm wide.

Cultural characteristics: Colonies on PDA erumpent, spreading, with moderate aerial mycelium and smooth, even, submerged margins; olivaceous-grey in central part, iron-grey in outer region (surface); colonies fertile.

Specimen examined: Colombia. Páramo de Guasca, 3400 m alt., isolated from dead leaf of Paepalanthus columbianus (Ericaceae). Aug. 1980, W. Gams, holotype CBS H-19937, culture ex-type CBS 486.80.

Notes: This isolate was originally identified as belonging to the Stenella araguata species complex. The latter name has been somewhat confused in the literature, and has been incorrectly applied to isolates associated with opportunistic human infections (de Hoog et al. 2000). The “araguata” species complex is treated elsewhere in the volume (see Crous et al. 2007a – this volume).

Penidiella columbiana (type material). A. Conidiophores on pine needle in vitro. B–H. Conidiophores with chains of disarticulating conidia. Scale bars: A = 450, B–C = 10 µm.

Penidiella cubensis (R.F. Castañeda) U. Braun, Crous & R.F. Castañeda, comb. nov. MycoBank MB504511. Fig. 10. Basionym: Cladosporium cubense R.F. Castañeda, Fungi Cubenses II (La Habana): 4. 1987.

In vivo: Colonies on fallen leaves, amphigenous, effuse, pilose, brown. Mycelium usually external, superficial, but also internal, composed of branched, septate, brown, thin-walled, smooth to rough-walled hyphae, 2–3 µm wide. Stromata present, 40–80 µm diam, brown, immersed. Conidiophores densely fasciculate or in distinct synnemata, arising from stromata, erect, synnemata up to about 1000 µm long and (10–)20–40(–50) µm wide, individual threads filiform, pluriseptate throughout, brown, thin-walled (≤ 0.5 µm), smooth or almost so to distinctly verruculose, apically penicillate. Conidiogenous cells integrated, terminal and intercalary, 10–30 µm long, subcylindrical, terminal conidiogenous cells often slightly enlarged at the tip, with (1–)2–3(–4) terminal or subterminal subdenticulate conidiogenous loci, short conically truncate, –2 µm diam, unthickened or almost so, but often slightly refractive or darkened-refractive, intercalary conidiogenous cells usually with a single lateral locus just below the upper septum, conidiogenous cells giving rise to a single set of primary ramoconidia, or a sequence of ramoconidia at different levels. Ramoconidia cylindrical to ellipsoid-fusoid, 8–18(–25) × 2–3 µm, aseptate, pale olivaceous, olivaceous-brown to brown, thin-walled, smooth or almost so to
faintly verruculose, ramoconidia with broadly truncate base, barely narrowed, or ramoconidia more or less attenuated at the base, hila 1–2 µm wide, unthickened or almost so, but often slightly refractive or darkened-refractive. Conidia in long acropetal chains, narrowly ellipsoid-ovoid, fusiform, 5–12(–15) × (1–)1.5–3 µm, aseptate, pale olivaceous to brownish, thin-walled, smooth to faintly rough-walled, ends attenuated, hila 1–1.5 µm wide, unthickened, not darkened, at most somewhat refractive.

Specimen examined: Cuba, Guantánamo, Maisí, on fallen leaves of Ficus sp., 24 Apr. 1986, M. Camino, holotype INIFAT C86/34 (HAL 209 F, ex holotype).

Notes: Cladosporium cubense was not available in culture and molecular sequence data are not available, but type material could be re-examined and revealed that this species is quite distinct from Cladosporium s. str., but agreeing with the concept of the genus Penidiella. Penidiella cubensis differs from all other species of this genus in having densely fasciculate conidiophores to synnematous conidiomata, arising from stromata.

Penidiella nectandrae Crous, U. Braun & R.F. Castañeda, nov. nov. MycoBank MB504512. Fig. 11. Basionym: Cladosporium ferrugineum R.F. Castañeda, Fungi Cubenses II (La Habana): 4. 1987, homonym, non C. ferrugineum Allesch., 1895.

In vivo: Colonies amphigenous, brown. Mycelium internal and external, superficial, composed of sparingly branched hyphae, septate, 1–3 µm wide, pale olivaceous-brown or brown, thin-walled (≤ 0.5 µm), smooth or almost so to distinctly verruculose, fertile cells giving rise to conidiophores somewhat swollen at the branching point, up to 5 µm diam, and somewhat darker. Stromata lacking. Conidiophores erect, straight, filiform, up to 350 µm long, 2.5–4 µm wide, pluriseptate throughout, brown, darker below and paler above, thin-walled, smooth, apex penicillate, terminal cell of the conidiophore with 2–4 short denticle-like loci giving rise to sets of conidiogenous cells or ramoconidia that then form a sequence of new sets of ramoconidia on different levels, i.e., the loose to dense, metula-like branching system is composed of conidiogenous cells and ramoconidia which are often barely distinguishable and turn into each other; conidiogenous loci terminal or subterminal, usually 1–3(–4), subdenticulate, 1–2 µm diam, conical, apically truncate, unthickened or almost so, not to somewhat darkened-refractive. Ramoconidia with truncate base, barely attenuated, or ramoconidia distinctly attenuated at the truncate base, up to 20 × 2 µm, aseptate, at the apex with 2–3(–4) subdenticulate hila, subcylindrical,
Phylogenetic lineages in the *Capnodiales*

very pale olivaceous, olivaceous-brown to brown, sometimes with different shades of brown (heterochromatous), thin-walled (≤ 0.5 µm), smooth to faintly verruculose. Conidia in long acropetal chains, narrowly ellipsoid-ovoid, fusiform to cylindrical, 5–16 × (1.5–)2(–2.5) µm, aseptate, very pale olivaceous, olivaceous-brown to brown, thin-walled, smooth to very faintly rough-walled, primary conidia with rounded apex and truncate base, somewhat attenuated, secondary conidia truncate at both ends, hila 1–1.5 µm diam, unthickened or almost so, at most slightly darkened-refractive.

Cultural characteristics: Colonies on PDA slimy, smooth, spreading; aerial mycelium absent, margins smooth, irregular; surface black with patches of cream. Colonies reaching 20 mm diam after 1 mo at 25 °C in the dark; colonies sterile on PDA, SNA and OA.

Specimen examined: Cuba, Matanzas, San Miguel de los Baños, isolated from living leaves of *Nectandra coriacea* (Lauraceae), 24 Jan. 1987, R.F. Cañeda and G. Arnold, holotype INIFAT C87/45, culture ex-type CBS 734.87, and HAL 2018 F (ex-holotype).

Notes: Although the ex-type strain of *Cladosporium ferrugineum* is sterile, its LSU DNA phylogeny reveals it to be unrelated to *Cladosporium s. str.* (see Fig. 1 in Crous et al. 2007a – this volume). Based on a re-examination of the type material it could clearly be shown that the morphology of this species fully agrees with the concept of the new genus *Penidiella*, which is supported by its phylogenetic position within *Capnodiales*.

*Penidiella rigidophora* Crous, R.F. Cañeda & U. Braun, sp. nov. MycoBank MB50453. Figs 12–13. ≡ *Cladosporium rigidophorum* R.F. Cañeda, nom. nud. (herbarium name).

Differt a specibus *Penidiellae* conidiophoris dimorphosis, hyphis et conidiis ad septa saepe distincte constrictis.

*Mycelium* consisting of strongly branched, septate, smooth or almost so, pale olivaceous to medium brown, guttulate, commonly constricted at septa, 2–6 µm wide hyphae, swollen cells up to 8 µm wide, wall up to 1(–1.5) µm wide. *Conidiophores* dimorphic. *Macronematous conidiophores* separate, erect, subcylindrical, predominantly straight to slightly curved, terminally loosely penicillate, up to 120 µm long, and 4–5 µm wide at the base, which is neither lobed nor swollen, and lacks rhizoids, up to 10-septate, medium to dark brown, wall up to 1(–1.5) µm wide. *Micronematous conidiophores* erect, subcylindrical, up to 40 µm tall, 3–4 µm wide, 1–3-septate, pale to medium brown (concolorous with hyphae). Conidiogenous cells predominantly terminal, rarely intercalary, medium brown, smooth, subcylindrical, but frequently swollen at apex, 10–20 × 5–6 µm, loci (predominantly single in micronematous conidiophores, but up to 4 in macronematous conidiophores) flat-tipped, sub-denticulate or not, 1–1.5 µm wide, barely to slightly darkened and thickened-refractive. Conidia in branched chains, medium brown, verruculose, (appearing like small spines under light microscope), ellipsoid to cylindrical-oblung, up to 1(–1.5) µm wide, frequently constricted at septa, which turn dark with age; ramoconidia (10–)13–17(–25) × 3–4(–5) µm, 1(–3)-septate; secondary conidia (7–)8–10(–12) × 3–4(–5); hila unthickened to very slightly thickened and darkened, not refractive, (0.5–)1(–1.5) µm.

Cultural characteristics: Colonies on PDA erumpent, spreading, with lobate margins and moderate aerial mycelium; iron-grey (surface), with a greenish black margin; reverse greenish black. Colonies reaching 20 mm diam after 1 mo at 25 °C in the dark; colonies fertile.
Specimen examined: Cuba, isolated from leaf litter of Smilax sp. (Smilacaceae), 6 Nov. 1994, R.F. Castañeda, holotype CBS H-19938, culture ex-type CBS 314.95.

Notes: Cladosporium rigidophorum is a herbarium name, which was never validly published. The ex-type strain, however, represents a new species of Penidiella, for which a valid name with Latin diagnosis is herewith provided. This species is easily distinguishable from all other taxa of Penidiella by forming distinct constrictions at hyphal and conidial septa as well as micronematous conidiophores (except for P. venezuelensis in which a few micronematous conidiophores have been observed). It is also phylogenetically distinct from the other taxa of Penidiella (see Fig. 1 in Crous et al. 2007a — this volume).

Fig. 12. Penidiella rigidophora (type material). A–F. Micronematous conidiophores giving rise to chains of conidia. G–H. Macronematous conidiophores (note base in G, and apex in H). I. Conidia. Scale bars = 10 µm.
**Penidiella strumelloidea** (Milko & Dunaev) Crous & U. Braun, **comb. nov.** MycoBank MB504514. Figs 14–15.

_Basionym:_ *Cladosporium strumelloideum* Milko & Dunaev, Novosti Sist. Nizsh. Rast. 23: 134. 1986.

_Mycelium_ consisting of branched, septate, smooth, hyaline to pale olivaceous, 1–4 µm wide hyphae, sometimes constricted at somewhat darker septa. _Conidiophores_ solitary, erect, arising from superficial mycelium, micronematous, i.e., reduced to conidiogenous cells, or macronematous, subcylindrical, straight to slightly curved, subcylindrical throughout or often somewhat attenuated towards the apex, 12–80 × (2–)2.5–4 µm, 0–6-septate, medium brown, smooth, wall ≤ 0.75 µm, penicillate apex formed by a terminal conidiogenous cell giving rise to a single set of ramoconidia. _Conidiogenous cells_ terminal, integrated, subcylindrical, straight, 8–12 × 1.5–2(–2.5) µm, pale brown, thin-walled, smooth, apex obtusely rounded to somewhat clavate; _loci_ terminal, occasionally subterminal or lateral, unthickened or almost so to slightly thickened and darkened, not refractive, 1–1.5 µm wide. _Conidia_ in branched chains; ramoconidia subcylindrical, with 1–3 terminal _loci_, olivaceous-brown, smooth; secondary conidia ellipsoidal, with one side frequently straight and the other convex, straight to slightly curved, (8–)10–12(–20) × 2(–3) µm, subhyaline to olivaceous-brown, smooth, thin-walled; _hila_ unthickened or almost so to somewhat thickened and darkened, not refractive, 1 µm wide.

_Cultural characteristics:_ Colonies on PDA erumpent, spreading, with abundant, dense to woolly aerial mycelium, and uneven, feathery margins; surface pale olivaceous grey, reverse iron-grey. Colonies reaching 25 mm diam after 1 mo at 25 °C in the dark; colonies fertile.

_Specimen examined:_ Russia, Yaroslavl Region, Rybinsk Reservoir, mouth of Sutka River, isolated from leaf of _Carex_ sp. (Cyperaceae), from stagnant water, S. Ozerskaya, **holotype** BKMF-2534, culture ex-type CBS 114484.

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_Fig. 13._ Penidiella rigidophora (type material). A. Hyphae. B. Conidiophores. C. Ramoconidia. D. Secondary conidia. Scale bar = 10 µm. U. Braun del.

_Fig. 14._ Penidiella strumelloidea (type material). A–B. Micronematous conidiophores. C–D. Macronematous conidiophores. E–G. Conidia. Scale bars = 10 µm.
Notes: *Penidiella strumelloidea* resembles other species of *Penidiella* by having penicillate conidiophores with a conidiogenous apparatus giving rise to branched conidial chains. It differs, however, from all other species of this genus in having a rather simple penicillate apex composed of a single terminal conidiogenous cell giving rise to one set of ramoconidia which form frequently somewhat curved conidia. It is also phylogenetically distinct from the other taxa of *Penidiella* (see Fig. 1 in Crous et al. 2007a – this volume).

*Penidiella venezuelensis* Crous & U. Braun, sp. nov. MycoBank MB504515. Figs 16–17.

Etymology: Named after the geographic location of its type strain, Venezuela.

Differs from *P..cmb0c0. rami3* (type material) in having conidiophores, about 10–15 × 2–3 µm. Conidiogenous cells terminal and intercalary, unbranched, subcylindrical, 5–12 × 3–4 µm, medium brown, smooth or almost so to finely verrucose, apex of conidiogenous cells frequently swollen, up to 8 µm diam, with 1–3(–4) flat-tipped, non to slightly thickened, non to slightly darkened-refractive loci, 1–1.5 µm wide, frequently appearing subdenticulate, up to 1.5 µm long, intercalary conidiogenous cells also slightly swollen at the conidiogenous portion just below the upper septum, which render the conidiophores subnodulose to nodulose, swellings round about the conidiophore axis or unilateral. Conidia ellipsoid-ovoid, subcylindrical, pale to medium olivaceous-brown or brown, finely verrucose, wall ≤ 0.5 µm wide, guttulate or not, occurring in branched chains. Ramoconidia 0–1(–3)-septate, 5–15(–22) × 3–4(–5) µm, with 1–3 subdenticulate apical hila; secondary conidia 0(–1)-septate, ellipsoid, obovoid to irregular, (4–)5–7(–8) × (2–)2.5–3(–4) µm; hila non to slightly thickened, non to slightly darkened-refractive, (0.5–)1(–1.5) µm wide.

Cultural characteristics: Colonies on OA erumpent, spreading, with dense, compact aerial mycelium, and even, smooth margins; olivaceous-grey (surface), margins iron-grey. Colonies reaching 22 mm diam after 1 mo at 25 °C in the dark.

Specimen examined: Venezuela, isolated from man with *tinea nigra*. Jan. 1975, D. Borelli, holotype CBS H-19934, culture ex-type CBS 106.75.

Notes: The type culture of *Penidiella venezuelensis* was originally determined as *Stenella araguata* from which it is, however, quite distinct by having smooth mycelium, long penicillate conidiophores with subdenticulate conidiogenous loci, smaller conidia, and agreeing with the concept of the genus *Penidiella*. It is phylogenetically distinct from the other taxa of *Penidiella* (see Fig. 1 in Crous et al. 2007a – this volume).

*Pseudotaeniolina* J.L. Crane & Schokn., Mycologia 78: 88. 1986.  

? = *Friedmanniomycetes* Onofri, Nova Hedwigia 68: 176. 1999.

Type species: *Pseudotaeniolina convolvuli* (Esfand.) J.L. Crane & Schokn., Mycologia 78: 88. 1986.

Description: Crane & Schoknecht (1986, figs 3–19).

Notes: No cultures or sequence data are available of the type species, and *Pseudotaeniolina globosa* De Leo, Urzi & De Hoog was placed in *Pseudotaeniolina* based on its morphology and ecology. The genus *Friedmanniomycetes* is presently known from two species (Selbmann et al. 2005). Morphologically *Friedmanniomycetes* is similar to *Pseudotaeniolina*, but fresh material of *Pseudotaeniolina convolvuli* needs to be recollected before this can be clarified.

*Readeriella* Syd. & P. Syd., Ann. Mycol. 6: 484. 1908.

? = *Kirramyces* J. Walker, B. Sutton & Pascoe, Mycol. Res. 96: 919. 1992.  

Collelophoeospora Crous & M.J. Wingf., Canad. J. Bot. 75: 668. 1997.

Synanamorphs: *Cibiessia* Crous, Fungal Diversity 26: 151. 2007; also pseudocercospora-like, see Crous (1998).

Type species: *Readeriella mirabilis* Syd. & P. Syd., Ann. Mycol. 6: 484. 1908.

Description: Crous et al. (2004b; figs 36–38).

Notes: Several coelomycete genera are presently available to accommodate anamorphs of *Capnodiales* that reside in *Teratosphaeriaceae*, for which *Readeriella* is the oldest name. Other genera such as *Phaeophleospora* Rangel, Sonderheria H.J. Swart & J. Walker and *Lecanosticta* Syd. belong to *Mycosphaerellaceae*.  

**Fig. 15.** Penidiella strumelloidea (type material). A. Hyphae. B. Conidiophores. C. Ramoconidia. D. Secondary conidia. Scale bars = 10 µm. U. Braun del.
**Readeriella** is polyphyletic within *Teratosphaeriaceae*. The recognition and circumscription (synonymy) of this genus follows the principles for anamorph genera within *Capnodiales* as outlined in the introduction to this volume. The only unifying character is conidial pigmentation, and the mode of conidiogenesis. Conidiogenous cells range from mono- to polyphialides with periclinal thickening, to phialides with percurrent proliferation, as observed in the type species, *R. mirabilis* (Fig. 8). Within the form genus conidia vary from aseptate to multi-septate, smooth to rough, and have a range of synanamorphs. *Readeriella mirabilis* has a synanamorph with cylindrical, aseptate conidia, while other species of *Readeriella* again have *Cibiessia* synanamorphs (scytalidium-like, with chains of dry, disarticulating conidia), suggesting the conidial morphology to be quite plastic. A re-examination of *R. readeriellophora* Crous & Mansilla revealed pycnidia to form a central cushion on which the conidiogenous cells are arranged (Fig. 18). This unique feature is commonly known in genera such as *Coniella* Höhn. and *Pilidiella* Petr. & Syd. (Diaporthales) (Van Niekerk et al. 2004), and has never been observed among anamorphs of the *Capnodiales*. Another species of *Readeriella*, namely "*Phaeophleospora*" *toledana* Crous & Bills, again forms paraphyses interspersed among conidiogenous cells, a rare feature in this group of fungi, while several species

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**Fig. 16.** *Penidiella venezuelensis* (type material). A. Microconidiophore. B. Apical part of macroconidiophore. C–F. Chains of conidia. Scale bars = 10 µm.

**Fig. 17.** *Penidiella venezuelensis* (type material). A. Hypha. B. Micronematous conidiophores. C. Macronematous conidiophores. D–E. Ramoconidia. F. Secondary conidia. Scale bar = 10 µm. U. Braun def.
have conidiomata ranging from acervuli to pycnidia (Cortinas et al. 2006). Phylogenetically this coelomycete morphology, with its characteristic conidiogenesis, has evolved several times in Teratosphaeriaceae.

**Readeriella blakelyi** (Crous & Summerell) Crous & U. Braun, **comb. nov.** MycoBank MB504516.  
*Basionym:* Coniothyrium blakelyi Crous & Summerell, Fungal Diversity 23: 342. 2006.

**Readeriella brunneotingens** Crous & Summerell, **sp. nov.** MycoBank MB504517.  
*Etymology:* Named after the diffuse brown pigment visible in agar when cultivated on MEA.

Readeriellae gauchensi similis, sed colonis viridi-atris et pigmento brunneo in agaro diffundente distinguenda.

Leaf spots amphigenous, irregular specs up to 3 mm diam, medium brown with a thin, raised, concolorous border. *Conidialoma* amphigenous, substomatal, exuding conidia in black masses; conidialoma pycnidial in vivo and in vitro, globose, brown to black, up to 120 µm diam; wall consisting of 3–4 cell layers of brown cells of *textura angularis*. Conidiogenous cells brown, verruculose, aseptate, doliform to ampulliform, or reduced to inconspicuous loci on hyphae (in vitro), proliferating percurrently near the apex, 5–7 × 3–5 µm; sympodial proliferation also observed in culture. *Conidia* brown, smooth to finely verruculose, ellipsoidal to subcylindrical, apex obtuse to subobtuse, tapering to a subtruncate or truncate base (–0.5 µm wide) with inconspicuous, minute marginal frill, (5–)6–7(–8) × 2–3(–3.5) µm in vitro, becoming 1-septate; in older cultures becoming swollen, and up to 2-septate, 15 µm long and 5 µm wide.

**Cultural characteristics:** Colonies on MEA reaching 20 mm diam after 2 mo at 25 °C; colonies erumpent, aerial mycelium sparse to abundant, greenish black, with profuse sporulation, visible as oozing brown, smooth to finely verruculose, ellipsoidal to subcylindrical, apex obtuse to subobtuse, tapering to a subtruncate or truncate base (1–1.5 µm wide) with inconspicuous, minute marginal frill, (5–)6–7(–8) × 2–3(–3.5) µm in vitro, becoming 1-septate; in older cultures becoming swollen, and up to 2-septate, 15 µm long and 5 µm wide.

**Notes:** The epithet “eucalypt” is preoccupied by *Readeriella eucalypti* (Gonz. Frag.) Crous (Summerell et al., 2006), and thus the synonym “pulcherrima” becomes the next available name for this species.

**Readeriella considenianae** (Crous & Summerell) Crous & U. Braun, **comb. nov.** MycoBank MB504523.  
*Basionym:* Colletogloeopsis considenianae Crous, Stud. Mycol. 55: 110. 2006.

**Readeriella zuluensis** (M.J. Wingf., Crous & T.A. Cout.) Crous & U. Braun, **comb. nov.** MycoBank MB504524.  
*Basionym:* Coniothyrium zuluense M.J. Wingf., Crous & T.A. Cout., Mycopathologia 136: 142. 1997.  
≡ *Colletogloeopsis zuluensis* (M.J. Wingf., Crous & T.A. Cout.) M.-N. Cortinas, M.J. Wingf. & Crous (zuluensis), Mycol. Res. 110: 235. 2006.

**Statinwardia** B. Sutton, Trans. Br. Mycol. Soc. 57: 540. 1971.  
*Type species:* Statinwardia breviscula B. Sutton, Trans. Br. Mycol. Soc. 57: 540. 1971.

**Description:** Sutton (1971; fig. 1).

**Notes:** The genus *Statinwardia* presently contains two species, namely *S. breviscula* and *Statinwardia suttonii* Crous & Summerell (Summerell et al., 2006), though its placement in *Capnodiales* was less well resolved. The genus forms acervuli on brown leaf spots, with brown, catenulate conidia covered in a mucilaginous sheath.

**Readeriella pulcherrima** (Gadgil & M. Dick) Crous & U. Braun, **comb. nov.** MycoBank MB504522.  
*Basionym:* Septoria pulcherrima Gadgil & M. Dick, New Zealand J. Bot. 21: 49. 1983.

≡ *Stagonospora destructans* (M.J. Wingf. & Crous) Crous, F.A. Ferreira & B. Sutton, S. African J. Bot. 63: 113. 1997.

**Readeriella dimorpha** (Crous & Carnegie) Crous & U. Braun, **comb. nov.** MycoBank MB504520.  
*Basionym:* Colletogloeopsis dimorpha Crous & Carnegie, Fungal Diversity 23: 345. 2006.

**Readeriella gauchensis** (M.-N. Cortinas, Crous & M.J. Wingf.) Crous & U. Braun, **comb. nov.** MycoBank MB504521.  
*Basionym:* Colletogloeopsis gauchensis M.-N. Cortinas, Crous & M.J. Wingf., Stud. Mycol. 55: 143. 2006.

**Readeriella delectans** (M.J. Wingf. & Crous) Crous & U. Braun, **comb. nov.** MycoBank MB504519.  
*Basionym:* Kirramyces delectans M.J. Wingf. & Crous, S. African J. Bot. 62: 325. 1996.

≡ *Phaeophleospora destructans* (M.J. Wingf. & Crous) Crous, F.A. Ferreira & B. Sutton, S. African J. Bot. 63: 113. 1997.
Fig. 18. A–E. Readeriella mirabilis. A. Conidium with conidial cirrus. B. Conidiogenous cells with percurrent proliferation. C. Macroconidia. D. Slightly pigmented, verruculose conidiogenous cell. E. Macro- and microconidia. F–I. Readeriella readeriellophora (type material). F. Colony on OA. G. Central stromatal tissue giving rise to conidiophores. H. Conidiogenous cells. I. Conidia. Scale bars = 10 μm.

Fig. 19. Readeriella brunneotingens (type material). A. Leaf spot. B. Colony on MEA. C–D. Conidia. Scale bar = 10 μm.
Schizothyriaceae clade

Schizothyrium Desm., Ann. Sci. Nat., Bot., sér. 3: 11. 1849.

Type species: Schizothyrium acerinum Desm., Ann. Sci. Nat., Bot., sér. 3: 11. 1849.

Description: Batzer et al. (2007; figs 3–7).

Notes: Species of Schizothyrium (Schizothyriaceae) have Zygophiala E.W. Mason anamorphs, and were recently shown to be allied to Mycosphaerellaceae (Batzer et al. 2007). Although species of Schizothyrium have thyrothecia, they cluster among genera with pseudothecal ascoporea, questioning the value of this character at the family level. Based on its bitunicate asci and 1-septate ascospores, the teleomorph is comparable to others in the Capnodiales.

Mycosphaerellaceae clade

Mycosphaerella Johanson, Övners. Förh. Kongl. Svenska Vetensk.-Akad. 41(9): 163. 1884.

Type species: Mycosphaerella punctiformis (Pers. : Fr.) Starbäck, Bih. Kongl. Svenska Vetensk.-Akad. Handl. 15(3, 2): 9. 1889.

Anamorph: Ramularia endophylla Verkley & U. Braun, Mycol. Res. 108: 1276. 2004.

Description: Verkley et al. (2004; figs 3–16).

Notes: The genus Mycosphaerella has in the past been linked to 23 anamorph genera (Crous 2000), while additional genera have been linked via DNA-based studies, bringing the total to at least 30 genera (Crous & Braun 2003, Crous et al. 2007b). However, based on ITS and SSU DNA phylogenetic studies and a reassessment of morphological characters and conidiogenesis, several anamorph genera have recently been reduced to synonymy (Crous & Braun 2003, Crous et al. 2006a). Furthermore, the DNA sequence data generated to date clearly illustrate that the anamorph genera in Mycosphaerellaceae are polyphyletic, residing in several clades within Mycosphaerella. If future collections not known from culture or DNA sequences are to be described in form genera, we recommend that the concepts as explained in Crous & Braun (2003) be used until such stage as they can be placed in Mycosphaerella, pending a modification of Art. 59 of the International Code of Botanical Nomenclature. The genus Mycosphaerella and its anamorphs represent a future topical issue of the Studies in Mycology, and will thus be treated separately.

Dissoconium subclade

Dissoconium de Hoog, Oorschot & Hijwegen, Proc. K. Ned. Akad. Wet., Ser. C, Biol. Med. Sci. 86(2): 198. 1983.

Type species: Dissoconium aciculare de Hoog, Oorschot & Hijwegen, Proc. K. Ned. Akad. Wet., Ser. C, Biol. Med. Sci. 86(2): 198. 1983.

Teleomorph: Mycosphaerella-like.

Description: de Hoog et al. (1983), Crous (1998), Crous et al. (2004b; figs 3–10).

Notes: The genus Dissoconium presently encompasses six species (Crous et al. 2007b), of which two, M. lateralis Crous & M.J. Wingf. (D. dekkerti de Hoog & Hijwegen), and M. communis Crous & Mansilla (D. commune Crous & Mansilla) are also known from their Mycosphaerella-like teleomorphs. No teleomorph genus will be introduced for this clade, however, until more sexual species have been collected to help clarify the morphological features of this genus. A further complication lies in the fact that yet other species, morphologically distinct from Dissoconium, also cluster in this clade (Crous, unpubl. data).

“Passalora” zambiae subclade

“Passalora” zambiae Crous & T.A. Cout., Stud. Mycol. 50: 209. 2004.

Description: Crous et al. (2004b; figs 32–33).

Notes: This fungus was placed in the form genus “Passalora” based on its smooth mycelium, giving rise to conidiophores forming branched chains of brown conidia with thickened, darkened, refractive hila. Although derived from single ascospores, the teleomorph material was lost, and thus it needs to be recollected before the relavance of its phylogenetic position can be fully understood.

Additional teleomorph genera considered

Coccodinium A. Massal., Atti Inst. Veneto Sci. Lett. Arti, Série 2, 5: 336. 1860. (Fig. 20).

Type species: Coccodinium bartschii A. Massal., Atti Inst. Veneto Sci. Lett. Arti, Série 2, 5: 337. 1860.

Description: Eriksson (1981, figs 34–35).

Notes: The genus Coccodinium (Coccodiniaceae) is characterised by having ascocarata that are sessile on a subiculum, or somewhat immersed, semiglobose, collapsed when dry, brownish, uniloculate, with a centrum that stains blue in IKI (iodine potassium iodide). Asci are bitunicate, stalked, 8-spored, saccate, and have a thick, undifferentiated endotunica. Periphyses and periphysoids are well-developed and numerous. Ascospores are elongate, fusiform, ellipsoidal or clavate, transversely septate or unseptate, hyaline or brownish (Eriksson 1981), and lack a mucous sheath. Based on a SSU sequence (GenBank accession U77668) derived from a strain identified as C. bartschii (Winka et al. 1998), Coccodinium appears to be allied to the taxon treated here in Teratosphaeria. Freshly collected cultures are relatively slow growing, and on MEA they form erumpent round, black colonies with sparse hyphal growth. On the surface of these colonies hyphal strands, consisting of brown, globose cells, give rise to conidia. Older cells (up to 15 µm diam) become fertile, giving rise to 1–3 conidia via inconspicuous phialidic loci. Conidia are fusoid-ellipsoidal to clavate, 3–5-septate, becoming constricted at the transverse septa, apex obtuse, base subtruncate, gultulate, smooth, widest in the upper third of the conidium, 15–40 × 4–7 µm. Phylogenetically Coccodinium is thus allied to the Chaetothyriales (Fig. 1), and not the Teratosphaeriaceae.
Fig. 20. Coccodinium bartschi. A. Ascomata on host. B. Ostiolar area. C. Periphysoids. D–E. Ascospores shot onto agar. F–I. Asci with thick ectotunica. J–K. Young ascospores. L–M. Mature ascospores. N. Colony on MEA. O–Q. Conidiogenous cells giving rise to conidia. R–S. Conidia. Scale bars: A, N = 250, B, D, F–G, I, L–M, O = 10 μm.
**Stigmidium** Trevis., Consp. Verruc.: 17. 1860. (Fig. 21).

*Type species:* *Stigmidium schaereri* (A. Massal.) Trevis., Consp. Verruc.: 17. 1860.

*Description:* Roux & Triebel (1994, figs 47–50).

*Notes:* The type species of the genus is lichenicolous, characterised by semi-immersed, black, globose ascomata with ostiolar periphyses and periphysoids. *Asci* are 8-spored, fasciculate, bitunicate, (endotunica not giving a special reaction in Congo red or toluidine blue). *Ascospores* are fusoid-ellipsoidal, medianly-septate, guttulate, thin-walled, lacking a sheath. Presently no culture is available, and thus the placement of *Stigmidium* remains unresolved.

**DISCUSSION**

From the LSU sequence data presented here, it is clear that *Mycosphaerella* is not monophyletic as previously suggested (Crous et al. 2001, Goodwin et al. 2001). The first step to circumscribe natural genera within this complex was taken by Braun et al. (2003), who separated *Cladosporium* anamorphs from this complex, and erected *Davidiella* (*Davidiellaceae*; Schoch et al. 2006) to accommodate their teleomorphs. The present study reinstates the genus *Teratosphaeria* for a clade of largely extremotolerant fungi (Selbmann et al. 2005) and foliar pathogens of *Myrtaceae* and *Proteaceae* (Crous et al. 2004a, b, 2006b, 2007b), and further separates generic subclades within the *Mycosphaerellaceae*, while Batzer et al. (2007) again revealed *Schizothyrium* Desm. (*Schizothyriaceae*) to cluster within the *Mycosphaerellaceae*. Our results, however, provide support for recognition of *Schizothyrium* as a distinct genus, although *Schizothyriaceae* was less well supported as being separate from *Mycosphaerellaceae* (*Capnodiales*).

Although pleomorphism represents a rather unstudied phenomenon in this group of fungi, it has been observed in several species. Within the *Teratosphaeria* clade, Crous et al. (2007b) recently demonstrated teleomorphs to have *Readeriella* and *Cibiessia* synanamorphs, while the black yeast genera that belong to this clade, commonly have more than one anamorph state in culture. The present study also revealed *Readeriella mirabilis* to have two conidial types in culture, and to be highly plastic regarding its mode of conidiogenesis, and *Readeriella* to be the oldest generic name available for a large group of leaf-spotting coelomycetes in the *Teratosphaeriaceae* (*Capnodiales*). Although not commonly documented, there are ample examples of synanamorphs in *Capnodiales*. Within *Mycosphaerella*, Beilharz et al. (2004) described *Passalora perplexa* Beilharz, Pascoe, M.J. Wingf. & Crous as a species with a coelomycete and yeast synanamorph, while Crous & Corlett (1998) described *Mycosphaerella stigmina-platani* F.A. Wolf to have a *Cercostigmina* and *Xenostigmina* synanamorphs, and recent collections also revealed the presence of a similar species that has typical "Stigmina" (distoseptate conidia) and *Pseudocercospora* (euseptate conidia) synanamorphs (Crous, unpubl. data), and Crous (1998) reported *Readeriella epicoccoides* (coelomycete) to...
have a Cercochlamys (hyphomycete) synanamorph in culture. Although the Mycosphaerella complex encompasses thousands of names, it may appear strange that it is only now that more clarity is obtained regarding the phylogenetic relationships among taxa in this group. This is partly due to the fact that these organisms are cultivated with difficulty, and also that the first paper to address the taxonomy of this complex based on DNA sequence data was only relatively recently published (Stewart et al. 1999). In the latter study, the genus Paracercospora Deighton (scars minutely thickened along the rim), was shown to be synonymous with the older genus Pseudocercospora. Similarly, Crous et al. (2001) showed that Cercochlamys (rough, irregular percurrent proliferations) was also synonymous with Pseudocercospora. This led Crous & Braun (2003) to conclude that conidomatal type, conidial catenulation, septation and proliferation of conidiogenous cells were of less importance in separating species at the generic level. Myceliossleri Rangel and Pheanoramulina Munj.-Cvetk. were subsequently reduced to synonymy with the older name, Passalora Fr., and characters identified as significant at the generic level were pigmentation (Cercospora vs. Passalora), scar structure (Passalora vs. Pseudocercospora), and verruculose superficial hyphae (Stenella vs. Passalora). Due to the unavailability of cultures, no decision was made regarding Stenella (verrucose conidia and mycelium), Stigmina (distoseptate conidia), and several other, less well-known genera such as Asperisporium Maubl., Denticularia Deighton, Distrocercospora N. Pons & B. Sutton, Prathigada Subram., Ramulispora, Pseudocercosporidium Deighton, Stenellopsis B. Huguenin and Verrucisporidia D.E. Shaw & Alcorn. In a recent study, however, Crous et al. (2006a) were able to show that Phaeoisariopsis (synnemata, conidia with slightly thickened hila) and Stigmina (distoseptate conidia) were also synonyms of Pseudocercospora.

The present study shows that most anamorph genera are polyphyletic within Teratosphaeriaceae, and paraphyletic within Capnodiales. In some cases, generic concepts of anamorphs based on morphology and conidium ontogeny conform well with phylogenetic relationships, though this is not true in all cases due to convergence. Nevertheless, anamorphs still convey valuable morphological information that is contained in the anamorph name, and naming anamorphs continue to provide a practical system to identify the various asexual taxa encountered.

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