

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 rDNA 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 *Mycosphaerella* complex.

Taxonomic novelties: *Batcheloromyces eucalypti* (Alcorn) Crous & U. Braun, comb. nov., *Catenulostroma* Crous & U. Braun, gen. nov., *Catenulostroma abietis* (Butin & Pehl) Crous & U. Braun, comb. nov., *Catenulostroma chromoblastomycosum* Crous & U. Braun, sp. nov., *Catenulostroma elginense* (Joanne E. Taylor & Crous) Crous & U. Braun, comb. nov., *Catenulostroma excentricum* (B. Sutton & Ganap.) Crous & U. Braun, comb. nov., *Catenulostroma germanicum* Crous & U. Braun, sp. nov., *Catenulostroma macowanii* (Sacc.) Crous & U. Braun, comb. nov., *Catenulostroma microsporium* (Joanne E. Taylor & Crous) Crous & U. Braun, comb. nov., *Catenulostroma protearum* (Crous & M.E. Palm) Crous & U. Braun, comb. nov., *Penidiella* Crous & U. Braun, gen. nov., *Penidiella columbiana* Crous & U. Braun, sp. nov., *Penidiella cubensis* (R.F. Castañeda) U. Braun, Crous & R.F. Castañeda, comb. nov., *Penidiella nectandrae* Crous, U. Braun & R.F. Castañeda, nom. nov., *Penidiella rigidophora* Crous, R.F. Castañeda & U. Braun, sp. nov., *Penidiella strumelloidea* (Milko & Dunaev) Crous & U. Braun, comb. nov., *Penidiella venezuelensis* Crous & U. Braun, sp. nov., *Readeriella blakelyi* (Crous & Summerell) Crous & U. Braun, comb. nov., *Readeriella brunneotingens* Crous & Summerell, sp. nov., *Readeriella consideniana* (Crous & Summerell) Crous & U. Braun, comb. nov., *Readeriella destructans* (M.J. Wingf. & Crous) Crous & U. Braun, comb. nov., *Readeriella dimorpha* (Crous & Carnegie) Crous & U. Braun, comb. nov., *Readeriella epicoccoides* (Cooke & Masee) Crous & U. Braun, comb. nov., *Readeriella gauchensis* (M.-N. Cortinas, Crous & M.J. Wingf.) Crous & U. Braun, comb. nov., *Readeriella molleriana* (Crous & M.J. Wingf.) Crous & U. Braun, comb. nov., *Readeriella nubilosa* (Ganap. & Corbin) Crous & U. Braun, comb. nov., *Readeriella pulcherrima* (Gadgil & M. Dick) Crous & U. Braun, comb. nov., *Readeriella stellenboschiana* (Crous) Crous & U. Braun, comb. nov., *Readeriella toledana* (Crous & Bills) Crous & U. Braun, comb. nov., *Readeriella zuluensis* (M.J. Wingf., Crous & T.A. Cout.) Crous & U. Braun, comb. nov., *Teratosphaeria africana* (Crous & M.J. Wingf.) Crous & U. Braun, comb. nov., *Teratosphaeria alistairii* (Crous) Crous & U. Braun, comb. nov., *Teratosphaeria associata* (Crous & Carnegie) Crous & U. Braun, comb. nov., *Teratosphaeria bellula* (Crous & M.J. Wingf.) Crous & U. Braun, comb. nov., *Teratosphaeria cryptica* (Cooke) Crous & U. Braun, comb. nov., *Teratosphaeria dentritica* (Crous & Summerell) Crous & U. Braun, comb. nov., *Teratosphaeria excentrica* (Crous & Carnegie) Crous & U. Braun, comb. nov., *Teratosphaeria fimbriata* (Crous & Summerell) Crous & U. Braun, comb. nov., *Teratosphaeria flexuosa* (Crous & M.J. Wingf.) Crous & U. Braun, comb. nov., *Teratosphaeria gamsii* (Crous) Crous & U. Braun, comb. nov., *Teratosphaeria jonkershoekensis* (P.S. van Wyk, Marasas & Knox-Dav.) Crous & U. Braun, comb. nov., *Teratosphaeria maxii* (Crous) Crous & U. Braun, comb. nov., *Teratosphaeria mexicana* (Crous) Crous & U. Braun, comb. nov., *Teratosphaeria molleriana* (Thüm.) Crous & U. Braun, comb. nov., *Teratosphaeria nubilosa* (Cooke) Crous & U. Braun, comb. nov., *Teratosphaeria ohnowa* (Crous & M.J. Wingf.) Crous & U. Braun, comb. nov., *Teratosphaeria parkiiifinis* (Crous & M.J. Wingf.) Crous & U. Braun, comb. nov., *Teratosphaeria parva* (R.F. Park & Keane) Crous & U. Braun, comb. nov., *Teratosphaeria perpendicularis* (Crous & M.J. Wingf.) Crous & U. Braun, comb. nov., *Teratosphaeria pluritubularis* (Crous & Mansilla) Crous & U. Braun, comb. nov., *Teratosphaeria pseudoafricana* (Crous & T.A. Cout.) Crous & U. Braun, comb. nov., *Teratosphaeria pseudocryptica* (Crous) Crous & U. Braun, comb. nov., *Teratosphaeria pseudosuberosa* (Crous & M.J. Wingf.) Crous & U. Braun, comb. nov., *Teratosphaeria quasircospora* (Crous & T.A. Cout.) Crous & U. Braun, comb. nov., *Teratosphaeria readeriellophora* (Crous & Mansilla) 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.A. Ferreira, Alfenas & M.J. Wingf.) Crous & U. Braun, comb. nov., *Teratosphaeria suttonii* (Crous & M.J. Wingf.) 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*, *Trimmatostroma*, 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 *Capnodiales*. 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, conidial 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

Table 1. Isolates for which new sequences were generated.

Anamorph	Teleomorph	Accession number ¹	Host	Country	Collector	GenBank Accession number
<i>Batcheloromyces eucaalypti</i>		CBS 313.76; CPC 3632	<i>Eucalyptus tessellaris</i>	Australia	J.L. Alcorn	EU019245
<i>Batcheloromyces leucadendri</i>		CBS 110892; CPC 1837	<i>Leucadendron</i> sp.	South Africa	L. Swart	EU019246
<i>Batcheloromyces proteae</i>		CBS 110696; CPC 1518	<i>Protea cynaroides</i>	South Africa	L. Viljoen	EU019247
<i>Capnobotryella renispora</i>		CBS 214.90*; CBS 176.88; IAM 13014; JCM 6932	<i>Capnobotrys neessii</i>	Japan	J. Sugiyama	EU019248
<i>Catenulostroma abietis</i>		CBS 290.90	Man, skin lesion	Netherlands	R.G.F. Wintermans	EU019249
<i>Catenulostroma castellanii</i>		CBS 105.75*; ATCC 24788	<i>Man, tineae nigra</i>	Venezuela	—	EU019250
<i>Catenulostroma chromoblastomycosum</i>		CBS 597.97	Man, chromoblastomycosis	Zaire	V. de Brouwere	EU019251
<i>Catenulostroma elghinense</i>		CBS 111030; CPC 1958	<i>Protea grandiceps</i>	South Africa	J.E. Taylor	EU019252
<i>Catenulostroma germanicum</i>		CBS 539.88	Stone	Germany	—	EU019253
<i>Catenulostroma macowanii</i>		CBS 110756; CPC 1872	<i>Protea nitida</i>	South Africa	J.E. Taylor	EU019254
<i>Catenulostroma microsporium</i>	<i>Teratosphaeria microspora</i>	CBS 110890; CPC 1832	<i>Protea cynaroides</i>	South Africa	L. Swart	EU019255
<i>Catenulostroma</i> sp.	<i>Teratosphaeria pseudosuberosa</i>	CBS 118911; CPC 12085	<i>Eucalyptus</i> sp.	Uruguay	M.J. Wingfield	EU019256
<i>Cercosporaella centaureicola</i>		CBS 120253	<i>Centaurea solstitiales</i>	Greece	D. Berner	EU019257
<i>Cibissia dimorphospora</i>		CBS 120034; CPC 12636	<i>Eucalyptus nitens</i>	Australia	—	EU019258
<i>Cibissia minutispora</i>		CPC 13071*	<i>Eucalyptus henryi</i>	Australia	A.J. Carnegie	EU019259
<i>Cibissia nontingens</i>	<i>Teratosphaeria</i> sp.	CBS 120725*; CPC 13217	<i>Eucalyptus tereticornis</i>	Australia	B. Summerell	EU019260
<i>Cladosporium bruhnei</i>	<i>Davidiella allicina</i>	CBS 115683; ATCC 66670; CPC 5101	CCA-treated Douglas-fire pole	U.S.A., New York	C.J. Wang	EU019261
<i>Cladosporium cladosporioides</i>		CBS 109.21; ATCC 11277; ATCC 200940; IFO 6368; IMI 049625	Sooty mould on <i>Hedera helix</i>	U.K.	—	EU019262
<i>Cladosporium sphaerospermum</i>		CBS 188.54; ATCC 11290; IMI 049638	—	—	—	EU019263
<i>Cladosporium uredinicola</i>		ATCC 46649	Hyperparasite on <i>Cronartium fusiforme</i> f. sp. <i>quercum</i>	U.S.A., Alabama	—	EU019264
<i>Coccodinium bartschii</i>		CBS 121708; CPC 13861–13863	Sooty mould on unidentified tree	Canada	K.A. Seifert	EU019265
<i>Dissoconium aciculare</i>		CBS 342.82*; CPC 1534	<i>Erysiphe</i> , on <i>Medicago lupulina</i>	Germany	T. Hijwegen	EU019266
<i>Dissoconium commune</i>	<i>"Mycosphaerella" communis</i>	CBS 114238*; CPC 10440	<i>Eucalyptus globulus</i>	Spain	J.P.M. Vazquez	EU019267
<i>Dissoconium dekkeri</i>	<i>"Mycosphaerella" lateralis</i>	CBS 567.89*; CPC 1535	<i>Juniperus chinensis</i>	Netherlands	T. Hijwegen	EU019268
<i>Fumagospora capnodiolebes</i>	<i>Capnodium salicinum</i>	CBS 131.34	Sooty mould on <i>Bursaria spinosa</i>	Indonesia	—	EU019269
<i>Hortaea werneckii</i>		CBS 107.67*	<i>Man, tineae nigra</i>	Portugal	—	EU019270
<i>Nothofrasseria dendritica</i>	<i>Teratosphaeria dendritica</i>	CPC 12820	<i>Eucalyptus nitens</i>	Australia	A.J. Carnegie	EU019271
<i>"Passalora" zambiae</i>		CBS 112970*; CPC 1228	<i>Eucalyptus globulus</i>	Zambia	T. Coutinho	EU019272
<i>Penidiella columbiana</i>		CBS 112971*; CIMW 14782; CPC 1227	<i>Eucalyptus globulus</i>	Zambia	T. Coutinho	EU019273
		CBS 486.80	<i>Paepalanthus columbianus</i>	Colombia	W. Gams	EU019274

Anamorph	Teleomorph	Accession number ¹	Host	Country	Collector	GenBank Accession number
<i>Penidiella nectandrae</i>		CBS 734.87*; ATCC 200932, INIFAT 87/45	<i>Nectandra coriacea</i>	Cuba	R.F. Castañeda & G. Arnold	EU019275
<i>Penidiella rigidophora</i>		CBS 314.95*	Leaf litter of <i>Smilax</i> sp.	Cuba	R.F. Castañeda	EU019276
<i>Penidiella strumelloidea</i>		CBS 114484*; VKM F-2534	<i>Carex</i> leaf, from stagnant water	Russia	S. Ozerskaya	EU019277
<i>Penidiella venezuelensis</i>		CBS 106.75*	<i>Man, tinea nigra</i>	Venezuela	D. Borelli	EU019278
<i>Phaeotheca triangularis</i>		CBS 471.90*	Wet surface of humidifier of airconditioning	Belgium	H. Beguin	EU019279
<i>Phaeothecoidea eucalypti</i>		CPC 13010	<i>Corymbia henryi</i>	Australia	B. Summerell	EU019280
<i>Pleurophoma</i> sp.		CPC 12918*	<i>Eucalyptus botryoides</i>	Australia	B. Summerell	EU019281
<i>Pseudotaeniolina globosa</i>	<i>Teratosphaeria fibrillosa</i>	CPC 1876	<i>Protea nitida</i>	South Africa	J.E. Taylor	EU019282
<i>Ramularia pratensis</i> var. <i>pratensis</i>		CBS 109889*	Rock	Italy	C. Urzi	EU019283
<i>Ramularia</i> sp.		CPC 11294	<i>Rumex crispus</i>	Korea	H.D. Shin	EU019284
<i>Readerella brunneotrigens</i>		CBS 324.87	On <i>Mycosphaerella</i> sp., leaf spot on <i>Brassica</i> sp.	Netherlands	—	EU019285
<i>Readerella destructans</i>		CPC 13303	<i>Eucalyptus tereticornis</i>	Australia	P.W. Crous	EU019286
<i>Readerella epicoccoides</i>		CBS 111369*; CPC 1366	<i>Eucalyptus grandis</i>	Indonesia	M.J. Wingfield	EU019287
<i>Readerella eucalypti</i>	<i>Teratosphaeria suttonii</i>	CPC 12352	<i>Eucalyptus</i> sp.	U.S.A., Hawaii	W. Gams	EU019288
<i>Readerella gauchensis</i>		CPC 11186	<i>Eucalyptus globulus</i>	Spain	M.J. Wingfield	EU019289
<i>Readerella mirabilis</i>		CBS 120303*; CMW 17331	<i>Eucalyptus grandis</i>	Uruguay	M.J. Wingfield	EU019290
<i>Readerella molleriana</i>	<i>Teratosphaeria molleriana</i>	CBS 116293; CPC 10506	<i>Eucalyptus fastigata</i>	New Zealand	W. Gams	EU019291
<i>Readerella ovata</i> complex		CBS 111164*; CMW 4940; CPC 1214	<i>Eucalyptus globulus</i>	Portugal	M.J. Wingfield	EU019292
<i>Readerella stellerboschiana</i>		CPC 18	<i>Eucalyptus cladocalyx</i>	South Africa	P.W. Crous	EU019293
<i>Readerella zuluensis</i>		CBS 111149; CPC 23	<i>Eucalyptus cladocalyx</i>	South Africa	P.W. Crous	EU019294
<i>Septoria tritici</i>	<i>Mycosphaerella graminicola</i>	CBS 116428; CPC 10886	<i>Eucalyptus</i> sp.	South Africa	P.W. Crous	EU019295
<i>Trimmatostroma betulinum</i>		CBS 120301*; CMW 17321	<i>Eucalyptus grandis</i>	South Africa	M.J. Wingfield	EU019296
<i>Trimmatostroma salicis</i>		CBS 100335; IPO 69001.61	<i>Triticum aestivum</i>	—	G.H.J. Kema	EU019297
		CBS 110744; CPC 658	<i>Triticum</i> sp.	South Africa	P.W. Crous	EU019298
		CBS 282.74	<i>Betula verrucosa</i>	Netherlands	W.M. Loerakker	EU019299
	<i>Teratosphaeria bellula</i>	CPC 13571	<i>Salix alba</i>	Germany	U. Braun	EU019300
	<i>Teratosphaeria mexicana</i>	CBS 111700; CPC 1821	<i>Protea eximia</i>	South Africa	J.E. Taylor	EU019301
	<i>Teratosphaeria nubifosa</i>	CPC 12349	<i>Eucalyptus</i> sp.	U.S.A., Hawaii	W. Gams	EU019302
		CBS 114419; CPC 10497	<i>Eucalyptus globulus</i>	New Zealand	—	EU019303
		CBS 116005*; CMW 3282; CPC 937	<i>Eucalyptus globulus</i>	Australia	A. Carnegie	EU019304

Table 1. (Continued).

Anamorph	Teleomorph	Accession number ¹	Host	Country	Collector	GenBank Accession number
	<i>Teratosphaeria ohnowa</i>	CBS 112896 [*] ; CMW 4937; CPC 1004	<i>Eucalyptus grandis</i>	South Africa	M.J. Wingfield	EU019305
	<i>Teratosphaeria secundaria</i>	CBS 115608; CPC 504	<i>Eucalyptus grandis</i>	Brazil	A.C. Alfenas	EU019306
	<i>Teratosphaeria</i> sp.	CBS 208.94; CPC 727	<i>Eucalyptus grandis</i>	Indonesia	A.C. Alfenas	EU019307

¹ATCC: American Type Culture Collection, Virginia, U.S.A.; CBS: Centraalbureau voor Schimmelcultures, Utrecht, The Netherlands; CPC: Culture collection of Pedro Crous, housed at CBS; CMW: Culture collection of Mike Wingfield, housed at FAO, Pretoria, South Africa; IAM: Institute of Applied Microbiology, University of Tokyo, Institute of molecular and cellular bioscience, Tokyo, Japan; IFO: Institute For Fermentation, Osaka, Japan; IMI: International Mycological Institute, CABI-Bioscience, Egham, Bokerham Lane, U.K.; INIFAT: Alexander Humboldt Institute for Basic Research in Tropical Agriculture, Ciudad de La Habana, Cuba; JCM: Japan Collection Of Microorganisms, RIKEN BioResource Center, Japan; VKM: All-Russian Collection of Microorganisms, Institute of Biochemistry and Physiology of Microorganisms, Russian Academy of Sciences, Pushchino, Russia.

^{*}Ex-type cultures.

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* Miura (Crous *et al.* 2003), *Batcheloromyces* Marasas, P.S. van Wyk & Knox-Dav. (Taylor *et al.* 2003), *Phaeophleospora* 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 ascospores 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 (MEA) (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 (ITS1), 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 LR16 (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 (\times 1 000 magnification)

were made of structures mounted in lactic acid, with the extremes of spore measurements given in parentheses. Ascospores were frequently also mounted in water to observe mucoid appendages and sheaths. Colony colours (surface and reverse) were assessed after 1–2 mo on MEA at 25 °C in the dark, using the colour charts of Rayner (1970). All cultures obtained in this study are maintained in the culture collection of the Centraalbureau voor Schimmelcultures (CBS) in Utrecht, the Netherlands (Table 1). Nomenclatural novelties and descriptions were deposited in MycoBank (www.MycoBank.org).

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 *Capnodiales* (100 % bootstrap support). These are discussed in detail in the Taxonomy and Discussion sections. A new collection of *Coccodinium bartschii* A. Massal clusters (100 % bootstrap support) with members of the *Herpotrichiellaceae* (*Chaetothyriales*), whereas the type species of the genus *Trimmatostroma* Corda, namely *T. salicis* Corda, as well as *T. betulinum* (Corda) S. Hughes, are allied (99 % bootstrap support) with the *Dermateaceae* (*Helotiales*). The *Capnodiales* encompasses members of the *Capnodiaceae*, *Trichosphaeriaceae*, *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 *Capnodiales* 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. Neighbour-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 *Trichosphaeriaceae* / *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 whereas the *Teratosphaeriaceae* clade obtained 74 %, 79 % and 78 % bootstrap support respectively with the same models. The *Schizothyriaceae* clade appeared basal in the *Capnodiales*, 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 238 815 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**
1. Ascomata pseudothecial 2
2. Ascospores with irregular, angular lumens typical of *Davidiella*; anamorph *Cladosporium* s. str. **Davidiella**
2. Ascospores guttulate or not, lacking angular lumens; anamorph other than *Cladosporium* 3
3. Ascomata frequently linked by superficial stroma; hamathecial tissue, ascospore sheath, multi-layered endotunica, prominent periphysoids, and ascospores turning brown in asci frequently observed **Teratosphaeria**
3. Ascomata not linked by superficial stroma; hamathecial tissue, ascospore sheath, multi-layered endotunica, prominent periphysoids, ascospores turning brown in asci not observed 4
4. Conidiophores solitary, pale brown, giving rise to primary and secondary, actively discharged conidia; anamorph *Dissoconium* teleomorph *Mycosphaerella*-like
4. Conidiomata variable from solitary conidiophores to sporodochia, fascicles to pycnidia, but conidia not actively discharged **Mycosphaerella** s. str.

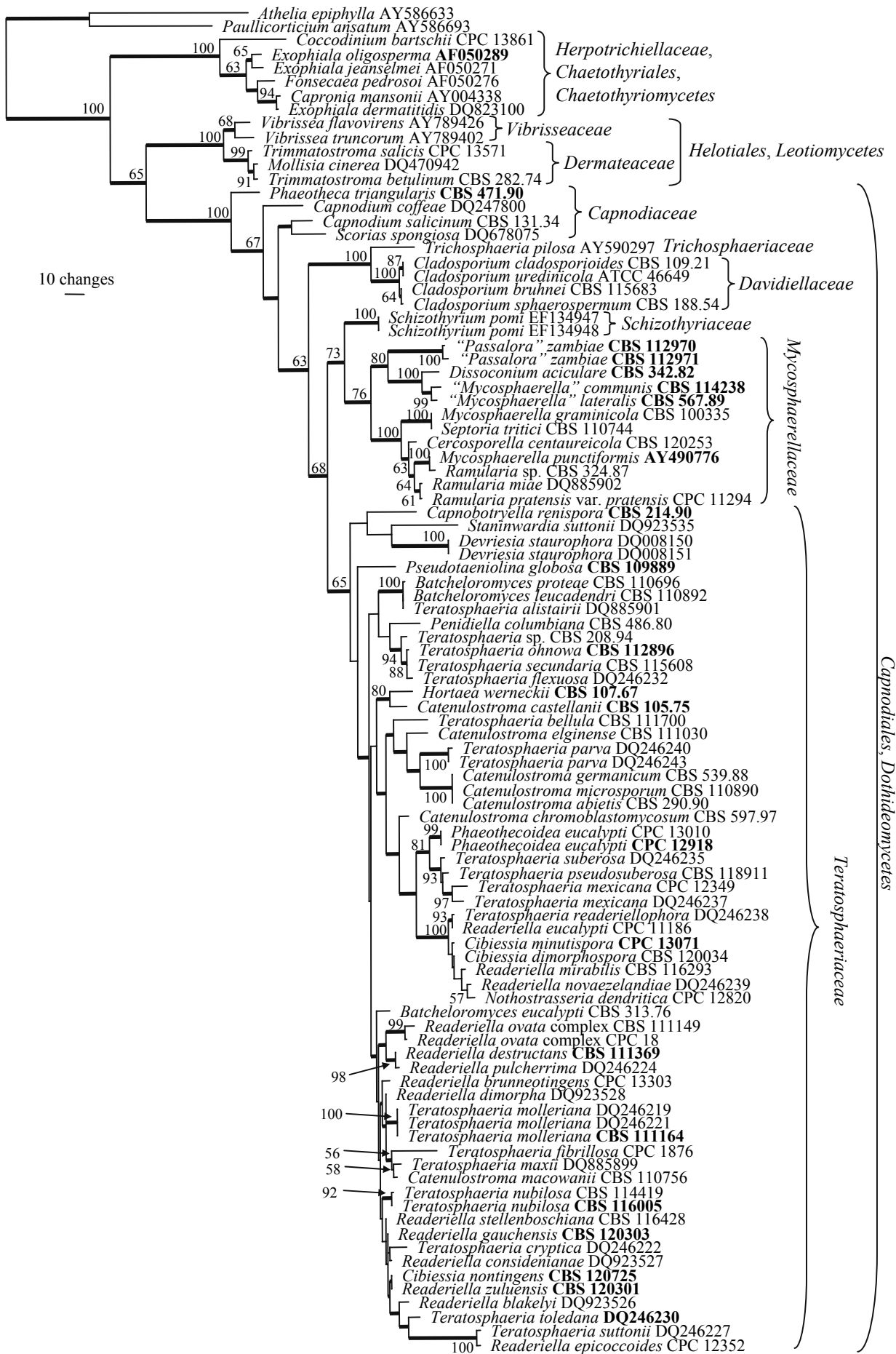


Fig. 1. One of 1 135 equally most parsimonious trees obtained from a heuristic search with 100 random taxon additions of the LSU sequence alignment using PAUP v. 4.0b10. The scale bar shows 10 changes, and bootstrap support values from 1 000 replicates are shown at the nodes. Thickened lines indicate 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).

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. Gesamten Naturk. 7: 37. 1816.

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

Basionym: Dematium herbarum Pers., Ann. Bot. (Usteri), 11 Stück: 32. 1794: Fr., Syst. Mycol. 3: 370. 1832.

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

Notes: The genus *Davidiella* (Davidiellaceae) was recently introduced for teleomorphs of *Cladosporium* s. str. (Braun *et al.* 2003). The genus *Cladosporium* is well-established, and contains around 772 names (Dugan *et al.* 2004), while *Davidiella* presently has 33 names (www.Mycobank.org), of which only around five have acknowledged *Cladosporium* 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. alistairii* 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. Asci 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. alistairii*, *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-arboreae* P.S. van Wyk, Marasas & Knox-Dav. have well-developed ostiolar 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 pseudotheciales, superficiales vel immersa, saepe in stromate ex cellulis brunneis pseudoparenchymatibus disposita, globulares, uniloculares, papillata, apice ostiolato, periphysata, saepe cum periphysoidibus; tunica multistratosa, ex cellulis brunneis angularibus composita, 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, 1-septatae, hyalinae, deinde pallide brunneae et verruculosae, saepe mucosae.

Ascomata pseudothecial, superficial to immersed, frequently situated in a stroma of brown pseudoparenchymatal cells, globose, unilocular, papillate, ostiolate, canal periphysate, with periphysoids frequently present; wall consisting of several layers of brown *textura 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.

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

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 alistairii (Crous) Crous & U. Braun, **comb. nov.** MycoBank MB504468.

Basionym: *Mycosphaerella alistairii* 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: *Sphaerella cryptica* Cooke, *Grevillea* 20: 5. 1891.

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

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

Basionym: *Colletogloeum nubilosum* Ganap. & Corbin, *Trans. Brit. Mycol. Soc.* 72: 237. 1979.

≡ *Colletogloeopsis nubilosum* (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: ***Catenulostroma 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. Doidge, **holotype** PREM; Stellenbosch, Jonkershoek valley, S33° 59' 44.7", E18° 58' 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: ***Catenulostroma 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: *Sphaerella 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 ambiphyllo* A. Maxwell, *Mycol. Res.* 107: 354. 2003.

Anamorph: ***Readeriella 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: *Sphaerella nubilosa* Cooke, *Grevillea* 19: 61. 1892.

≡ *Mycosphaerella nubilosa* (Cooke) Hansf., *Proc. Linn. Soc. New South Wales* 81: 36. 1965.

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

Basionym: *Mycosphaerella parkii* (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.* 98: 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 pseudaficana (Crous & T.A. Cout.) Crous & U. Braun, **comb. nov.** MycoBank MB504491.

Basionym: *Mycosphaerella pseudaficana* 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 quasercospora (Crous & T.A. Cout.) Crous & U. Braun, **comb. nov.** MycoBank MB504494.

Basionym: *Mycosphaerella quasercospora* 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 & Masee) Crous & U. Braun, **comb. nov.** MycoBank MB504500.

Basionym: *Cercospora epicoccoides* Cooke & Masee apud Cooke, Grevillea 19: 91. 1891.

≡ *Phaeophleospora epicoccoides* (Cooke & Masee) Crous, F.A. Ferreira & B. Sutton, S. African J. Bot. 63: 113. 1997.

≡ *Kirramyces epicoccoides* (Cooke & Masee) J. Walker, B. Sutton & Pascoe, Mycol. Res. 96: 919. 1992.

= *Hendersonia grandispora* McAlp., Proc. Linn. Soc. New South Wales 28: 99. 1903.

= *Phaeoseptoria eucalypti* Hansf., Proc. Linn. Soc. New South Wales 82: 225. 1957.

= *Phaeoseptoria luzonensis* T. Kobayashi, Trans. Mycol. Soc. Japan 19: 377. 1978.

Synanamorph: **Pseudocercospora** sp.

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
1. 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** (= *Friedmanniomyces*)
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, pseudocladosprium-like in morphology, but scars and hila not excessively thickened, nor refractive, producing chlamydospores in culture; species are mostly heat resistant **Devriesia**
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 pycnidial, conidiogenous cells phialidic, but also percurrent, subhyaline **Nothotrasseria**
7. Conidia brown, but basal appendages lacking, amero- to scolecospores 8
8. Conidiomata pycnidial 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 synnematosus (*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 unilocal, with conspicuous annellations, 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 distoseptate **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. inval.)

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

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 & Schokn.

Batcheloromyces Marasas, P.S. van Wyk & Knox-Dav., J. S. African Bot. 41: 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 *Stigmina* (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 conidiogenesis on hyphal tips of the aerial mycelium, forming elongate-globose to ellipsoid, muriformly septate, thick-walled conidia, that occur in clusters.

The finding that *Stigmina s. str.* [based on *S. platani* (Fuckel) Sacc., the type species] is a generic synonym of *Pseudocercospora* Speg. (Crous *et al.* 2006a), and that the type species of *Trimmatostroma* (*T. salicis*, Fig. 5) belongs to the *Helotiales* (Fig. 1), raises the question of where to place *stigmina*- and *trimmatostroma*-like anamorphs that reside in the *Teratosphaeria* clade. Although the *stigmina*-like species can be accommodated in *Batcheloromyces* (see Sutton & Pascoe 1989), a new genus is required for *Teratosphaeria* anamorphs that have a *trimmatostroma*-like morphology. The recognition of *Batcheloromyces* and the introduction of a new anamorph genus for *trimmatostroma*-like anamorphs of *Teratosphaeria* are also morphologically justified. *Batcheloromyces* is easily distinguishable from *Stigmina 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. *Trimmatostroma*-like anamorphs of *Teratosphaeria* are morphologically also sufficiently distinct from *Trimmatostroma s. str.* (see notes under *Catenulostroma* Crous & U. Braun) as well as *Batcheloromyces* (see key above).

Batcheloromyces eucalypti (Alcorn) Crous & U. Braun, **comb. nov.** MycoBank MB504503.

Basionym: *Stigmina eucalypti* Alcorn, 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).

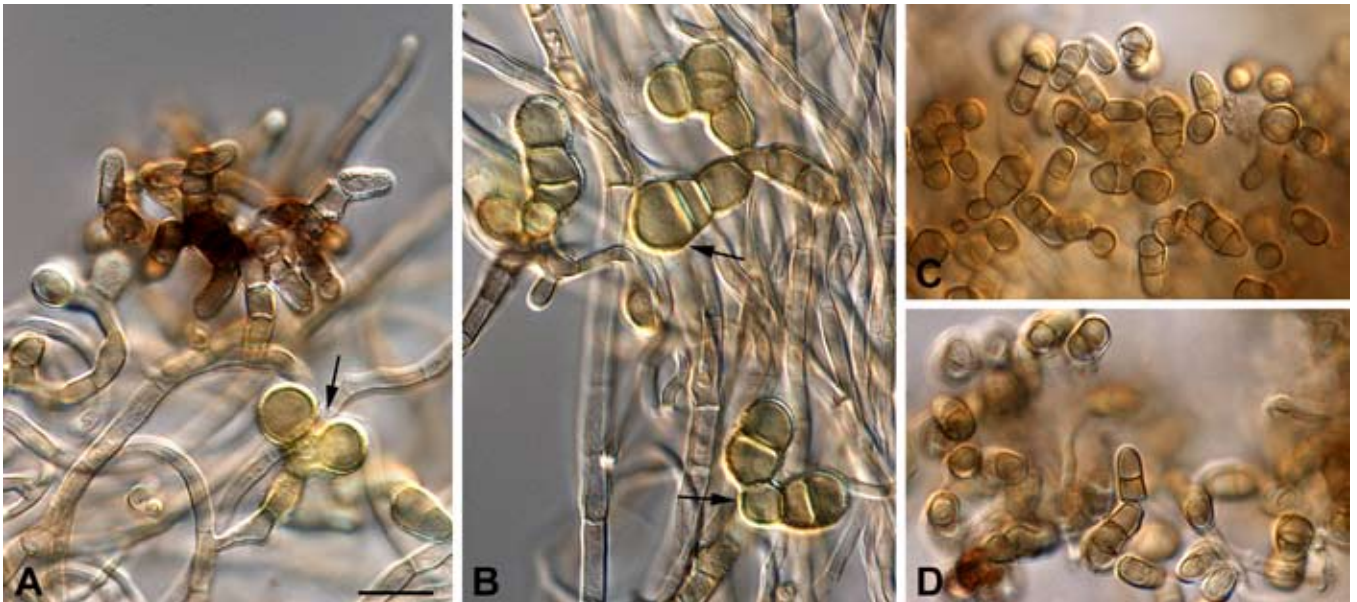


Fig. 4. *Batcheloromyces leucadendri* in vitro. A–B. *Batcheloromyces* state with synanamorph (arrows). C–D. Conidia occurring solitary or in short chains. Scale bar = 10 µm.

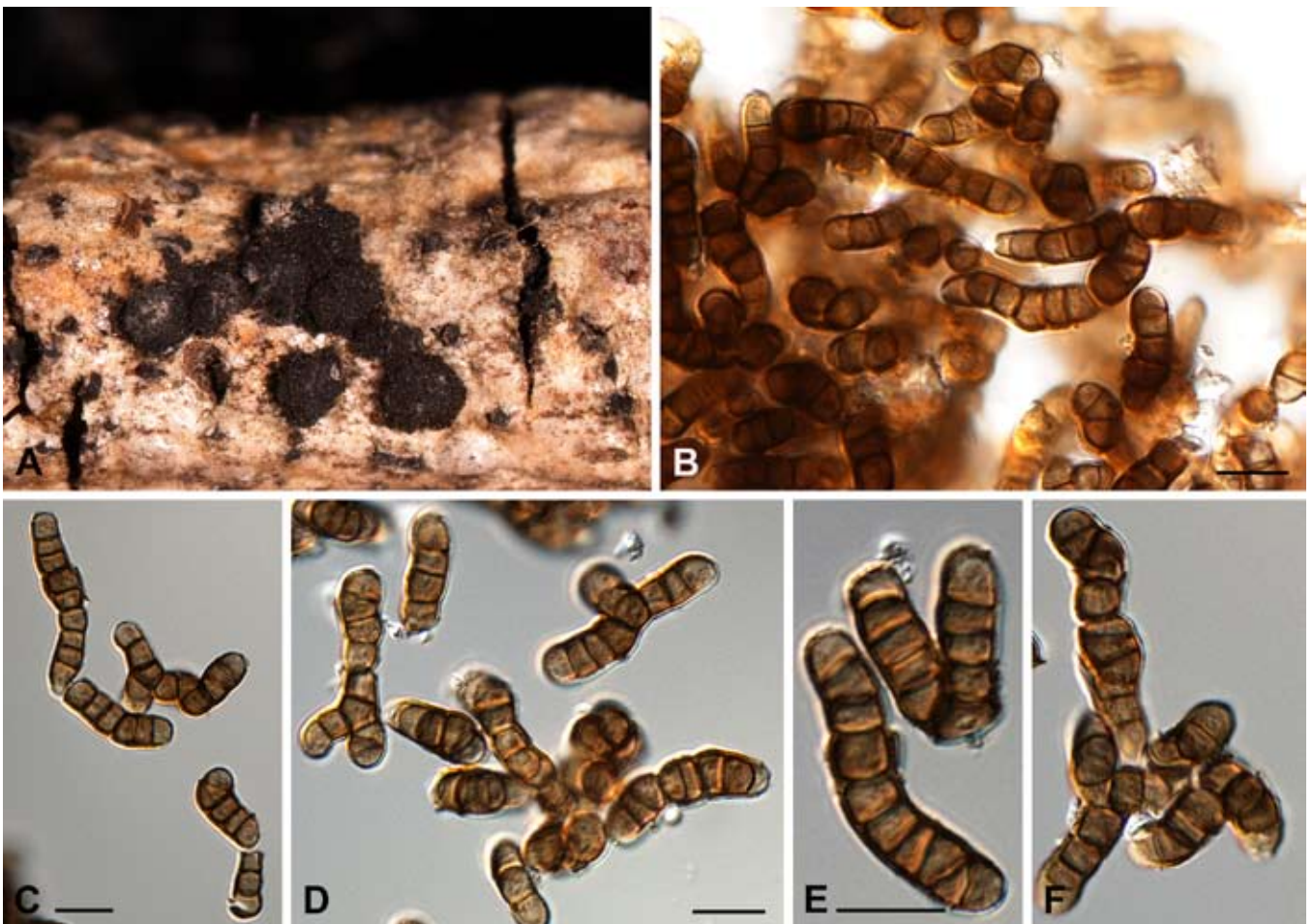


Fig. 5. *Trimmatostroma salicis*. A. Sporodochia on twig. B–E. Chains of disarticulating conidia. Scale bars = 10 µm.

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-saprophytico, 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 *hyphopodia* absent. *Conidiophores* arising from hyphae or stromata, solitary, fasciculate to sporodochial, in biotrophic, plant pathogenic species emerging through stomata, little differentiated, semimacronematous, branched or not, continuous to septate, brown, smooth to verruculose. *Conidiogenous cells* integrated, terminal or conidiophores reduced to conidiogenous cells, holoblastic-thalloblastic, meristematic, unilocal, 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, micronematous 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

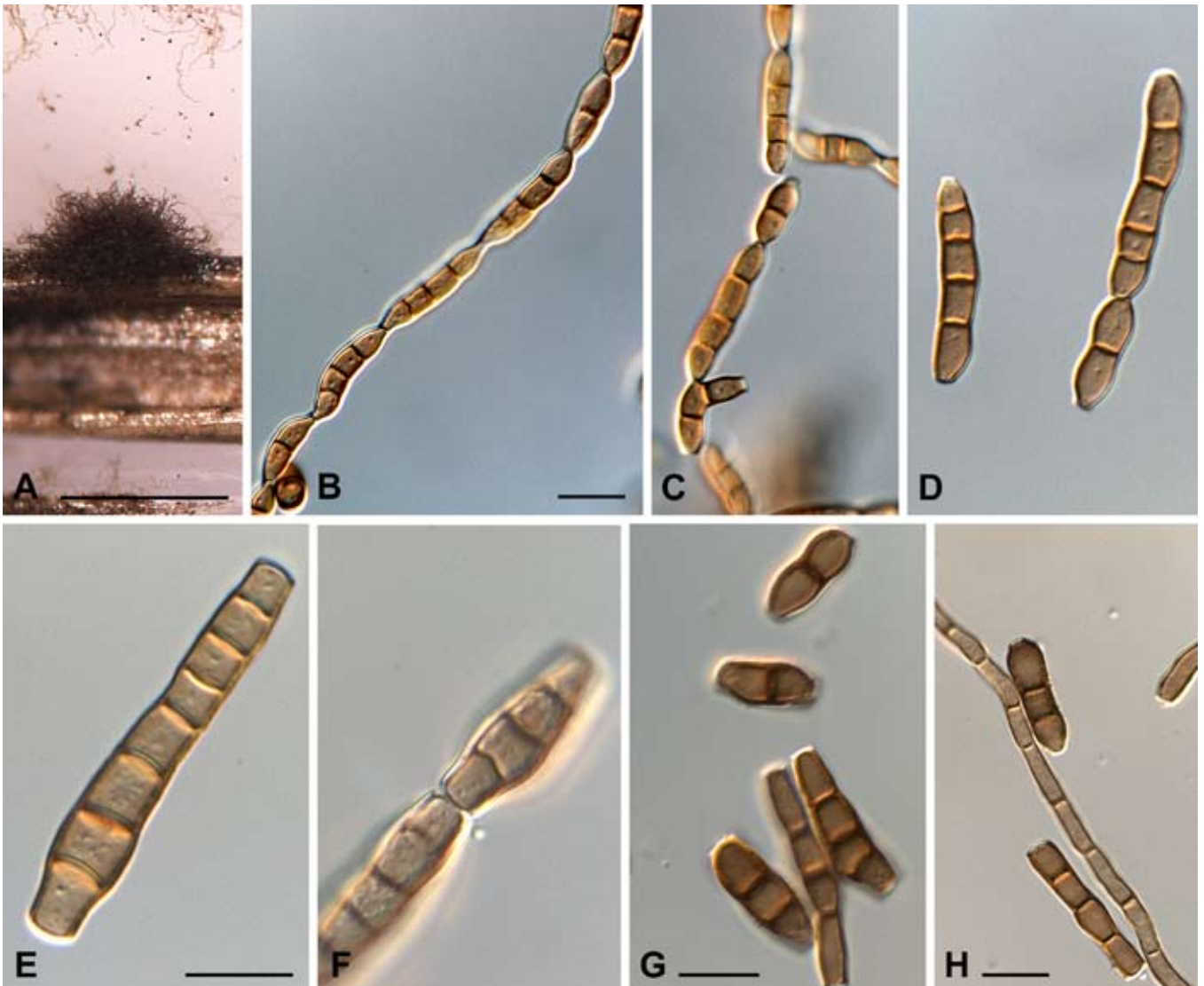


Fig. 6. *Catenulostroma chromoblastomycosum* (type material). A. Sporodochium on pine needle *in vitro*. B–H. Chains of disarticulating conidia. Scale bars: A = 350, B, E, G, H = 10 μm.

- 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–)16–20(–36) × (10–)14–18(–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. abietis* 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,



Fig. 7. *Catenulostroma germanicum* (type material). A–D. Chains of disarticulating conidia *in vitro*. Scale bars = 10 μm .

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) \times 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-19935, 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. abietis* conidiis 1–2 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, unilocal, 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.

≡ *Coniothecium punctiforme* G. Winter, Hedwigia 24: 33. 1885, non *C. punctiforme* Corda, *Icones Fungorum* (Prague) 1: 2. 1837.
≡ *Trimmatostroma macowanii* (Sacc.) M.B. Ellis, *More Dematiaceous Hyphomycetes*: 29. 1976.

Catenulostroma microsporum, see ***Teratosphaeria microspora***.

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 hila, forming chlamydospores in culture, and being heat resistant. Morphologically they resemble taxa placed in *Pseudocladosporium* U. Braun (= *Fusicladium* 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).

Notes: The genus forms brown, septate, thick-walled hyphae, with ellipsoidal, 0–1-septate (becoming muriformly septate), hyaline to pale brown conidia forming directly on the hyphae, via phialides with percurrent proliferation. Isolates of *H. werneckii* are restricted to tropical or subtropical areas, where they occur as halophilic saprobes, frequently being associated with *tinea nigra* of humans (de Hoog *et al.* 2000). The generic distinction with *Capnobotryella* is less clear, except that the latter tends to have darker, thick-walled conidia, and reduced, less prominent phialides.

Penidiella Crous & U. Braun, **gen. nov.** MycoBank MB504463.

Etymology: Named after its penicillate conidiophores.

Differt a Periconiellae conidiophoris apice penicillato ex cellulis conidiogenis et ramoconidiis compositis, cellulis conidiogenis saepe 1–3(–4) locis conidiogenis, terminalibus vel subterminalibus, subdenticulatis, non vel subincrassatis, non vel leviter fuscatis-refractivis, ramoconidiis praesentibus, saepe numerosis, conidiis ramificatis.

Mycelium consisting of branched, septate, smooth to verruculose, subhyaline to pale brown hyphae. *Conidiophores* macronematous, occasionally also with some micronematous conidiophores; macronematous conidiophores arising from superficial mycelium or stromata, solitary, fasciculate or in synnemata, erect, brown, thin- to thick-walled, smooth to finely verruculose; terminally penicillate, branched terminal part consisting of a conidiogenous apparatus composed of a series of conidiogenous cells and/or ramoconidia. *Conidiogenous cells* integrated, terminal, intercalary or pleurogenous, unbranched, pale to medium brown, smooth to finely verruculose, tapering to a flattened or rounded apical region or tips slightly inflated, polyblastic, sympodial, giving rise to a single or several sets of ramoconidia on different levels; with relatively few conidiogenous loci, 1–3(–4), terminal or subterminal, subdenticulate, denticle-like loci usually conical, terminally truncate, usually unthickened or at most very slightly thickened, not to slightly darkened or somewhat refractive. *Conidia* in branched acropetal chains. *Ramoconidia* 0–1-septate, pale to medium brown, smooth to verruculose, thin-walled, ellipsoidal, obovoid, fusiform, subcylindrical to obclavate; conidia subcylindrical, fusiform to ellipsoid-ovoid, 0–1-septate, pale olivaceous to brown, smooth to verruculose, thin-walled, catenate; hila truncate, unthickened or almost so, barely to somewhat darkened-refractive.

Type species: *Penidiella columbiana* Crous & U. Braun, sp. nov.

Notes: Three ramichloridium-like genera cluster within *Capnodiales*, namely *Periconiella* Sacc. [type: *P. velutina* (G. Winter) Sacc.], *Ramichloridium* Stahel ex de Hoog [type: *R. apiculatum* (J.H. Mill., Giddens & A.A. Foster) de Hoog] and *Penidiella* [type: *P. columbiana* Crous & U. Braun]. All three genera have brown, macronematous conidiophores with similar conidial scars. Within this complex, *Ramichloridium* is distinct in having a prominent rachis giving rise to solitary conidia. *Periconiella* and *Penidiella* are branched in the apical part of their conidiophores, and lack a rachis. In *Periconiella* conidia are solitary or formed in short, mostly simple chains, ramoconidia are lacking. The apical conidiogenous apparatus is composed of conidiogenous cells or branches with integrated, usually terminal conidiogenous cells, which are persistent. The conidiogenous cells are subcylindrical to somewhat clavate, usually not distinctly attenuated towards the tip, and have several, often numerous loci, aggregated or spread over the whole cell, terminal to usually lateral, flat, non-protuberant, not denticle-like, usually distinctly thickened and darkened, at least at the rim. In contrast, *Penidiella* has a quite distinct branching

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 micronematous conidiophores. *Penidiella* species with less pronounced penicillate apices, e.g. *P. strumelloidea* (Milko & Dunaev) Crous & U. Braun, are comparable with species of the genus *Pleurotheciopsis* 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.

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***
1. Conidiophores solitary, at most loosely aggregated 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***
2. Penicillate apex of the conidiophores composed of a system of true branchlets, conidiogenous cells and ramoconidia or at least a sequence of ramoconidia on several levels; conidia usually straight 3
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***
3. Mycelium more or less smooth; penicillate apex at least partly with true branchlets; conidia wider, 2–5 μm , at least partly septate, uniformly pigmented 4
4. Hyphae, conidiophores and conidia frequently distinctly constricted at the septa; penicillate apex of the conidiophores sparingly developed, branchlets more or less divergent; isolated from leaf litter of *Smilax* sp., Cuba ***P. rigidophora***
4. Hyphae and conidia without distinct constrictions at the septa; penicillate apex of the conidiophores usually well-developed, with abundant branchings 5
5. Conidiophores short, up to 120 \times 3–4 μm , frequently with intercalary conidiogenous cell, swollen at the conidiogenous portion just below the upper septum which render the conidiophores subnodulose to distinctly nodulose, apex \pm loosely penicillate; conidia (4–)5–7(–8) μm long; occasionally with micronematous conidiophores; isolated from man with *tinea nigra*, Venezuela ***P. venezuelensis***
5. Conidiophores much longer, up to 800 μm , 7–9 μm wide at the base, not distinctly nodulose, penicillate apex loose to often more compact, tight, metula-like; conidia longer, 7–25 \times 2–5 μm ; micronematous conidiophores lacking; isolated from dead leaf of *Paepalanthus columbianus*, Colombia ***P. columbiana***

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, crassitunicata, minute verruculosa, ad 800 μm longa, ad basim 7–9 μm lata, ad apicem pluriramosa, ex ramibus diversibus et cellulis conidiogenis composita, ramibus primariis (–2) subcylindratis, 1–7-septatis, 50–120 \times 4–6 μm ; ramibus secundariis (–2) subcylindratis, 1–5-septatis, 40–60 \times 4–6 μm ; ramibus tertiariis et subsequentibus 1–4-septatis, 10–30 \times 3–5 μm . Cellulae conidiogenae terminales vel laterales, non ramosae, 5–15 \times 3–5 μm , modice brunneae, minute verruculosae, apicem versus attenuatae, truncatae vel rotundatae, polyblasticae, sympodiales, cicatrices conidiales incrassatae, sed leviter fuscatae et non refractivae. Ramoconidia 0–1-septata, modice brunnea, levia, ellipsoidea, obclavata vel obovoidea, cum 1–3 hiliis terminalibus, 10–20 \times 3–5 μm ; conidia subcylindrica vel ellipsoidea, 0–1-septata, pallide brunnea, catenata (–10), hila truncata, non incrassata, vix vel leviter fuscata.

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 \times 4–6 μm ; secondary branches (–2), subcylindrical, 1–5-septate, 40–60 \times 4–6 μm ; tertiary and additional branches 1–4-septate, 10–30 \times 3–5 μm . *Conidiogenous cells* terminal, intercalary or lateral, unbranched, 5–15 \times 3–5 μm , medium brown, finely verruculose, tapering to a flattened or rounded (frequently swollen) apical region, scars thickened, but only somewhat darkened, not refractive. *Ramoconidia* 0–1-septate,

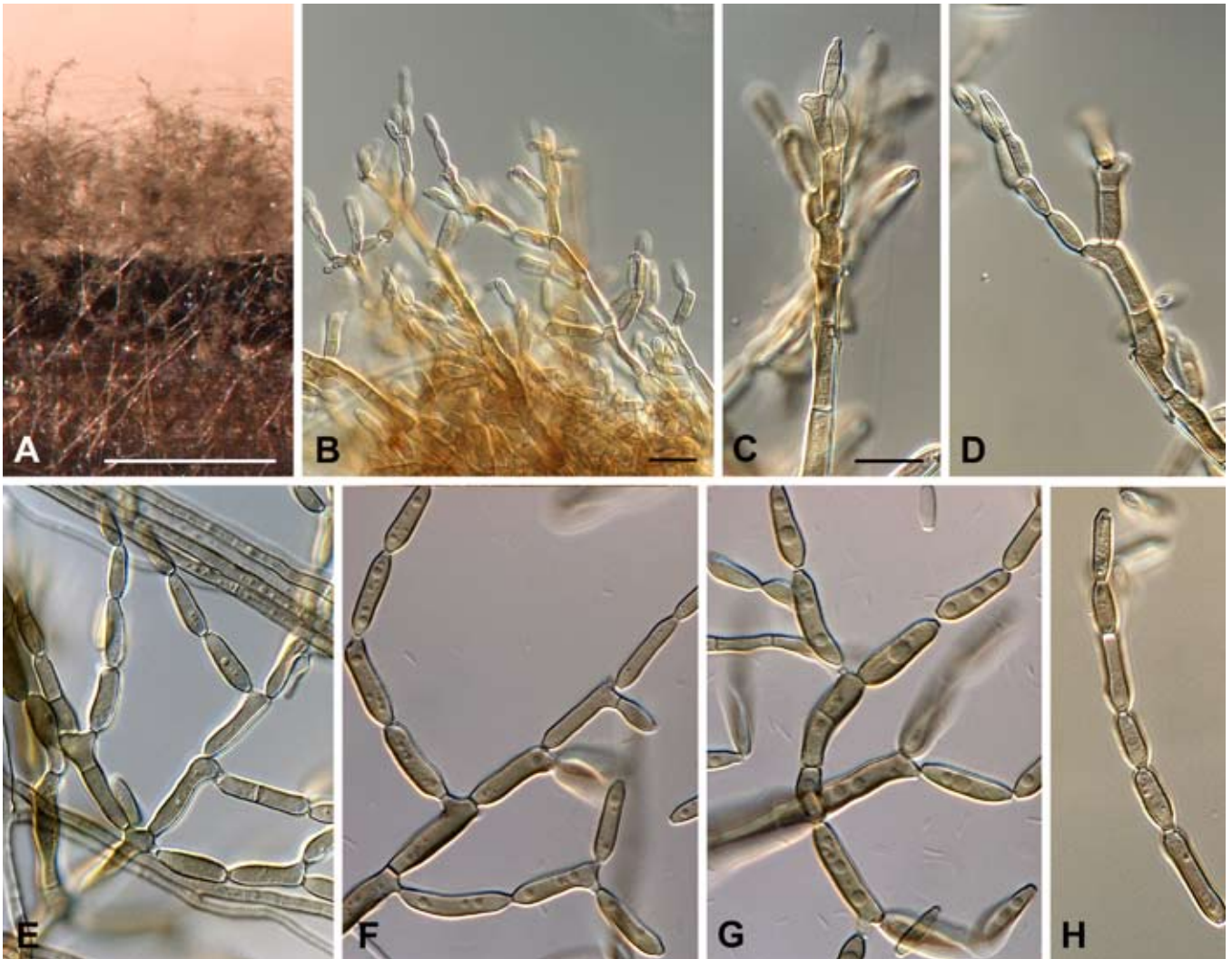


Fig. 8. *Penidiella columbiana* (type material). A. Conidiophores on pine needle *in vitro*. B–H. Conidiophores with chains of disarticulating conidia. Scale bars: A = 450, B–C = 10 μ m.

medium brown, smooth, wall ≤ 1 μ m wide, ellipsoidal to obclavate or obovoid, with 1–3 apical hila, 10–25 \times 3–5 μ m, ramoconidia with broadly truncate base, not or barely attenuated, up to 4 μ m wide, or at least somewhat attenuated at the base, hila 1.5–3 μ m wide. *Conidia* subcylindrical to ellipsoid, 0(–1)-septate, pale brown, in chains of up to 10, 7–15 \times 2–3 μ m, hila truncate, unthickened, barely to somewhat darkened, 1–2 μ m 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* (*Eriocaulaceae*), 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 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 μ m wide. *Stromata* present, 40–80 μ m diam, brown, immersed. *Conidiophores* densely fasciculate or in distinct synnemata, arising from stromata, erect, synnemata up to about 1000 μ m long and (10–)20–40(–50) μ m wide, individual threads filiform, pluriseptate throughout, brown, thin-walled (≤ 0.5 μ m), smooth or almost so to distinctly verruculose, apically penicillate. *Conidiogenous cells* integrated, terminal and intercalary, 10–30 μ m 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, 1–2 μ m 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) \times 2–3 μ m, aseptate, pale olivaceous, olivaceous-brown to brown, thin-walled, smooth or almost so to

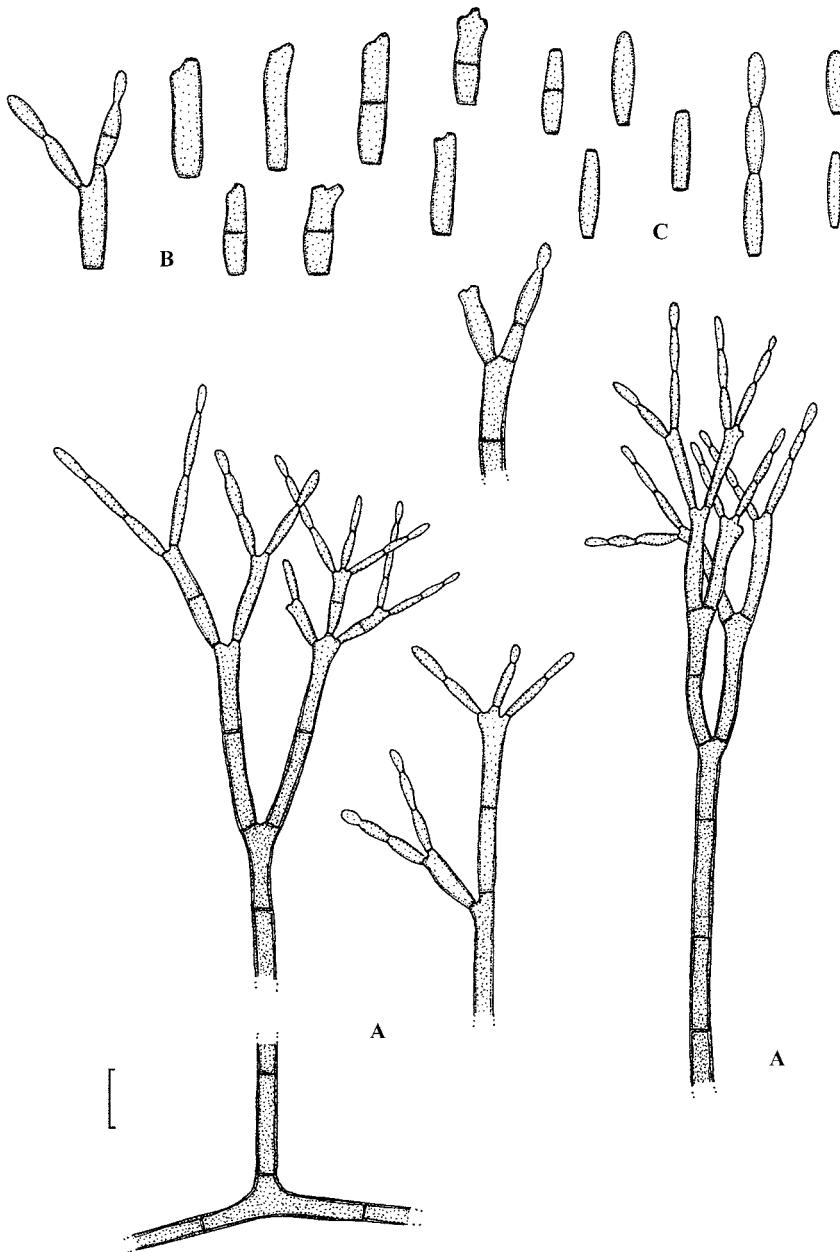


Fig. 9. *Penidiella columbiana* (type material). A. Conidiophores. B. Ramoconidia. C. Secondary conidia. Scale bar = 10 μ m. U. Braun del.

faintly verruculose, ramoconidia with broadly truncate base, barely narrowed, or ramoconidia more or less attenuated at the base, hila 1–2 μ m wide, unthickened or almost so, but often slightly refractive or darkened-refractive. *Conidia* in long acropetal chains, narrowly ellipsoid-ovoid, fusiform, 5–12(–15) \times (1–)1.5–3 μ m, aseptate, pale olivaceous to brownish, thin-walled, smooth to faintly rough-walled, ends attenuated, hila 1–1.5 μ m 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 C86/134 (HAL 2019 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 synnematus conidiomata, arising from stromata.

Penidiella nectandrae Crous, U. Braun & R.F. Castañeda, *nom. 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 μ m wide, pale olivaceous-brown or brown, thin-walled (\leq 0.5 μ m), smooth or almost so to distinctly verruculose, fertile cells giving rise to conidiophores somewhat swollen at the branching point, up to 5 μ m diam, and somewhat darker. *Stromata* lacking. *Conidiophores* erect, straight, filiform, up to 350 μ m long, 2.5–4 μ m 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 μ m 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 \times 2 μ m, aseptate, at the apex with 2–3(–4) subdenticulate hila, subcylindrical,

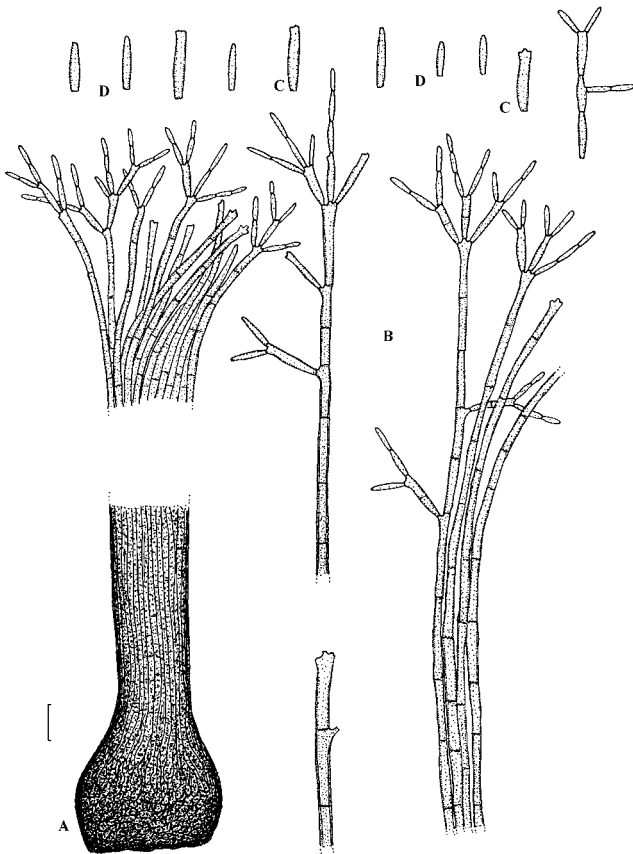


Fig. 10. *Penidiella cubensis* (type material). A. Swollen stromatic base of synnema. B. Conidiophores. C. Ramoconidia. D. Secondary conidia. Scale bar = 10 µm. U. Braun del.

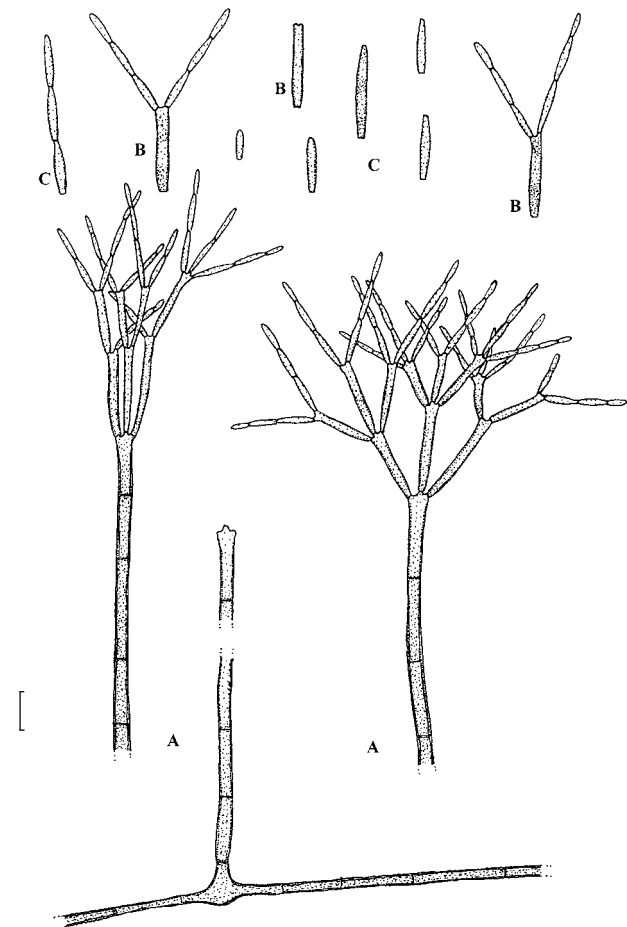


Fig. 11. *Penidiella nectandrae* (type material). A. Conidiophores. B. Ramoconidia. C. Secondary conidia. Scale bar = 10 µm. U. Braun del.

very pale olivaceous, olivaceous-brown to brown, sometimes with different shades of brown (heterochromatous), thin-walled ($\leq 0.5 \mu\text{m}$), smooth to faintly verruculose. *Conidia* in long acropetal chains, narrowly ellipsoid-ovoid, fusiform to cylindrical, $5\text{--}16 \times (1.5\text{--}2)(\text{--}2.5) \mu\text{m}$, 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 $1\text{--}1.5 \mu\text{m}$ 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. Castañeda 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. Castañeda & U. Braun, **sp. nov.** MycoBank MB504513. Figs 12–13.

= *Cladosporium rigidophorum* R.F. Castañeda, 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, $2\text{--}6 \mu\text{m}$ wide hyphae, swollen cells up to $8 \mu\text{m}$ wide, wall up to $1(\text{--}1.5) \mu\text{m}$ wide. *Conidiophores* dimorphic. *Macronematous conidiophores* separate, erect, subcylindrical, predominantly straight to slightly curved, terminally loosely penicillate, up to $120 \mu\text{m}$ long, and $4\text{--}5 \mu\text{m}$ wide at the base, which is neither lobed nor swollen, and lacks rhizoids, up to 10-septate, medium to dark brown, wall up to $1(\text{--}1.5) \mu\text{m}$ wide. *Micronematous conidiophores* erect, subcylindrical, up to $40 \mu\text{m}$ tall, $3\text{--}4 \mu\text{m}$ 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, $10\text{--}20 \times 5\text{--}6 \mu\text{m}$, loci (predominantly single in micronematous conidiophores, but up to 4 in macronematous conidiophores) flat-tipped, sub-denticulate or not, $1\text{--}1.5 \mu\text{m}$ 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-oblong, up to $1(\text{--}1.5) \mu\text{m}$ wide, frequently constricted at septa, which turn dark with age; ramoconidia $(10\text{--})13\text{--}17(\text{--}25) \times 3\text{--}4(\text{--}5) \mu\text{m}$, 1(–3)-septate; secondary conidia $(7\text{--})8\text{--}10(\text{--}12) \times 3\text{--}4(\text{--}5)$; hila unthickened to very slightly thickened and darkened, not refractive, $(0.5\text{--})1(\text{--}1.5) \mu\text{m}$.

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.

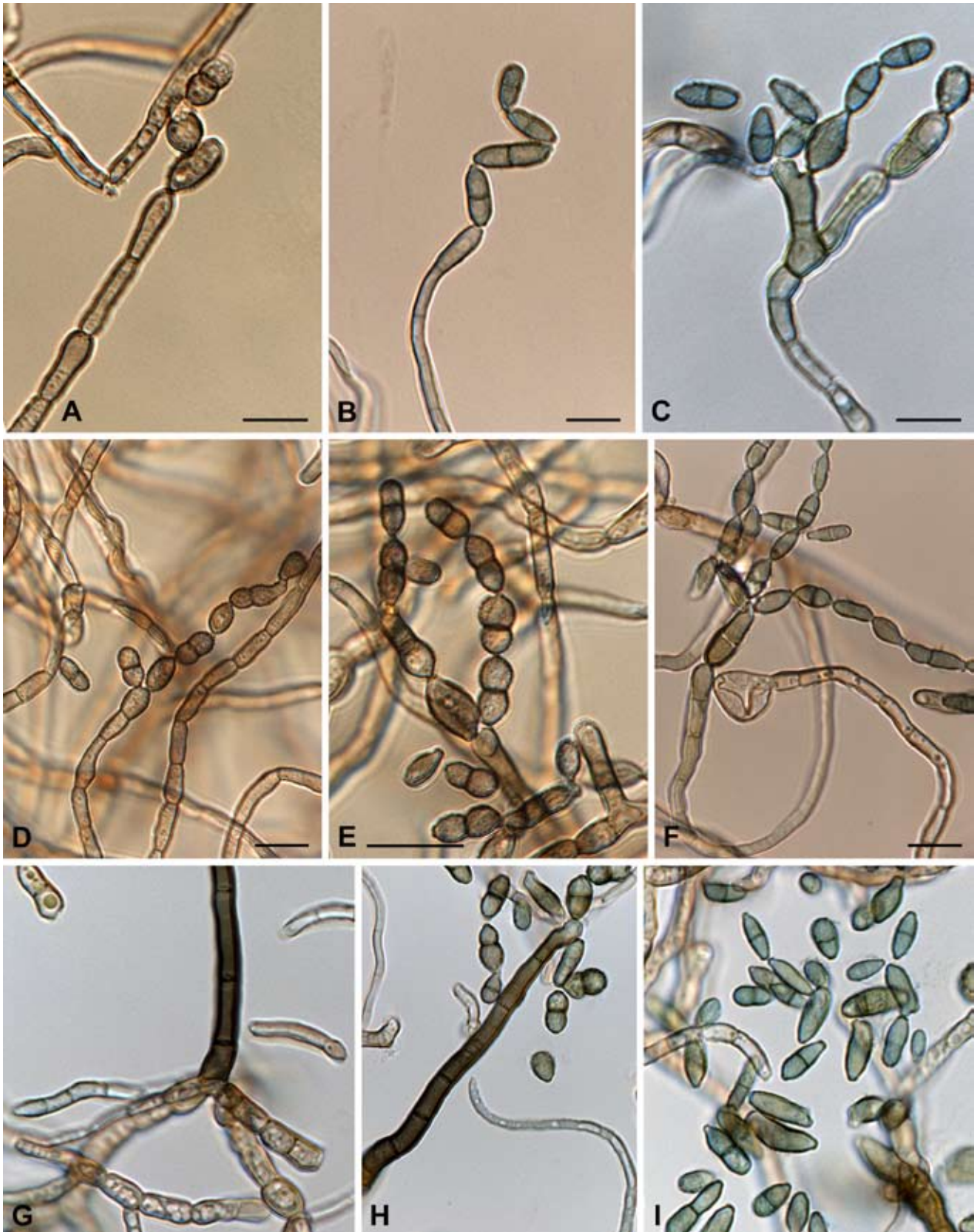


Fig. 12. *Penidiella rigidophora* (type material). A–F. Micronematous conidiophores giving rise to chains of conidia. G–H. Macronematous conidiophores (note base in G, and apex in H). I. Conidia. Scale bars = 10 μ m.

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).

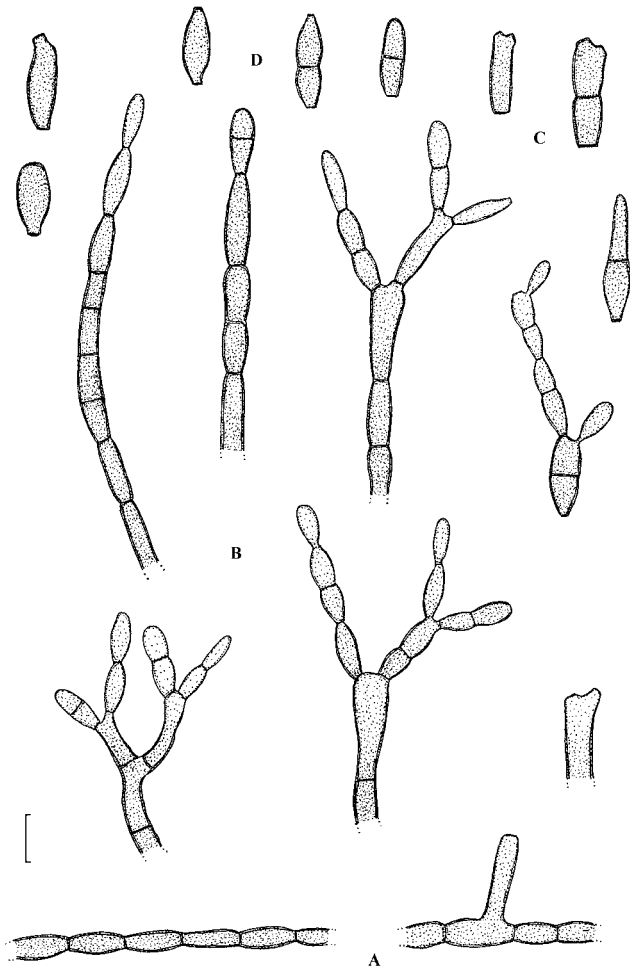


Fig. 13. *Penidiella rigidophora* (type material). A. Hyphae. B. Conidiophores. C. Ramoconidia. D. Secondary conidia. Scale bar = 10 μ m. U. Braun del.

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 μ m 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 \times (2–)2.5–4 μ m, 0–6-septate, medium brown, smooth, wall \leq 0.75 μ m, penicillate apex formed by a terminal conidiogenous cell giving rise to a single set of ramoconidia. *Conidiogenous cells* terminal, integrated, subcylindrical, straight, 8–12 \times 1.5–2(–2.5) μ m, 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 μ m 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) \times 2(–3) μ m, subhyaline to olivaceous-brown, smooth, thin-walled; hila unthickened or almost so to somewhat thickened and darkened, not refractive, 1 μ m 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 $^{\circ}$ 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.

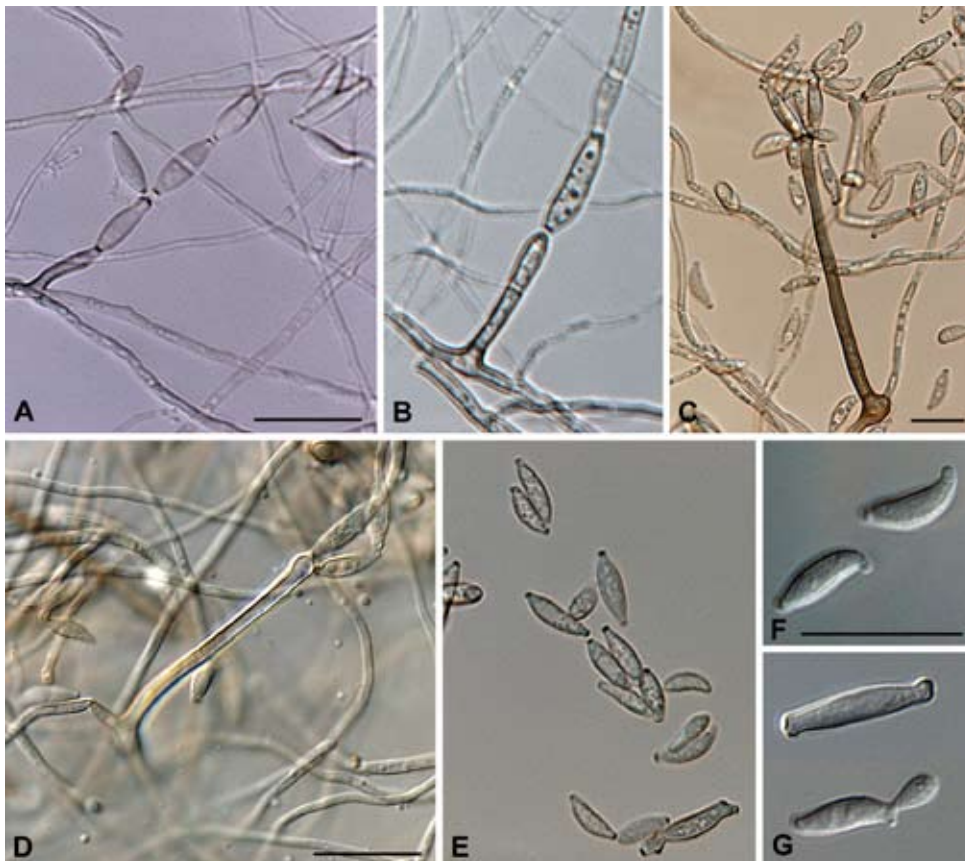


Fig. 14. *Penidiella strumelloidea* (type material). A–B. Micronematous conidiophores. C–D. Macronematous conidiophores. E–G. Conidia. Scale bars = 10 μ m.

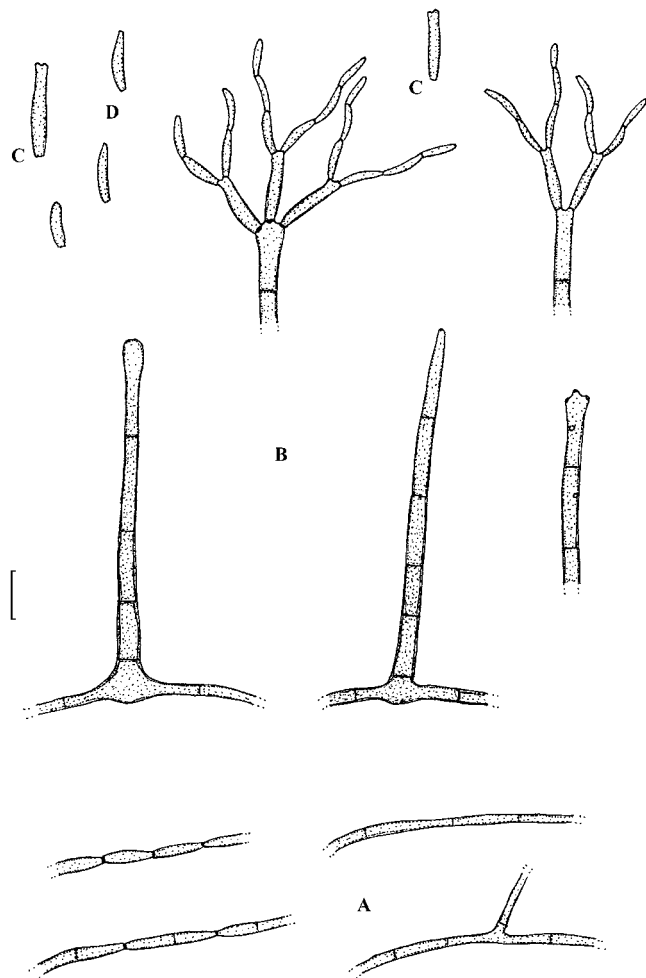


Fig. 15. *Penidiella strumelloidea* (type material). A. Hyphae. B. Conidiophores. C. Ramoconidia. D. Secondary conidia. Scale bars = 10 µm. U. Braun del.

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.

Differt a *P. columbiana* conidiophoris beavioribus et angustioribus, ad $120 \times 3\text{--}4$ µm, subnodulosis, apice plus minusve laxe penicillatis et conidiis brevioribus, $(4\text{--}5\text{--}7\text{--}8)$ µm longis.

Mycelium consisting of branched, septate, smooth to faintly rough-walled, thin-walled, subhyaline, pale olivaceous to medium brown, $(1.5\text{--})2\text{--}3$ µm wide hyphae. **Conidiophores** solitary, erect, macronematous, subcylindrical, straight to flexuous to once geniculate, up to 120 µm long, $3\text{--}4$ µm wide, $1\text{--}12$ -septate, pale to medium olivaceous-brown or brown, thin-walled (up to about 1 µm), terminally penicillate, branched portion composed of true branchlets and/or a single set or several sets of ramoconidia, branchlets up to 50 µm long; occasionally with a few additional micronematous

conidiophores, about $10\text{--}15 \times 2\text{--}3$ µm. **Conidiogenous cells** terminal and intercalary, unbranched, subcylindrical, $5\text{--}12 \times 3\text{--}4$ µm, medium brown, smooth or almost so to finely verruculose, apex of conidiogenous cells frequently swollen, up to 6 µm diam, with $1\text{--}3(4)$ flat-tipped, non to slightly thickened, non to slightly darkened-refractive loci, $1\text{--}1.5$ µm wide, frequently appearing subdentate, 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 verruculose, wall ≤ 0.5 µm wide, guttulate or not, occurring in branched chains. **Ramoconidia** $0\text{--}1(3)$ -septate, $5\text{--}15(22) \times 3\text{--}4(5)$ µm, with $1\text{--}3$ subdentate apical hila; secondary conidia $0(1)$ -septate, ellipsoid, obovoid to irregular, $(4\text{--}5\text{--}7(8)) \times (2\text{--})2.5\text{--}3(4)$ µm; hila non to slightly thickened, non to slightly darkened-refractive, $(0.5\text{--})1(1.5)$ 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 subdentate 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.
? = *Friedmanniomyces* 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 *Friedmanniomyces* is presently known from two species (Selbmann *et al.* 2005). Morphologically *Friedmanniomyces* 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.

= *Colletogloeopsis* 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, *Sonderhenia* H.J. Swart & J. Walker and *Lecanosticta* Syd. belong to *Mycosphaerellaceae*.

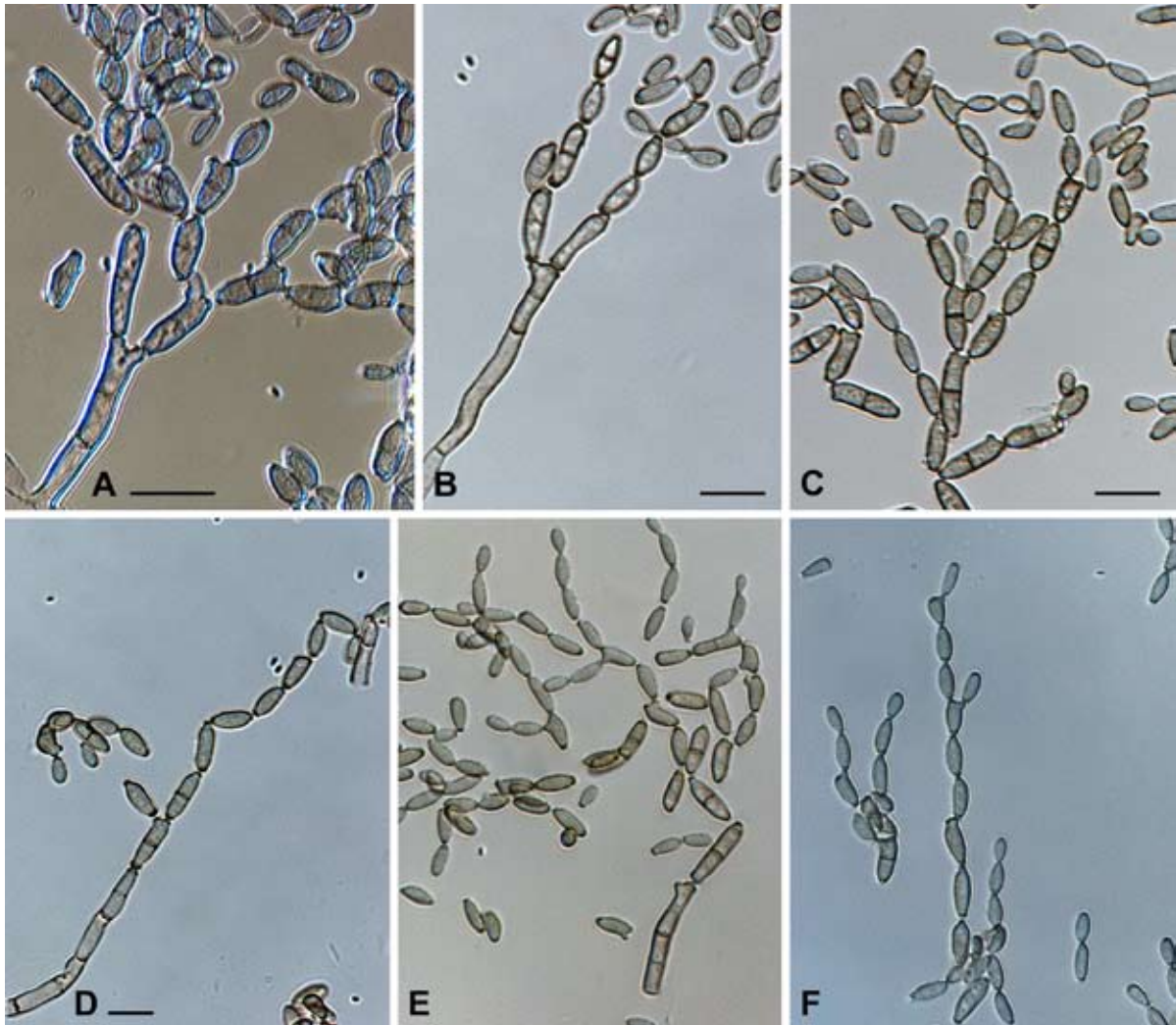
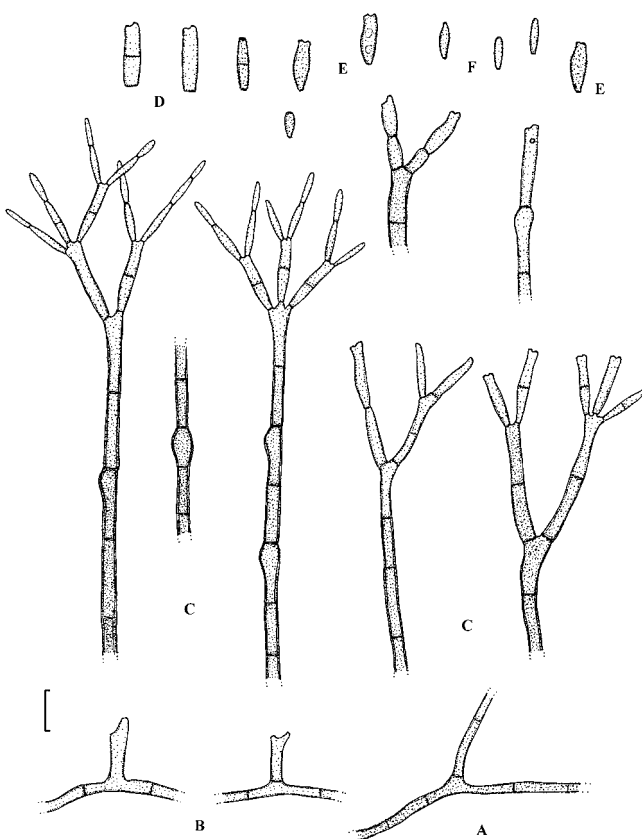


Fig. 16. *Penidiella venezuelensis* (type material). A. Microconidiophore. B. Apical part of macroconidiophore. C–F. Chains of conidia. Scale bars = 10 μ m.



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. 18). Within the form genus conidia vary from aseptate to multiseptate, 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

Fig. 17. *Penidiella venezuelensis* (type material). A. Hypha. B. Micronematous conidiophores. C. Macronematous conidiophores. D–E. Ramoconidia. F. Secondary conidia. Scale bar = 10 μ m. U. Braun *del.*

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: *Colletogloeopsis blakelyi* Crous & Summerell, Fungal Diversity 23: 342. 2006.

Readeriella brunneotagens Crous & Summerell, **sp. nov.** MycoBank MB504517. Fig. 19.

Etymology: Named after the diffuse brown pigment visible in agar when cultivated on MEA.

Readeriellae gauchensis similis, sed coloniis viridi-atris et pigmento brunneo in agaro diffundente distinguenda.

Leaf spots amphigenous, irregular specks up to 3 mm diam, medium brown with a thin, raised, concolorous border. *Conidiomata* amphigenous, substomatal, exuding conidia in black masses; conidiomata 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 (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.

Cultural characteristics: Colonies on MEA reaching 20 mm diam after 2 mo at 25 °C; colonies erumpent, aerial mycelium sparse to absent, margins smooth but irregularly lobate; surface irregularly folded, greenish black, with profuse sporulation, visible as oozing black conidial masses; a diffuse dark-brown pigment is also produced, resulting in inoculated MEA plates appearing dark-brown.

Specimen examined: **Australia**, Queensland, Cairns, Eureka Creek, 48 km from Mareeba, S 17° 11' 13.2", E 145° 02' 27.4", 468 m, on leaves of *Eucalyptus tereticornis*, 26 Aug. 2006, P.W. Crous, CBS-H 19838 **holotype**, culture ex-type CPC 13303 = CBS 120747.

Notes: Conidial dimensions of *R. brunneotagens* closely match those of *Readeriella gauchensis* (M.-N. Cortinas, Crous & M.J. Wingf.) Crous (Cortinas *et al.* 2006). The two species can be distinguished in culture, however, in that colonies of *R. brunneotagens* are greenish black in colour, sporulate profusely, and exude a diffuse, brown pigment into the agar, whereas colonies of *R. gauchensis* are more greenish olivaceous, and exude a yellow pigment into the agar (Cortinas *et al.* 2006).

Readeriella considerianae (Crous & Summerell) Crous & U. Braun, **comb. nov.** MycoBank MB504518.

Basionym: *Colletogloeopsis considerianae* Crous & Summerell, Fungal Diversity 23: 343. 2006.

Readeriella destructans (M.J. Wingf. & Crous) Crous & U. Braun, **comb. nov.** MycoBank MB504519.

Basionym: *Kirramyces destructans* 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.

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 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 pulcherrima* (Gadgil & M. Dick) H.J. Swart, Trans. Brit. Mycol. Soc. 90: 285. 1988.

= *Cercospora eucalypti* Cooke & Massee, *Grevillea* 18: 7. 1889.

≡ *Kirramyces eucalypti* (Cooke & Massee) J. Walker, B. Sutton & Pascoe, Mycol. Res. 96: 920. 1992.

≡ *Phaeophleospora eucalypti* (Cooke & Massee) Crous, F.A. Ferreira & B. Sutton, S. African J. Bot. 63: 113. 1997.

Notes: The epithet “*eucalypti*” 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 readeriellophora, see ***Teratosphaeria readeriellophora***. Fig. 18.

Readeriella stellenboschiana (Crous) Crous & U. Braun, **comb. nov.** MycoBank MB504523.

Basionym: *Colletogloeopsis stellenboschiana* 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 (*zuluense*), Mycol. Res. 110: 235. 2006.

Staninwardia B. Sutton, Trans. Br. Mycol. Soc. 57: 540. 1971.

Type species: *Staninwardia breviuscula* B. Sutton, Trans. Br. Mycol. Soc. 57: 540. 1971.

Description: Sutton (1971; fig. 1).

Notes: The genus *Staninwardia* presently contains two species, namely *S. breviuscula* and *Staninwardia 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.

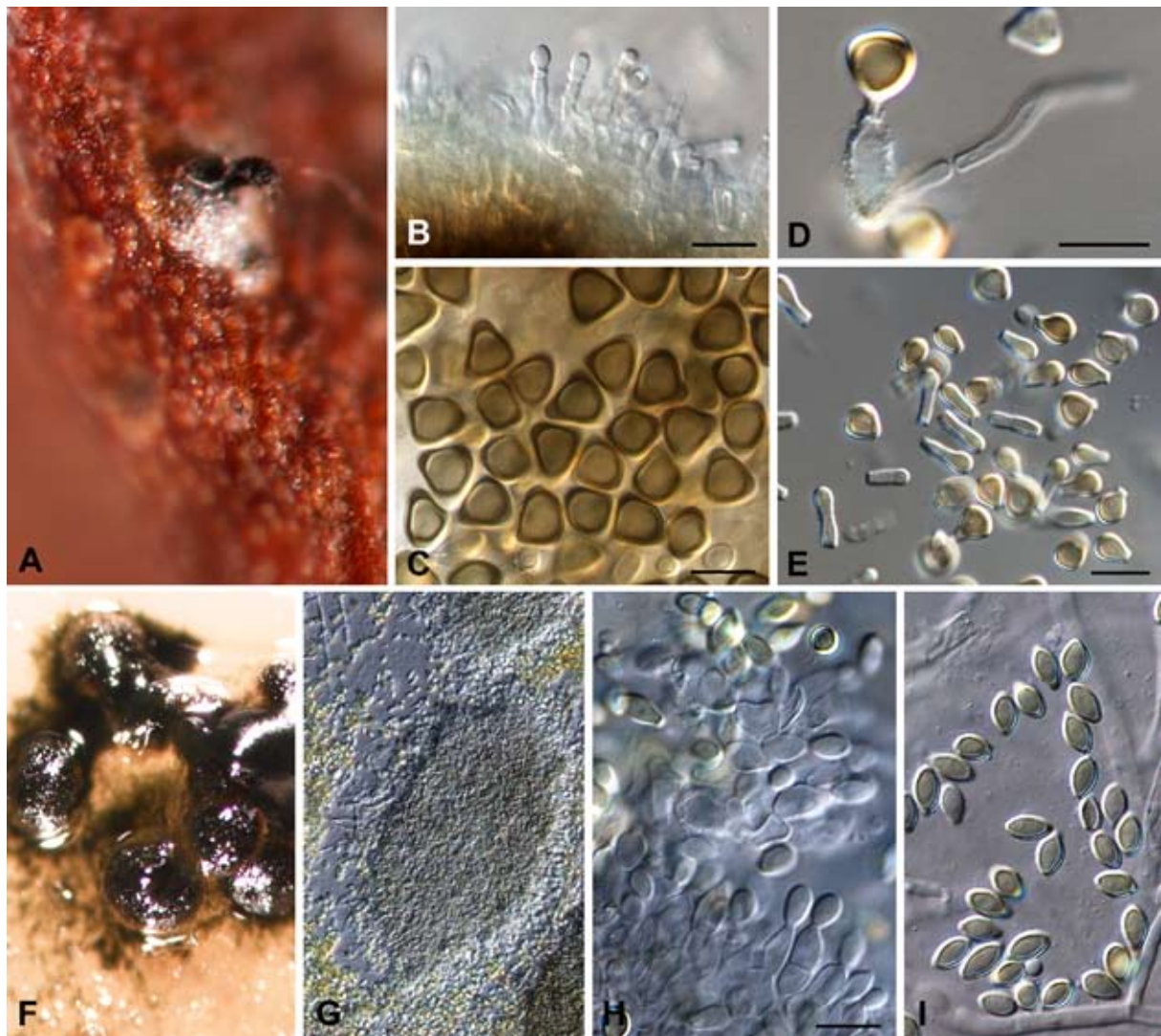


Fig. 18. A–E. *Readeriella mirabilis*. A. Conidium with conidial cirrus. B. Conidiogenous cells with percurrent proliferation. C. Macroconidia. D. Slightly pigmented, verruculose conidiogenous cell. E. Macro- and microconidia. F–I. *Readeriella readeriellophora* (type material). F. Colony on OA. G. Central stromatal tissue giving rise to conidiophores. H. Conidiogenous cells. I. Conidia. Scale bars = 10 μ m.

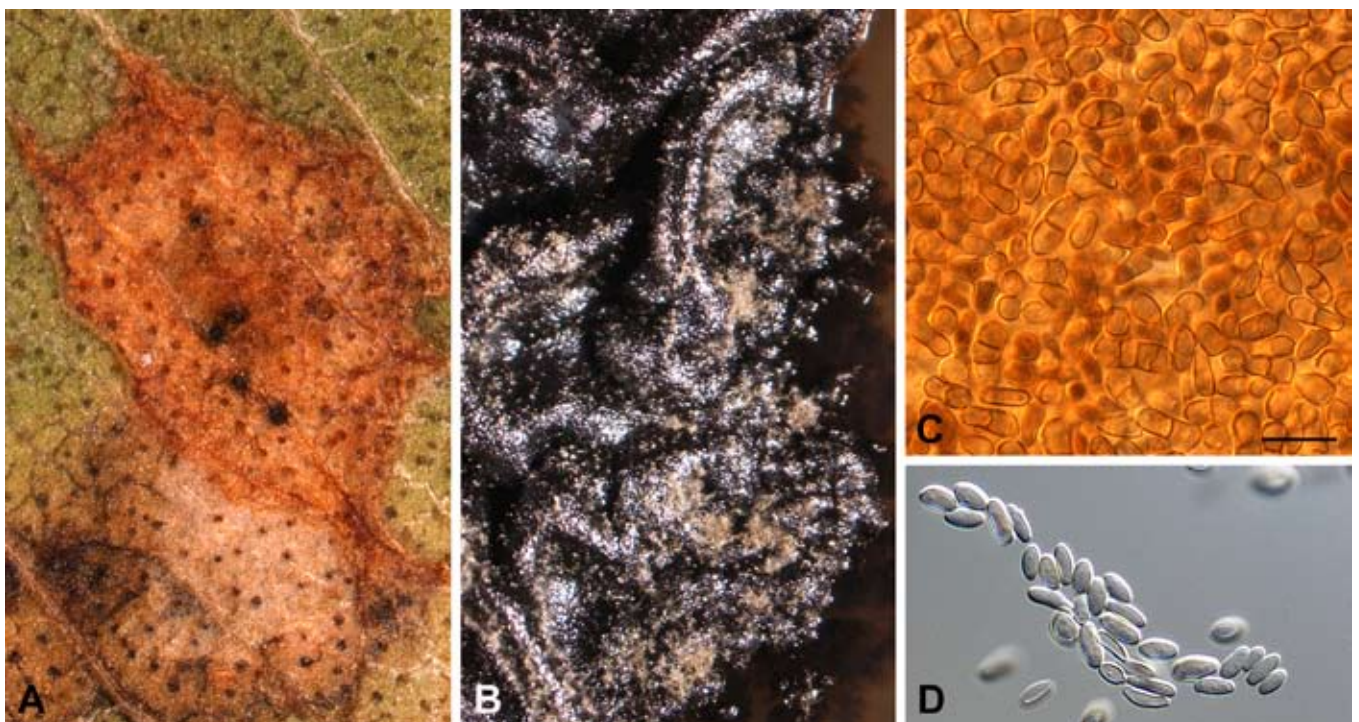


Fig. 19. *Readeriella brunneotingens* (type material). A. Leaf spot. B. Colony on MEA. C–D. Conidia. Scale bar = 10 μ m.

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 Zygothiala 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 pseudothecial ascomata, 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 subclade

Mycosphaerella Johanson, Öfvers. 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 et al. 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 Mycosphaerella 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.

? = *Uwebraunia* Crous & M.J. Wingf., Mycologia 88: 446. 1996.

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. dekkeri 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 relevance 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 ascomata 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 muriform, 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 taxa 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, guttulate, 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 bartschii*. 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 μ m.

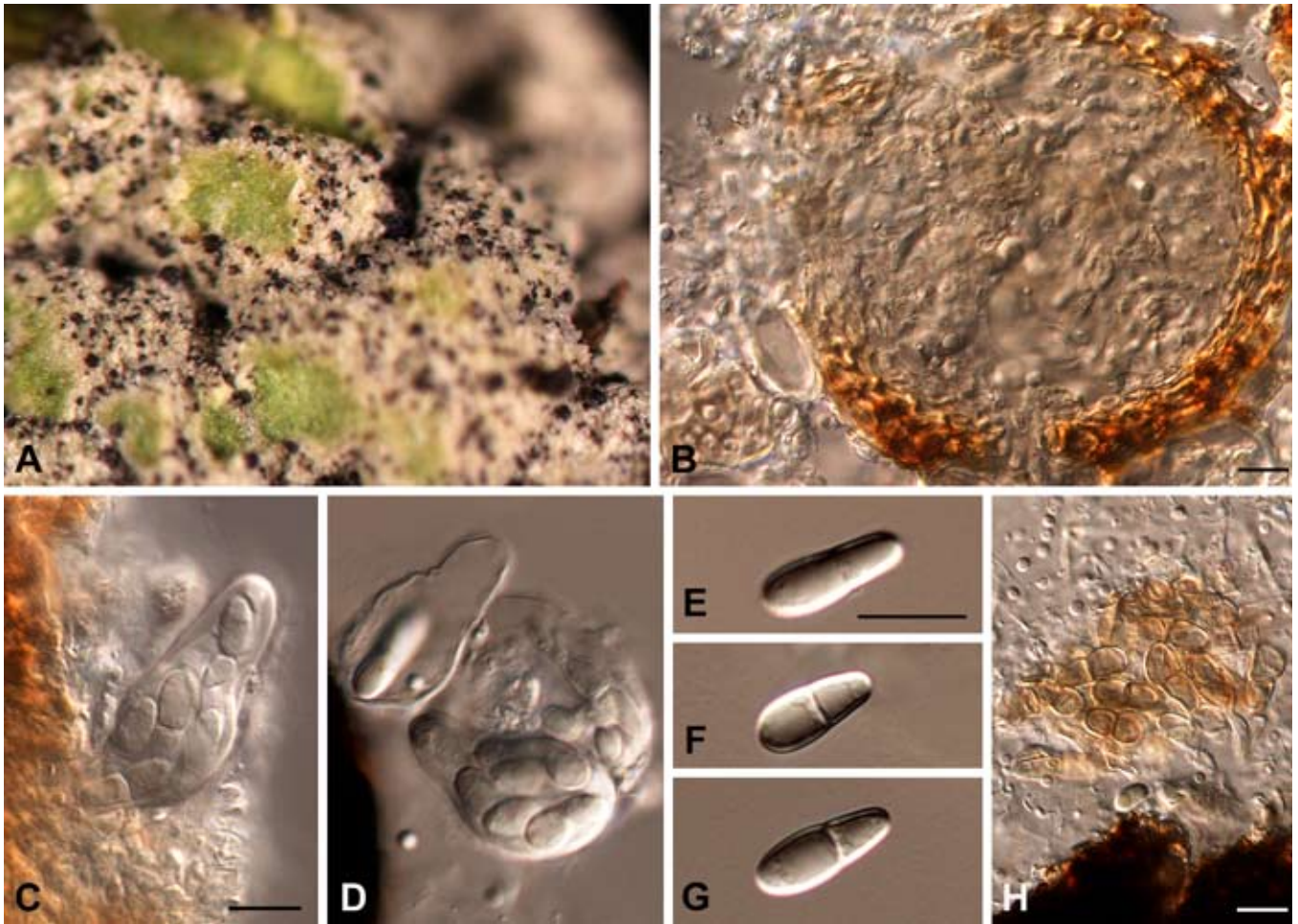


Fig. 21. *Stigmidium schaeferi*. A. Lichenicolous habit on *Dacampia hookeri*. B. Vertical section through an ascoma. C–D. Asci. E–G. Ascospores. H. Older, brown ascospores. Scale bars = 10 µm.

Stigmidium Trevis., Consp. Verruc.: 17. 1860. (Fig. 21).

Type species: *Stigmidium schaeferi* (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 1-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 stigmata-platani* F.A. Wolf to have a *Cercostigmata* U. Braun and *Xenostigmata* Crous synanamorph, and recent collections also revealed the presence of a similar species that has typical “*Stigmata*” (distoseptate conidia) and *Pseudocercospora* (euseptate conidia) synanamorphs (Crous, unpubl. data), and Crous (1998) reported *Readeriella epicoccoides* (coelomycete) to

have a *Cercostigmina* (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 *Cercostigmina* (rough, irregular percurrent proliferations) was also synonymous with *Pseudocercospora*. This led Crous & Braun (2003) to conclude that conidiomatal type, conidial catenulation, septation and proliferation of conidiogenous cells were of less importance in separating species at the generic level. *Mycovellosiella* Rangel and *Phaeoramularia* Munt.-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), *Stigmia* (distoseptate conidia), and several other, less well-known genera such as *Asperisporium* Maubl., *Denticularia* Deighton, *Distocercospora* N. Pons & B. Sutton, *Prathigada* Subram., *Ramulispora*, *Pseudocercosporidium* Deighton, *Stenellopsis* B. Huguenin and *Verrucisporota* 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 *Stigmia* (distoseptate conidia) were also synonyms of *Pseudocercospora*.

The present study shows that most anamorph genera are polyphyletic within *Teratosphaeria*, 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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