



## Unravelling *Mycosphaerella*: do you believe in genera?

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### Key words

*Cibiessia*  
*Colletogloeum*  
*Dissoconium*  
*Kirramyces*  
*Mycosphaerella*  
*Passalora*  
*Penidiella*  
*Phaeophleospora*  
*Phaeothecoidea*  
*Pseudocercospora*  
*Ramularia*  
*Readeriella*  
*Stenella*  
*Teratosphaeria*  
*Zasmidium*

**Abstract** Many fungal genera have been defined based on single characters considered to be informative at the generic level. In addition, many unrelated taxa have been aggregated in genera because they shared apparently similar morphological characters arising from adaptation to similar niches and convergent evolution. This problem is aptly illustrated in *Mycosphaerella*. In its broadest definition, this genus of mainly leaf infecting fungi incorporates more than 30 form genera that share similar phenotypic characters mostly associated with structures produced on plant tissue or in culture. DNA sequence data derived from the LSU gene in the present study distinguish several clades and families in what has hitherto been considered to represent the *Mycosphaerellaceae*. In some cases, these clades represent recognisable monophyletic lineages linked to well circumscribed anamorphs. This association is complicated, however, by the fact that morphologically similar form genera are scattered throughout the order (*Capnodiales*), and for some species more than one morph is expressed depending on cultural conditions and media employed for cultivation. The present study shows that *Mycosphaerella* s.s. should best be limited to taxa with *Ramularia* anamorphs, with other well defined clades in the *Mycosphaerellaceae* representing *Cercospora*, *Cercosporella*, *Dothistroma*, *Lecanosticta*, *Phaeophleospora*, *Polythrincium*, *Pseudocercospora*, *Ramulispora*, *Septoria* and *Sonderhenia*. The genus *Teratosphaeria* accommodates taxa with *Kirramyces* anamorphs, while other clades supported in the *Teratosphaeriaceae* include *Baudoinea*, *Capnobotryella*, *Devriesia*, *Penidiella*, *Phaeothecoidea*, *Readeriella*, *Staninwardia* and *Stenella*. The genus *Schizothyrium* with *Zygophiala* anamorphs is supported as belonging to the *Schizothyriaceae*, while *Dissoconium* and *Ramichloridium* appear to represent a distinct family. Several clades remain unresolved due to limited sampling. *Mycosphaerella*, which has hitherto been used as a term of convenience to describe ascomycetes with solitary ascomata, bitunicate asci and 1-septate ascospores, represents numerous genera and several families yet to be defined in future studies.

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## INTRODUCTION

When Colin Booth delivered his Presidential address to the British Mycological Society in 1977, he chose the title 'Do you believe in genera?'. This, interestingly, was the question Mr Mason asked him when he first arrived at the Commonwealth Mycological Institute. This question raised a very complex issue, and it was sufficient to silence anyone embarking on a career in mycology. However, Booth went on to research this topic, and delivered his interpretation in his published Presidential address (Booth 1978). In addressing this issue, he chose the *Nectriaceae*, a group that he knew very well. For the purpose of the present study, we focus on the genus *Mycosphaerella* that was a core focus of Booth's colleague, J.A. von Arx, who worked at the 'sister' Institute, the Centraalbureau voor Schimmelcultures (CBS) in the Netherlands.

To believe in genera, Booth (1978) emphasised the need to clarify what a genus represents. Here he followed the definition of Singer (1975), namely that a genus represents an assemblage of species separated from others by a gap larger or more abrupt than that existing between species. Since 2009 is also

the 150th celebration of Darwin's 'On the Origin of Species', it is fitting to reflect on the quote Booth cited from this book, namely, 'that our classifications will come to be genealogies: and that they will then truly give what may be called the plan of creation'. Booth (1978) made the point that particularly for microfungi, taxonomy was largely at the alpha or descriptive phase, and that mycology and generic concepts had suffered from what he referred to as 'shoe-box taxonomy'.

The shoe-box taxonomy referred to by Booth led mycologists to place taxa with similar primary characters that were considered important at the time, in the same box. This resulted in many *genera trivialia*, their members often genetically widely separated reflecting distinct evolutionary histories. He further noted that conidiomatal and ascomatal morphology frequently reflected a response to a particular niche, rather than genealogical relationship. What this implied was that many generic names reflected 'terms of convenience', rather than genealogical relationships. This is especially true for *Mycosphaerella* and its anamorphs that we discuss in this study.

Subsequent to the time when Booth (1978) published his views on genera, mycology has undergone a major revolution in the way that fungal groupings at all levels are recognised. This has emerged from the now widely adopted application of DNA sequence comparisons to define fungal groups (Taylor et al. 2000). Phylogenetic relationships derived from various gene regions have allowed mycologists to revise the classification schemes to coincide with molecular phylogenetic relationships. This has resulted in major changes reflecting higher order relationships (James et al. 2006, Hibbett et al. 2007). Thus, many

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**Table 1** Details of the isolates for which novel sequences were generated.

Species	Accession number <sup>1</sup>	GenBank number (28S nrDNA)
<i>Baudoinia compniacensis</i>	CBS 123031; DAOM 238773; UAMH 10808	GQ852580
	CBS 123032; DAOM 237864; UAMH 10764	GQ852581
<i>Capnobotryella renispora</i>	CBS 215.90; IAM 13015	GQ852582
<i>Cercospora apii</i>	CBS 118712	GQ852583
<i>Cercospora zebrinae</i>	CBS 118790; IMI 262766; WAC 7973	GQ852584
<i>Cercospora virgaureae</i>	CBS 113304	GQ852585
<i>Dissoconium aciculare</i>	CBS 201.89	GQ852586
	CBS 204.89	GQ852587
<i>Dissoconium australiensis</i>	CBS 120729; CPC 13282	GQ852588
<i>Dissoconium commune</i>	CBS 110747; CPC 831	GQ852589
	CBS 114239; CPC 10492	GQ852590
	CPC 12397	GQ852591
<i>Dissoconium dekkeri</i>	CPC 13098	GQ852592
	CPC 13264	GQ852593
	CPC 13279	GQ852594
	CPC 13479	GQ852595
<i>Dothistroma pini</i>	CBS 116487; CMW 10951	GQ852596
<i>Dothistroma septosporum</i>	CBS 112498; CPC 3779	GQ852597
<i>Lecanosticta acicola</i>	CBS 871.95; MPFN 314	GQ852598
' <i>Mycosphaerella</i> ' <i>acaciigena</i>	CBS 112515; CPC 3837	GQ852599
	CBS 112516; CPC 3838	GQ852600
' <i>Mycosphaerella</i> ' <i>africana</i>	CBS 116154; CMW 4945; CPC 794	GQ852601
' <i>Mycosphaerella</i> ' <i>ellipsoidea</i>	CBS 110843; CPC 850	GQ852602
' <i>Mycosphaerella</i> ' <i>endophytica</i>	CBS 114662; CPC 1193	GQ852603
' <i>Mycosphaerella</i> ' <i>heimii</i>	CBS 110682; CMW 4942; CPC 760	GQ852604
	CPC 11000	GQ852605
	CPC 13099	GQ852606
' <i>Mycosphaerella</i> ' <i>heimioides</i>	CBS 111190; CMW 3046; CPC 1312	GQ852607
' <i>Mycosphaerella</i> ' <i>holualoana</i>	CBS 110699; CPC 2155	GQ852608
' <i>Mycosphaerella</i> ' <i>irregulariramosa</i>	CBS 111211; CPC 1362	GQ852609
' <i>Mycosphaerella</i> ' <i>keniensis</i>	CBS 111001; CMW 5147; CPC 1084	GQ852610
' <i>Mycosphaerella</i> ' <i>konae</i>	CPC 10992	GQ852611
' <i>Mycosphaerella</i> ' <i>marksii</i>	CBS 110942; CPC 982	GQ852612
	CPC 11222	GQ852613
	CPC 13273	GQ852614
	CPC 13724	GQ852615
' <i>Mycosphaerella</i> ' <i>parkii</i>	CBS 387.92; CMW 14775; CPC 353	GQ852616
<i>Mycosphaerella pyri</i>	CBS 222.31; CPC 3677	GQ852617
<i>Passalora bellynckii</i>	CBS 150.49; CPC 3635	GQ852618
<i>Passalora brachycarpa</i>	CBS 115124	GQ852619
' <i>Passalora</i> ' <i>eucalypti</i>	CBS 111318; CPC 1457	GQ852620
' <i>Passalora</i> ' <i>graminis</i>	CBS 113303	GQ852621
' <i>Passalora</i> ' sp.	CPC 11876	GQ852622
	CPC 12319	GQ852623
' <i>Passalora</i> ' <i>vaginae</i>	CBS 140.34; DSM 1148; IMI 303641	GQ852624
' <i>Penidiella</i> ' sp.	CBS 124991; CPC 12400	GQ852625
	CBS 124993; CPC 13692	GQ852626
' <i>Phacellium</i> ' <i>paspali</i>	CBS 113093; RoKI 1144	GQ852627
<i>Phaeothecoidea</i> sp.	CBS 124994; CPC 13711	GQ852628
	CBS 124995; CPC 13710	GQ852629
<i>Pseudocercospora bixae</i>	CBS 111804; CPC 2554	GQ852630
<i>Pseudocercospora crousii</i>	CBS 119487; Lynfield 1260	GQ852631
<i>Pseudocercospora fijiensis</i>	X300	GQ852632
<i>Pseudocercospora griseola</i> forma <i>griseola</i>	CPC 10779	GQ852633
<i>Pseudocercospora paraguayensis</i>	CBS 111317; CPC 1458	GQ852634
<i>Pseudocercospora platani</i>	CBS 110755; IMI 136770; CPC 4299	GQ852635
<i>Pseudocercospora pseudoeucalyptorum</i>	CBS 114242; CMW 14908; CPC 10390	GQ852636
	CPC 12406	GQ852637
	CPC 12568	GQ852638
	CPC 12802	GQ852639
	CPC 12957	GQ852640
	CPC 13455	GQ852641
	CPC 13769	GQ852642
	CPC 13816	GQ852643
	CPC 13926	GQ852644
<i>Pseudocercospora punctata</i>	CPC 10532	GQ852645
<i>Pseudocercospora schizobii</i>	CBS 124990; CPC 13492	GQ852646
<i>Pseudocercospora</i> sp.	CBS 124996; CPC 12960	GQ852647
	CPC 13008	GQ852648
	CPC 13299	GQ852649
	CPC 13315	GQ852650
	CPC 14621	GQ852651
<i>Pseudocercospora sphaerulinae</i>	CBS 112621; CPC 4314	GQ852652
<i>Ramulispora sorghi</i>	CBS 110578; CPC 905	GQ852653
	CBS 110579; CPC 906	GQ852654
<i>Readeriella callista</i>	CBS 124986; CPC 13615	GQ852655
	CPC 12715	GQ852656
	CPC 12727	GQ852657
	CPC 12841	GQ852658
	CPC 13605	GQ852659

<i>Readeriella eucalypti</i>	CPC 13401	GQ852660
<i>Readeriella mirabilis</i>	CPC 12379	GQ852661
	CPC 13611	GQ852662
<i>Readeriella nontingens</i>	CPC 14444	GQ852663
<i>Readeriella patrickii</i>	CBS 124987; CPC 13602	GQ852664
<i>Readeriella</i> sp.	CBS 124997; CPC 13608	GQ852665
	CBS 124998; CPC 13618	GQ852666
	CBS 124999; CPC 13026	GQ852667
	CBS 125001; CPC 13599	GQ852668
	CBS 125002; CPC 13631	GQ852669
	CBS 125003; CPC 14447	GQ852670
	CPC 13621	GQ852671
	CPC 13630	GQ852672
<i>Septoria aceris</i>	CBS 652.85	GQ852673
<i>Septoria apiicola</i>	CBS 400.54; IMI 092628	GQ852674
<i>Septoria convolvuli</i>	CBS 102325	GQ852675
<i>Septoria cucubali</i>	CBS 102368	GQ852676
<i>Septoria leucanthemi</i>	CBS 109090	GQ852677
<i>Septoria senecionis</i>	CBS 102366	GQ852678
<i>Sonderhenia eucalypticola</i>	CPC 11252	GQ852679
<i>Teratosphaeria considerianae</i>	CPC 13032	GQ852680
	CPC 14057	GQ852681
<i>Teratosphaeria cryptica</i>	CBS 110975; CMW 3279; CPC 936	GQ852682
	CPC 12415	GQ852683
	CPC 12424	GQ852684
	CPC 12559	GQ852685
	CPC 12562	GQ852686
	CPC 12565	GQ852687
	CPC 13839	GQ852688
	CPC 13842	GQ852689
<i>Teratosphaeria destructans</i>	CBS 111370; CPC 1368	GQ852690
<i>Teratosphaeria eucalypti</i>	CPC 12552	GQ852691
<i>Teratosphaeria molleriana</i>	CPC 12232	GQ852692
	CPC 12246	GQ852693
<i>Teratosphaeria nubilosa</i>	CPC 11926	GQ852694
	CPC 12235	GQ852695
	CPC 12243	GQ852696
	CPC 12830	GQ852697
	CPC 13452	GQ852698
	CPC 13825	GQ852699
	CPC 13828	GQ852700
	CPC 13831	GQ852701
	CPC 13833	GQ852702
	CPC 13835	GQ852703
	CPC 13837	GQ852704
	CPC 13844	GQ852705
	CPC 13847	GQ852706
	CPC 13849	GQ852707
' <i>Teratosphaeria</i> ' <i>parva</i>	CPC 12249	GQ852708
	CPC 12419	GQ852709
' <i>Teratosphaeria</i> ' sp.	CBS 120040; CPC 12712	GQ852710
	CBS 125006; CPC 14514	GQ852711
	CPC 12200	GQ852712
	CPC 13680	GQ852713
	CPC 14535	GQ852714
<i>Teratosphaeria stellenboschiana</i>	CBS 124989; CPC 13767	GQ852715
	CPC 12283	GQ852716
	CPC 13764	GQ852717
' <i>Teratosphaeria</i> ' <i>suberosa</i>	CPC 11032	GQ852718
	CPC 13091	GQ852719
	CPC 13093	GQ852720
	CPC 13094	GQ852721
	CPC 13095	GQ852722
	CPC 13096	GQ852723
	CPC 13104	GQ852724
	CPC 13106	GQ852725
	CPC 13111	GQ852726
	CPC 13115	GQ852727
	CPC 13736	GQ852728
<i>Teratosphaeria suttonii</i>	CBS 119973; CMW 23440	GQ852729
<i>Verrucisporota daviesiae</i>	CBS 116002; VPRI 31767	GQ852730
<i>Verrucisporota proteacearum</i>	CBS 116003; VPRI 31812	GQ852731
<i>Zasmidium anthuriicola</i>	CBS 118742	GQ852732
<i>Zasmidium citri</i>	CPC 13467	GQ852733
' <i>Zasmidium</i> ' sp.	CPC 12748	GQ852734
	CPC 14044	GQ852735
	CPC 14636	GQ852736

<sup>1</sup> CBS: Centraalbureau voor Schimmelcultures, Utrecht, The Netherlands; CMW: Culture Collection of the Forestry and Agricultural Biotechnology Institute (FABI) of the University of Pretoria, Pretoria, South Africa; CPC: Culture collection of Pedro Crous, housed at CBS; DAOM: Plant Research Institute, Department of Agriculture (Mycology), Ottawa, Canada; DSM: Deutsche Sammlung von Mikroorganismen und Zellkulturen GmbH, Braunschweig, Germany; IMI: International Mycological Institute, CABI-Bioscience, Egham, Basingstoke, UK; MPFN: Culture collection at the Laboratoire de Pathologie Forestière, INRA, Centre de Recherches de Nancy, 54280 Champenoux, France; UAMH: University of Alberta Microfungus Collection and Herbarium, Edmonton, Alberta, Canada; VPRI: Victorian Department of Primary Industries, Knoxfield, Australia; WAC: Department of Agriculture Western Australia Plant Pathogen Collection, Perth, Australia; X: Private culture collection of Mahdi Arzanlou; RoKI: Private culture collection Roland Kirschner; Lynfield: Private culture collection Frank Hill.

genera have been shown as poly- or paraphyletic (Halleen et al. 2004, Lee et al. 2004, Réblová et al. 2004, Verkley et al. 2004b, Crous et al. 2006b, c, 2007a, b, Arzanlou et al. 2007, Wang et al. 2007, Phillips et al. 2008), and cosmopolitan species have been shown to represent assemblages of often large numbers of cryptic taxa (Barnes et al. 2004, Crous et al. 2004b, c, 2006a, d, 2008a, b, Groenewald et al. 2005, Mostert et al. 2006, Andjic et al. 2007b, Cheewangkoon et al. 2008).

The genus *Mycosphaerella* s.l. together with its associated anamorph genera (especially *Cercospora*, *Pseudocercospora*, *Septoria*, *Ramularia*, etc.), represents more than 10 000 taxa (Crous et al. 2000, 2001, 2004b, c, 2006a, b, d, 2007a–c, 2008a, b, Crous & Braun 2003, Arzanlou et al. 2007, 2008). In a treatment of the *Mycosphaerella* species and associated anamorphs occurring on *Eucalyptus*, Crous (1998) showed that the genus is polyphyletic, and suggested that it would eventually be subdivided to reflect natural groups as defined by its anamorphs. However, results obtained in the first phylogenetic trees published for the genus based on ITS DNA sequence data, suggested that *Mycosphaerella* was monophyletic (Stewart et al. 1999, Crous et al. 1999, 2000, 2001, Goodwin et al. 2001).

As greater numbers of DNA sequences were included in phylogenetic analyses for *Mycosphaerella* species, the view of this genus as being monophyletic has gradually collapsed. Thus it has now been aptly demonstrated that *Mycosphaerella* is polyphyletic (Hunter et al. 2006, Crous et al. 2007a), and the complex has in recent years been separated into *Davidiella* species with *Cladosporium* anamorphs (*Davidiellaceae*) (Braun et al. 2003, Crous et al. 2007b, Schubert et al. 2007, Zalar et al. 2007, Dugan et al. 2008), *Schizothyrium* species with *Zygothia* anamorphs (*Schizothyriaceae*) (Batzer et al. 2008), *Teratosphaeria* species with more than 12 anamorphs (*Teratosphaeriaceae*) (Crous et al. 2007a) and *Mycosphaerella* species with more than 20 anamorph genera (*Mycosphaerellaceae*) (Crous & Braun 2003). All of these groups reside in the *Capnodiales* in the *Dothideomycetes* (Schoch et al. 2006). Although *Davidiella* (*Cladosporium*) and *Schizothyrium* (*Zygothia*) have a clear one to one relationship with anamorph genera, this is far from true for *Mycosphaerella* (*Mycosphaerellaceae*) and *Teratosphaeria* (*Teratosphaeriaceae*), where the teleomorph morphology is relatively conserved throughout the two respective families. To complicate the situation further, similar anamorph morphologies have evolved in different clades, and in some cases even outside the family (Crous et al. 2007a).

Redefining generic concepts with the incorporation of molecular phylogenetic data has, in many cases, led to the recognition of several natural groups in larger assemblages formerly defined solely based on alpha taxonomy. A further complication arises from dual nomenclature, where generic names linked to anamorph genera have to be linked to teleomorph genera. Two options are thus available for mycologists. One is to use anamorph generic names as nouns, and to accept that they can be poly- and paraphyletic (Halleen et al. 2004, Lee et al. 2004, Réblová et al. 2004, Verkley et al. 2004b, Crous et al. 2006b, c, 2007a, b, Arzanlou et al. 2007, Wang et al. 2007, Phillips et al. 2008). The alternative is to provide new anamorph genus names for well-defined clades, and in the process identify the characters that can be used to distinguish them.

In order to halt the unnecessary proliferation of generic names, Crous et al. (2007a) proposed to use anamorph genera for the same phenotype, regardless of where it clustered within the *Capnodiales*. This approach has flaws as taxa in different clades inevitably end up with the same generic names suggesting that they are related, and such a situation has led to substantial disagreement among *Mycosphaerella* taxonomists

(see Cortinas et al. 2006, Andjic et al. 2007a, Crous et al. 2007a, 2008a, 2009a). A solution to this dilemma lies in the introduction of generic names for discrete monophyletic lineages, but concurrently not to perpetuate the problems that arise from maintaining dual nomenclature. Here a single generic name, based on priority but regardless of whether it is an 'anamorph' or 'teleomorph' generic name, is used for all unambiguous monophyletic phylogenetic lineages, as also done recently in other groups of fungi (Rossman & Samuels 2005, Crous et al. 2006d, 2008a, b, Damm et al. 2008, Phillips et al. 2008).

In the present study this approach is applied to the *Mycosphaerellaceae* and *Teratosphaeriaceae*. The aim is to provide a more natural classification for the genera in these families.

## MATERIALS AND METHODS

### Isolates

Leaves with leaf spot symptoms typical of infection by '*Mycosphaerella*' were collected from various parts of the world. Excised lesions were soaked in water for approximately 2 h, after which they were attached to the bottom of Petri dish lids, with the top half of the dish containing 2 % malt extract agar (MEA; Oxoid, Hampshire, England) (Crous et al. 1991). Ascospore germination patterns were examined after 24 h, and single ascospore cultures established as described by Crous (1998). For those symptoms where no teleomorph was observed, cultures were established from single conidia.

### DNA phylogeny

Genomic DNA was extracted from mycelium taken from fungal colonies on MEA using the UltraClean™ Microbial DNA Isolation Kit (Mo Bio Laboratories, Inc., Solana Beach, CA, USA). A 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 first 900 bp at the 5' end of the 28S rRNA gene (LSU) was amplified and sequenced as described by Cheewangkoon et al. (2008).

The generated LSU sequences were compared with other fungal DNA sequences from NCBI's GenBank sequence database using a megablast search of the nr database; sequences with high similarity were added to the alignment. The alignment was subjected to neighbour-joining phylogenetic analyses as described by Cheewangkoon et al. (2008) and to a RAXML v7.0.4 analysis (Stamatakis et al. 2005a, b) using a maximum likelihood (ML) search with 1 000 bootstrap replicates (Stamatakis et al. 2008) as implemented at the CIPRES portal v1.15 (<http://www.phylo.org/portal/Home.do>). Search parameters assigned by the search engine included a GAMMA model of rate heterogeneity, ML estimation of the alpha-parameter and a GTR substitution matrix. Novel sequences were lodged in GenBank (Table 1) and the alignments and phylogenetic trees in TreeBASE (<http://www.treebase.org>).

### Taxonomy

To confirm the morphology of the included strains, fungal structures were mounted in lactic acid for microscopic examination. Colonies were sub-cultured onto 2 % potato-dextrose agar (PDA), synthetic nutrient-poor agar (SNA), MEA, and oatmeal agar (OA) (Crous et al. 2009b), and incubated under continuous near-ultraviolet light at 25 °C to promote sporulation. Colony colours were rated according to the colour charts of Rayner (1970). All cultures obtained in this study are maintained in the culture collection of the CBS (Table 1). Nomenclatural novelties and descriptions were deposited in MycoBank ([www.MycoBank.org](http://www.MycoBank.org); Crous et al. 2004a).



## RESULTS

### Phylogenetic analysis

The manually adjusted LSU alignment contained 316 taxa (including the outgroup sequence) and 773 characters were included in the phylogenetic analysis. As the focus of this paper was the higher-order phylogeny of these fungi, the ITS sequences obtained were not used in the phylogenetic analyses. They were, however, used in a follow-up study on species (Crous et al. 2009c) and lodged in GenBank as part of that study, if not present there already. The three distance analyses yielded trees with identical overall topologies and supported the same lineages as the RAXML phylogeny but with some rearrangements of lineages at the deeper nodes (data not shown). Examples of these rearrangements include the swapping of Clade 18 (*Dissoconium*) and Clade 19 (*Schizothyrium*) from the *Teratosphaeriaceae* to the *Mycosphaerellaceae* compared to the RAXML phylogeny, highlighting the insecure phylogenetic position of these two genera. No significant increase or decrease in bootstrap support values was observed between the distance and RAXML analyses and the low bootstrap support values observed for some clades (see below) could be due to the choice of gene and/or the sampling for the analyses. The obtained RAXML phylogeny with a tree length of 2 357 547 is shown in Fig. 1. The final ML optimisation likelihood value obtained was -9197.49319 and the alpha value was estimated as 0.236078.

### Taxonomy

Numerous anamorph genera have been associated with '*Mycosphaerella*', although the genus has largely been used as a convenient mycological concept, rather than a phylogenetic entity. As increasing numbers of asexual 'genera' are collected and subjected to DNA sequence analysis, many of these reside in the *Capnodiales* (Schoch et al. 2006, Crous et al. 2007a). The present study addresses the question of logical groupings for some of these genera. Many remain unresolved, chiefly due to low numbers of taxa presently available in culture that can thus be used for DNA sequence analyses. As greater numbers of taxa are collected, the generic boundaries of more clades will be resolved. For the present, however, we treat only those genera that could be resolved based on available cultures. In each case the generic name to use for a specific clade is indicated if that clade is resolved. Many phylogenetically distinct taxa still remain in '*Mycosphaerella*', '*Teratosphaeria*' or in one of the associated asexual genera, and these can only be disposed to their correct genera as their taxonomy and DNA phylogeny are clarified. The clade numbers below refer to the numbers indicated on Fig. 1. Several unresolved clades are left untreated and are thus not discussed.

#### Clade 1: *Polythrincium* (*Cymadothea* teleomorph; *Mycosphaerellaceae*)

*Polythrincium trifolii* (teleomorph *Cymadothea trifolii*), an important foliar pathogen of clover, was recently treated by Simon et al. (2009). The anamorph genus *Polythrincium* (1817) predates the *Mycosphaerella*-like teleomorph genus, *Cymadothea* (1935), and morphologically the most informative morph. The older generic name *Polythrincium* is thus preferred for this clade.

#### Clade 2: *Zasmidium*-like (*Mycosphaerellaceae*)

Although the following taxa resemble others in the *Zasmidium* clade, they cluster as sister to *Zasmidium* s.s. (Clade 8), which is poorly resolved. Taxa in this clade all form hyaline propagules of a synanamorph in their aerial mycelium, although this feature is not restricted to taxa in this clade. Presently it is still unclear

which features separate this clade from *Zasmidium* s.s., and thus the latter name is applied to both clades.

#### Clade 3: *Ramularia* (*Mycosphaerella* s.s. teleomorphs; *Mycosphaerellaceae*)

The genus *Mycosphaerella* is typified by *M. punctiformis*, which has a *Ramularia* anamorph, *R. endophylla* (Verkley et al. 2004a). *Ramularia* represents a well-known genus of anamorphs that has been monographed (Braun 1998), representing hyaline hyphomycetes with solitary to fasciculate conidiophores, and aseptate to transversely septate hyaline conidia with thickened, darkened, refractive scars. Given the fact that *Mycosphaerella* has been applied in the broad sense to many diverse genera in the family, and has become a 'name of convenience' rather than one indicative of genealogical relationship, we consider that it would be best to use the older name for this clade, namely *Ramularia* (1833), rather than *Mycosphaerella* (1884). The recently reported unique scar structure separating *Cercospora* from *Ramularia* should also be noted here. Based on these observations on *Cercospora centaureicola* (CBS 120253) by Kirschner (2009), as well as its phylogenetic placement, *C. centaureicola* is accepted as a likely synonym of *R. nagornyii*, as discussed by Kirschner (2009).

#### Clade 4: *Lecanosticta* (*Mycosphaerellaceae*)

This lineage includes only *Lecanosticta acicola* (teleomorph: *M. dearnessii*) and additional taxa will need to be added before it can be adequately resolved. *Lecanosticta acicola* (= *L. pini*) is the type species of the genus *Lecanosticta* and represents the generic name that should be used for this clade.

#### Clade 5: *Phaeophleospora* (*Mycosphaerellaceae*)

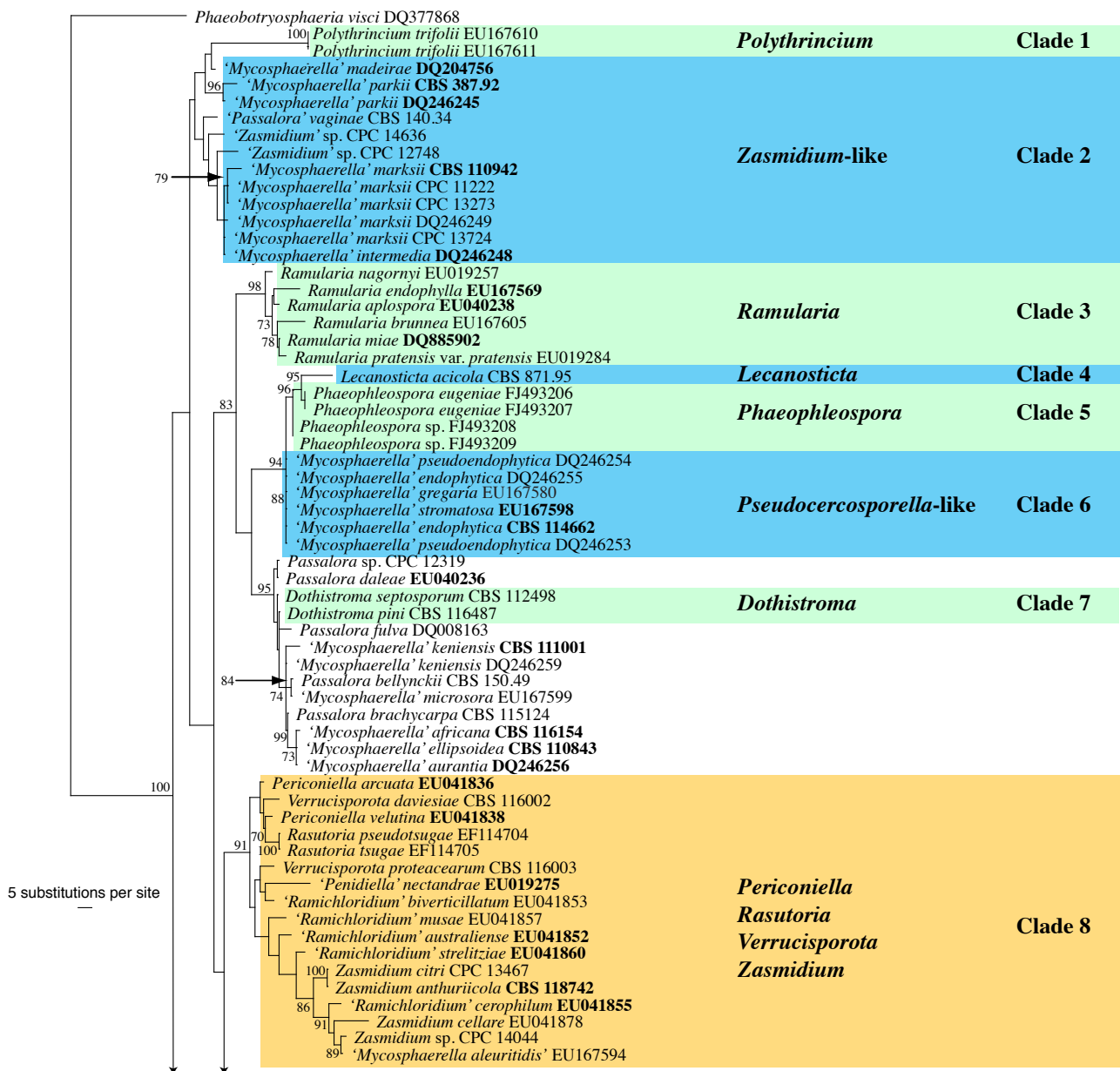
*Phaeophleospora* is characterised by pycnidia that give rise to conidia via brown, percurrently proliferating conidiogenous cells (Crous et al. 1997), and by brown, scolecosporous conidia with transverse septa. This morphology has evolved several times in the *Capnodiales*. Andjic et al. (2007a) separated *Phaeophleospora* from the phylogenetically distant *Kirramyces* based on the pigment gradient observed in conidia of *P. eugeniae*, the type species of *Phaeophleospora*. Crous et al. (2007a) showed that *Phaeophleospora* belonged to the *Mycosphaerellaceae*, whilst *Kirramyces* belonged to the *Teratosphaeriaceae*. Very few species of *Phaeophleospora* are presently known from culture, and most need to be recollected, and their morphological features and classification re-evaluated.

#### Clade 6: *Pseudocercospora*-like (*Mycosphaerellaceae*)

Taxa residing in this clade have anamorphs and teleomorphs that resemble *Pseudocercospora* and *Mycosphaerella*, respectively. However, the type species of *Pseudocercospora*, *P. ipomoeae*, needs to be recollected before the generic name applicable to this clade can be resolved.

#### Clade 7: *Dothistroma* (*Mycosphaerellaceae*)

*Dothistroma* (1941) is based on *D. pini*, and is linked to a *Mycosphaerella*-like (or *Scirrhia*, *Eruptio*) teleomorph. The two species of *Dothistroma* that have been subjected to DNA sequence analysis cluster together in this clade, which is closely related to *Passalora*-like fungi, for which the status remains unclear. The appropriate name for this clade is still unclear, as we suspect that adding more taxa would lead to a better resolution of morphological types within the larger clade in which *Dothistroma* resides.



**Fig. 1 (five parts)** Maximum likelihood tree from RAxML showing the phylogenetic relationships based on the LSU sequence alignment. The scale bar shows 5 substitutions per site, and bootstrap support values (> 69%) from 1000 replicates are shown at the nodes. Ex-type sequences are printed in bold face. The tree was rooted to *Phaeobotryosphaeria visci* (GenBank accession DQ377868).

#### **Clade 8: Zasmidium-complex (Mycosphaerella-like and Rasutoria teleomorphs; Mycosphaerellaceae)**

*Zasmidium* is characterised by coarsely verrucose, olivaceous-green hyphae, that give rise to conidiophores with integrated conidiogenous cells that proliferate sympodially near the apex, with conspicuously pigmented, darkened, somewhat refractive planate scars. Conidia are formed singly or in short chains, and are cylindrical to fusiform, verrucose, obovate to obconical, subhyaline to pigmented, 0–pluri-septate, with conspicuous, slightly pigmented, thickened, refractive hila. Morphologically, *Zasmidium* resembles *Stenella*, but the type species of the latter genus clusters in the *Teratosphaeriaceae* (Arzanlou et al. 2008), whereas *Zasmidium* clusters in the *Mycosphaerellaceae*. Conidia of *Stenella* (*S. araguata*) have pileate scars (David 1993), while those of *Zasmidium* (*Z. cellare*) and former *Stenella* species belonging in the *Mycosphaerellaceae* are planate, i.e. *Cercospora*-like.

The *Zasmidium* clade remains poorly resolved (Fig. 1, part 1), and it also includes the type species of *Periconiella* (*P. velu-*

*tina*) and *Verrucisporota* (*V. proteacearum*). Furthermore, the *Zasmidium*-like morphology has also evolved elsewhere in the *Mycosphaerellaceae* (Fig. 1, clade 2). Additional collections need to be added to clarify the relationships among taxa with the morphology type (verrucose superficial hyphae with pigmented structures, and thickened, darkened, refractive, convex scars). The identity of *Mycosphaerella aleuritidis* (CBS 282.62) could not be confirmed in culture, and hence its position in this clade, and purported *Pseudocercospora aleuritidis* anamorph, remains uncertain. *Zasmidium* is presently paraphyletic in the *Mycosphaerellaceae*. The genus *Zasmidium* s.s. should be applied to this clade, though more taxa need to be added to resolve the status of other morphotypes (genera) clustering in this clade.

***Zasmidium anthuriicola*** (U. Braun & C.F. Hill) Crous & U. Braun, *comb. nov.* — MycoBank MB509715

*Basionym.* *Stenella anthuriicola* U. Braun & C.F. Hill, Fung. Diversity 22: 33. 2006.

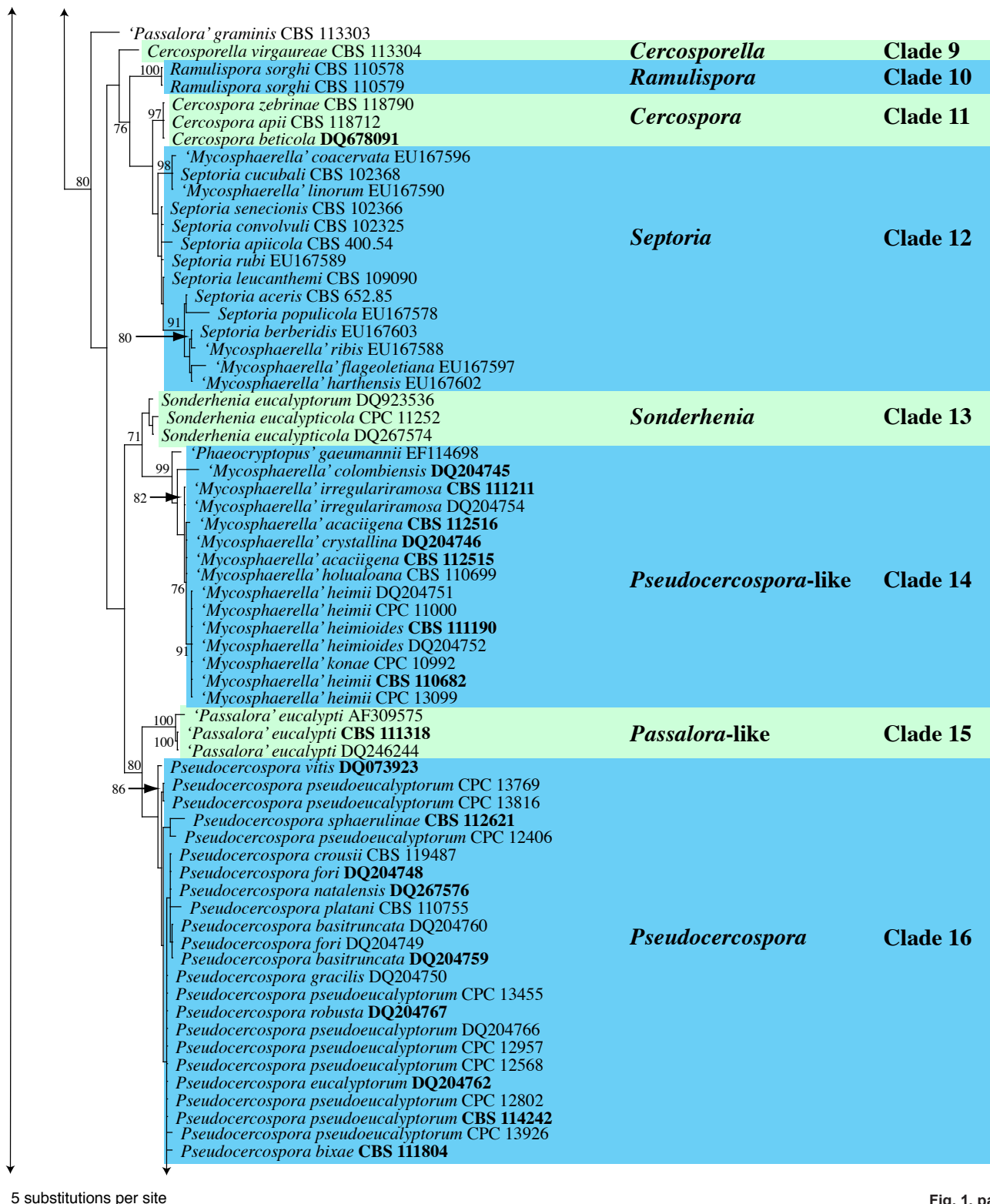


Fig. 1, part 2

***Zasmidium citri*** (Whiteside) Crous, *comb. nov.* — MycoBank MB509716

*Basionym.* *Mycosphaerella citri* Whiteside, *Phytopathology* 62: 263. 1972.

*Anamorph.* *Cercospora citri-grisea* F.E. Fisher, *Phytopathology* 51: 300. 1961.

≡ *Stenella citri-grisea* (F.E. Fisher) Sivan., in Sivanesan, *Bitunicate ascomycetes and their anamorphs*: 226. 1984.

#### Clade 9: *Cercospora* (*Mycosphaerellaceae*)

*Cercospora* (1880), which is based on *C. virgaureae* (= *C. cana*), has hyaline conidiophores and conidia with planate, slightly

thickened and somewhat refractive, inconspicuous, smooth conidial scars (Braun 1995, Kirschner 2009). Although hardly any species are known from culture, the genus appears to be phylogenetically distinct.

#### Clade 10: *Ramulispora* (*Mycosphaerellaceae*)

*Ramulispora* is typified by *R. sorghi*, a pathogen that causes prominent leaf spots on sorghum called sooty stripe, due to the abundant production of microsclerotia on the leaf surface (Braun 1995, Crous et al. 2003a). It is further characterised by forming sporodochia with hyaline, transversely euseptate, scolecosporous conidia.



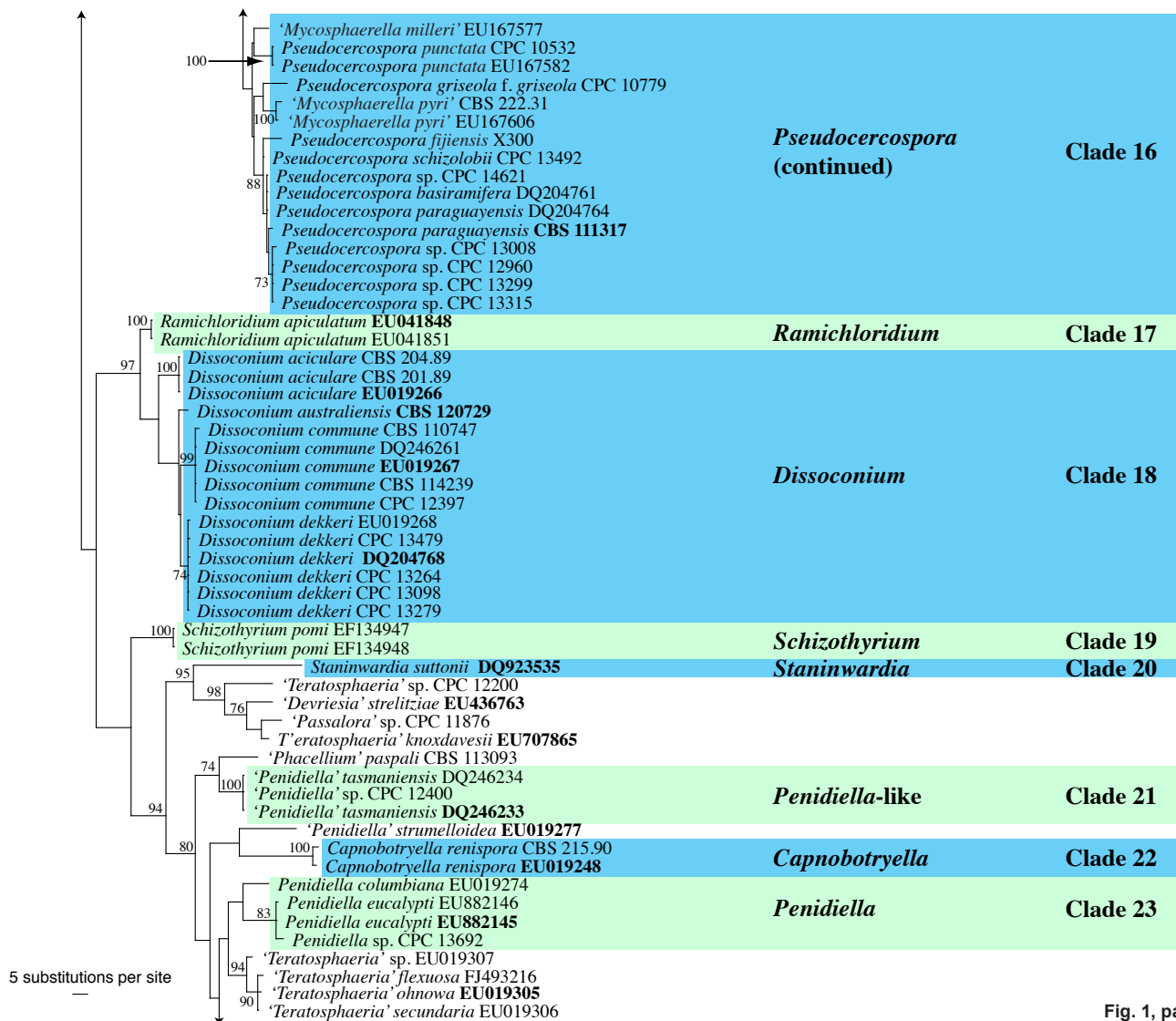


Fig. 1, part 3

### Clade 11: *Cercospora* (*Mycosphaerellaceae*)

The genus *Cercospora*, which is based on *Cercospora penicillata* (= *C. depazeoides*), contains more than 600 species that are saprobic or plant pathogenic (Crous & Braun 2003, Groenewald et al. 2005, 2006, Crous et al 2006a). Conidiophores are solitary to fasciculate, arising from internal hyphae or stromata, erect, continuous to pluriseptate, subhyaline to pigmented, smooth to finely roughened, with integrated, terminal or intercalary conidiogenous cells, proliferating sympodially, and conspicuously thickened, darkened, planate scars. Conidia are predominantly solitary, scolecosporous, obclavate to cylindrical-filiform, acicular, hyaline or subhyaline, mostly pluriseptate, smooth, with thickened, darkened, planate hila. Species of *Cercospora* form a well-defined clade in the *Mycosphaerellaceae*. Species with brown, pigmented conidia are accommodated in *Passalora*, though the latter concept has evolved in several clades in the *Capnodiales*, and remains to be resolved. The name to use for this clade is *Cercospora*, which represents a monophyletic genus (J.Z. Groenewald et al. in prep.).

### Clade 12: *Septoria* (*Mycosphaerellaceae*)

*Septoria* (1884) includes more than 2 000 plant pathogenic coelomycetes that are associated with leaf spot diseases. The genus is characterised by pycnidial conidiomata, and hyaline conidiogenous cells with sympodial and/or percurrent proliferation, giving rise to filiform, hyaline, smooth-walled, multiseptate conidia (Verkley & Priest 2000). The majority of known species

cluster within the *Mycosphaerellaceae*, although this morphology type has also evolved outside the family, and the genus is poly- and paraphyletic. The type species, *S. cytisi*, needs to be recollected to determine which *Septoria*-like clade is applicable to *Septoria* s.s. This clade, including Clade 11, was supported with a bootstrap support value of 68 % (not shown).

### Clade 13. *Sonderhenia* (*Mycosphaerellaceae*)

Swart & Walker (1988) introduced the genus *Sonderhenia* to accommodate pycnidial anamorphs of *Mycosphaerella* that formed brown, transversely distoseptate conidia on brown, percurrently proliferating conidiogenous cells. Two species are known from the genus, namely *S. eucalypticola* and *S. eucalyptorum*, which appear to form a monophyletic clade (68 % bootstrap support value, not shown).

### Clade 14. *Pseudocercospora*-like (*Mycosphaerellaceae*)

The fact that *Pseudocercospora* species cluster in two well defined clades is not surprising. What was unexpected, is that *Pseudocercospora* s.s. (Clade 16), clusters apart from a complex commonly referred to as the *Ps. heimii* clade, including species such as *Ps. crystallina*, *Ps. heimii*, *Ps. heimioides*, *Ps. konae*, *Ps. irregulariramosa*, *Ps. thailandica*, etc. These species all have smooth, pale brown, subcylindrical to narrowly obclavate conidia, conidiogenous cells that proliferate sympodially and occur singly on hyphae in culture, and colonies that form red crystals in agar when cultivated (Crous & Wingfield 1996, Crous



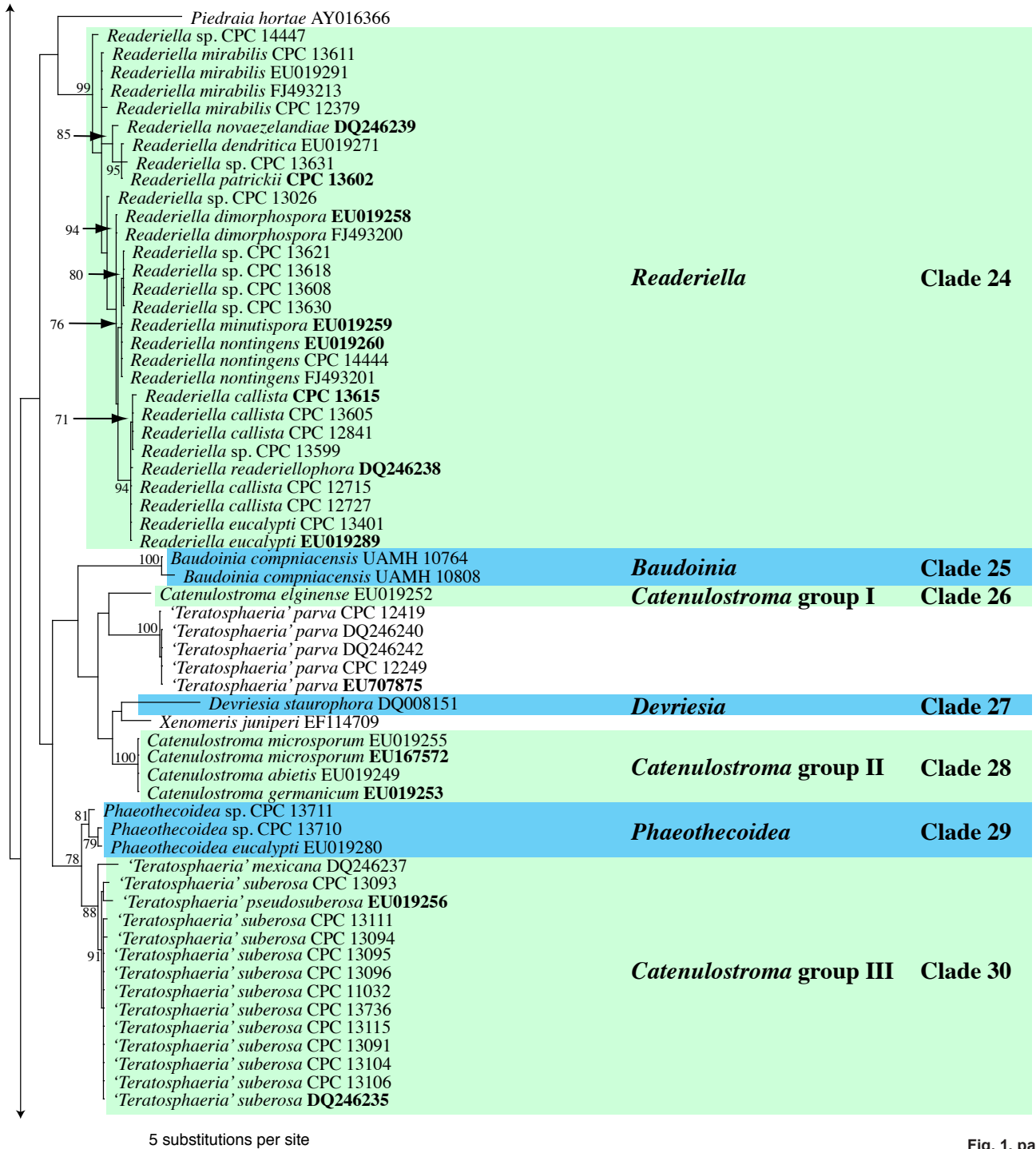


Fig. 1, part 4

1998). The taxonomic status of this clade remains unresolved, and will be dealt with in a revision of the *Pseudocercospora* complex (Hunter et al. in prep.).

**Clade 15. *Passalora*-like (*Mycosphaerellaceae*)**

Hyphomycetes with pigmented conidia, and darkened, thickened, refractive scars, formed on fasciculate conidiophores, have traditionally been placed in *Passalora* (Braun 1995). Crous & Braun (2003) extended this concept to include taxa with superficial mycelium (*Mycovellosiella*, based on *M. cajani*) and conidia in chains (*Phaeoramularia*, based on *Ph. gomphrenicola*). This definition, however, appears to be inordinately wide, as several clades have taxa exhibiting the *Passalora*-like morphology. The type species of *Passalora*, *P. bacilligera*, must be recollected before the taxonomy of this complex can be fully resolved.

**Clade 16. *Pseudocercospora* (*Mycosphaerellaceae*)**

The genus *Pseudocercospora* represents species with pigmented conidiophores arranged singly on superficial hyphae, synnemata (in the type species, *P. vitis*, and in *Phaeoisariopsis*) to fascicles arising from a submerged to erumpent stroma, almost becoming sporodochial to acervular in some cases (Crous et al. 2006b). Conidiophores give rise to terminal and intercalary conidiogenous cells that form conidia via sympodial and/or percurrent proliferations. Proliferations can be rough and irregular (*Cercostigmina*), or smooth and inconspicuous. Conidia are mostly scolecosporous, smooth or finely roughened, pigmented, thin- to thick-walled (*Scolecostigmina*), transverse or with oblique eu- to distosepta (*Stigmina*). Conidiogenous loci are inconspicuous, or slightly thickened around the rim (*Paracercospora* and *Passalora*-like). *Pseudocercospora* has recently been conserved over *Stigmina* (Braun & Crous 2006),

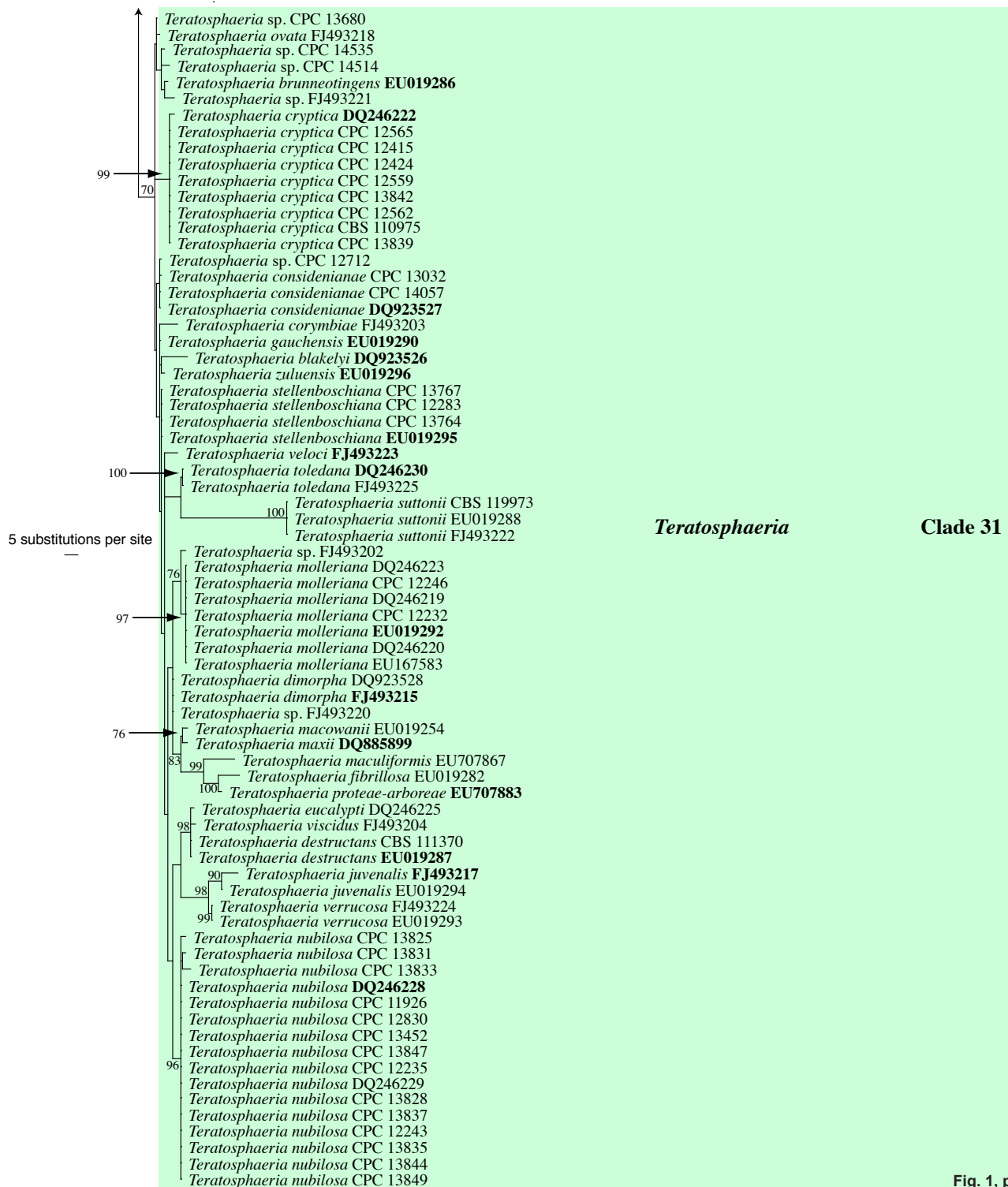


Fig. 1, part 5

and is the recommended generic name for this clade. Cultures of some taxa in this clade could not be confirmed morphologically, and probably represent misidentifications, namely *Mycosphaerella milleri* (CBS 541.63), which is supposed to have *Passalora magnoliae* as an anamorph, and *Mycosphaerella pyri* (CBS 222.31), which is supposedly linked to *Septoria pyricola*. This clade was supported with a bootstrap support value of 62 % (not shown).

***Pseudocercospora fori*** (G.C. Hunter, Crous & M.J. Wingf.)  
G.C. Hunter, Crous & M.J. Wingf., *comb. nov.* — MycoBank MB509717

*Basionym.* *Mycosphaerella fori* G.C. Hunter, Crous & M.J. Wingf., Mycol. Res. 108: 677. 2004.

Notes — This species commonly forms its *Pseudocercospora* state in culture and on host material. Although originally named in '*Mycosphaerella*' (Hunter et al. 2004), this fungus is better accommodated in *Pseudocercospora*. Both sexual and asexual states are fully described in the original publication by Hunter et al. (2004).

***Pseudocercospora schizolobii*** (M.J. Wingf. & Crous) M.J. Wingf. & Crous, *comb. nov.* — MycoBank MB509718

*Basionym.* *Passalora schizolobii* M.J. Wingf. & Crous, Fungal Planet 2. 2006.

Culture characteristics — Colonies on MEA erumpent, irregular, sectored, with sparse aerial mycelium, margin catenulate,

smooth, surface crenate, olivaceous-grey; reverse iron-grey; reaching 20 mm diam after 1 mo; on OA erumpent, spreading with moderate aerial mycelium, and smooth, catenulate margins, pale olivaceous-grey to olivaceous-grey; reaching 25 mm after 1 mo.

*Specimens examined.* ECUADOR, Buenos Aires, Pacheco, on leaves of *Schizolobium parahybum*, 17 Jan. 2006, M.J. Wingfield, culture ex-type CPC 12962 = CBS 120029. – THAILAND, on leaves of *Eucalyptus camaldulensis*, Oct. 2006, W. Himaman, CPC 13492 = CBS 124990.

**Notes** — *Passalora schizolobii* was described as a leaf spot pathogen of *Schizolobium parahybum* from Ecuador (Wingfield et al. 2006). The present collection represents what appears to be the same species (on ITS sequence data, and morphology), but occurring on *Eucalyptus*. Conidia are 1–7-septate, and (30–)40–55(–80) × (2.5–)3(–3.5) µm, with inconspicuous hila, 1–1.5 µm wide. *Passalora schizolobii* was placed in *Passalora* due to the slightly darkened, thickened hila. Morphologically it represents an intermediate between *Passalora* and *Pseudocercospora*, which explains why it clusters among other species of *Pseudocercospora*, suggesting that taxa with scars and hila that are slightly darkened and thickened, but not refractive, should rather be placed in *Pseudocercospora* than in *Passalora* (Crous & Braun 2003). A multi-gene approach and inoculation studies are required to clarify if the *Eucalyptus* isolates are really the same as those causing a serious disease on *Schizolobium*.

#### **Clade 17: *Ramichloridium***

In the past *Ramichloridium* included a heterogeneous group of fungi with diverse life styles, viz. saprobes, human and plant pathogens. *Ramichloridium* is characterised by taxa with erect, dark, more or less differentiated, branched or unbranched conidiophores and predominantly aseptate conidia produced on a sympodially proliferating rachis (de Hoog 1977). No teleomorph has been linked to the genus. *Ramichloridium* was accepted as paraphyletic by Arzanlou et al. (2008), with taxa clustering in the *Mycosphaerellaceae* and *Teratosphaeriaceae*. The type species of the genus, *R. apiculatum*, clusters with *Dissoconium*, but its higher order phylogenetic relationship has not been resolved.

#### **Clade 18. *Dissoconium* (*Mycosphaerella*-like teleomorphs)**

*Dissoconium* is unique in the *Capnodiales* in that it is characterised by producing pairs of forcibly discharged primary and secondary conidia on sympodially proliferating conidiogenous cells, which gives rise to a conidium-bearing rachis (Crous et al. 2007c, 2008a, Arzanlou et al. 2008). The genus is peculiar in that the two conidial types frequently anastomose after being forcibly discharged, and some species form microsclerotial bodies in culture (Crous et al. 2008a). Where known, teleomorphs have been accommodated in '*Mycosphaerella*' (Crous et al. 2004b). Morphologically there is little to choose between these teleomorphs and *Mycosphaerella* s.s., except that they tend to have a non-persistent mucilaginous sheath surrounding their ascospores, and periphyses lining the ostiolar cavity. These features, however, also occur in several species of *Mycosphaerella* s.s. It has thus not been possible to identify morphological features in the teleomorph that could be used to separate these clades. The recommended genus name for this clade is *Dissoconium*, although additional taxa need to be added to clarify its higher order phylogeny. This clade was supported with a bootstrap support value of 60 % (not shown).

#### **Clade 19: *Schizothyrium* (*Zygothiala* anamorphs)**

In former classification schemes, the genus *Schizothyrium* was placed in the *Schizothyriaceae*, *Dothideales* (von Arx & Müller 1975), *Microthyriales* (Kirk et al. 2001), and *Dothideomycetes*

(Eriksson 2006). *Schizothyrium* is characterised by strongly flattened, crustose, rounded or elongated ascomata, opening by irregular splits, with bitunicate asci, and some interascal tissue composed of remnants of stomatal cells, and transversely 1-septate, hyaline to pale brown ascospores. Recent phylogenetic studies (Schoch et al. 2006, Batzer et al. 2008) support *Schizothyrium* as residing in the *Dothideomycetes*, subclass *Dothideomycetidae*, order *Capnodiales*. Results obtained here support the family *Schizothyriaceae* as sister to the *Mycosphaerellaceae*. It should be noted, however, that the type species, *S. acerinum*, is presently not known from culture, and needs to be recollected.

#### **Clade 20: *Staninwardia* (*Teratosphaeriaceae*)**

*Staninwardia* is known from two species occurring on leaf spots of *Eucalyptus* (Summerell et al. 2006). It is characterised by acervuli with brown, catenulate conidia covered in a mucilaginous sheath. No teleomorph state has been reported for this genus.

#### **Clades 21, 23: *Penidiella* complex (*Teratosphaeriaceae*)**

The genus *Penidiella*, which is based on *P. columbiana*, is polyphyletic. Species of *Penidiella* have synnematosus to solitary conidiophores, consisting of a single terminal conidiogenous cell giving rise to several ramoconidia that form secondary ramoconidia, or a branched apparatus composed of several terminal and sometimes lateral conidiogenous cells giving rise to sequences of 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. Species that have thus far been found to cluster apart from the type, *P. columbiana*, appear to have a different conidiogenous apparatus. Inordinately few taxa are known from this complex, and it is premature to subdivide *Penidiella*. We thus retain it as paraphyletic taxon.

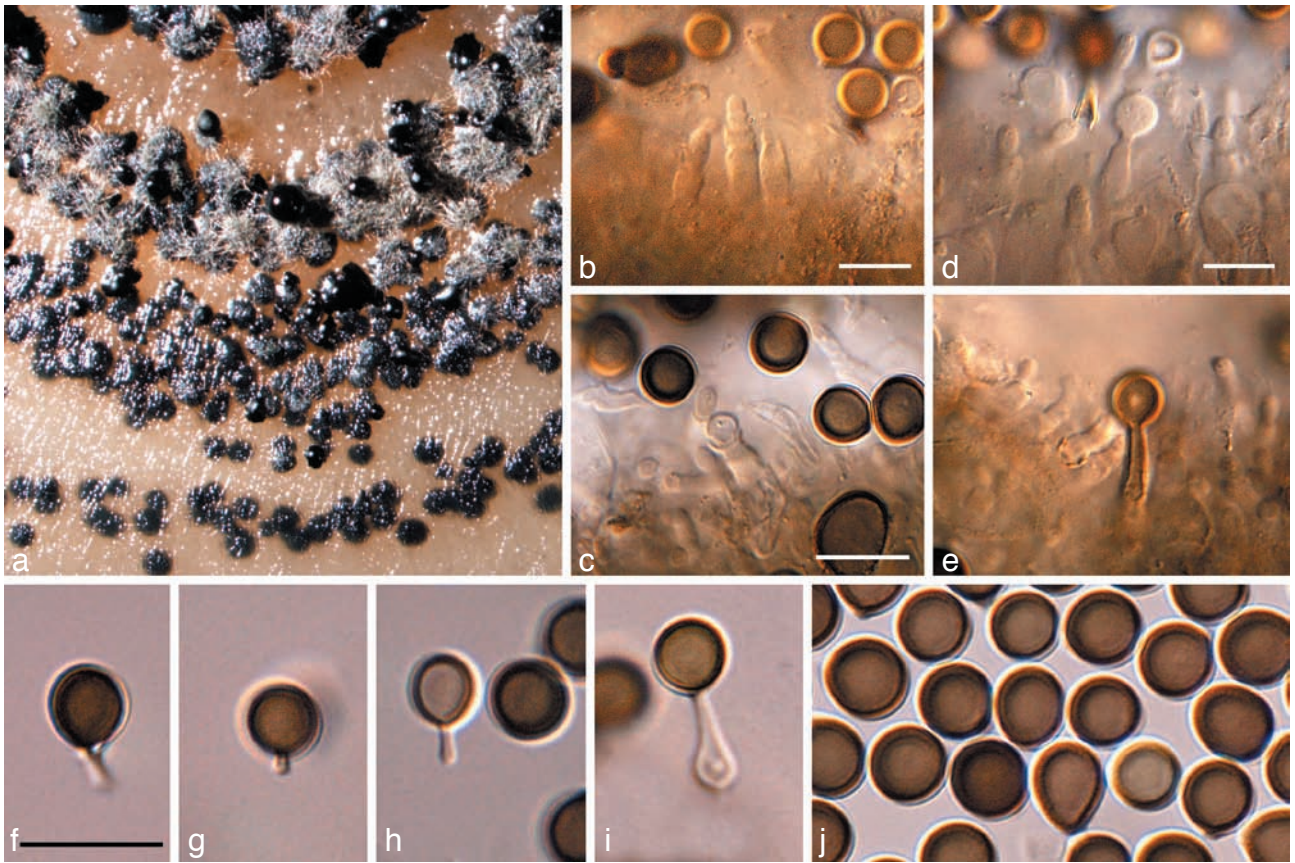
#### **Clade 22: *Capnobotryella* (*Teratosphaeriaceae*)**

*Capnobotryella* (based on *C. renispora*) is characterised by forming brown, septate, thick-walled hyphae, with ellipsoidal, 0–1-septate conidia forming directly on the hyphae, via minute phialides, and the production of endoconidia (Sugiyama & Amano 1987). No teleomorph state has been reported for this genus.

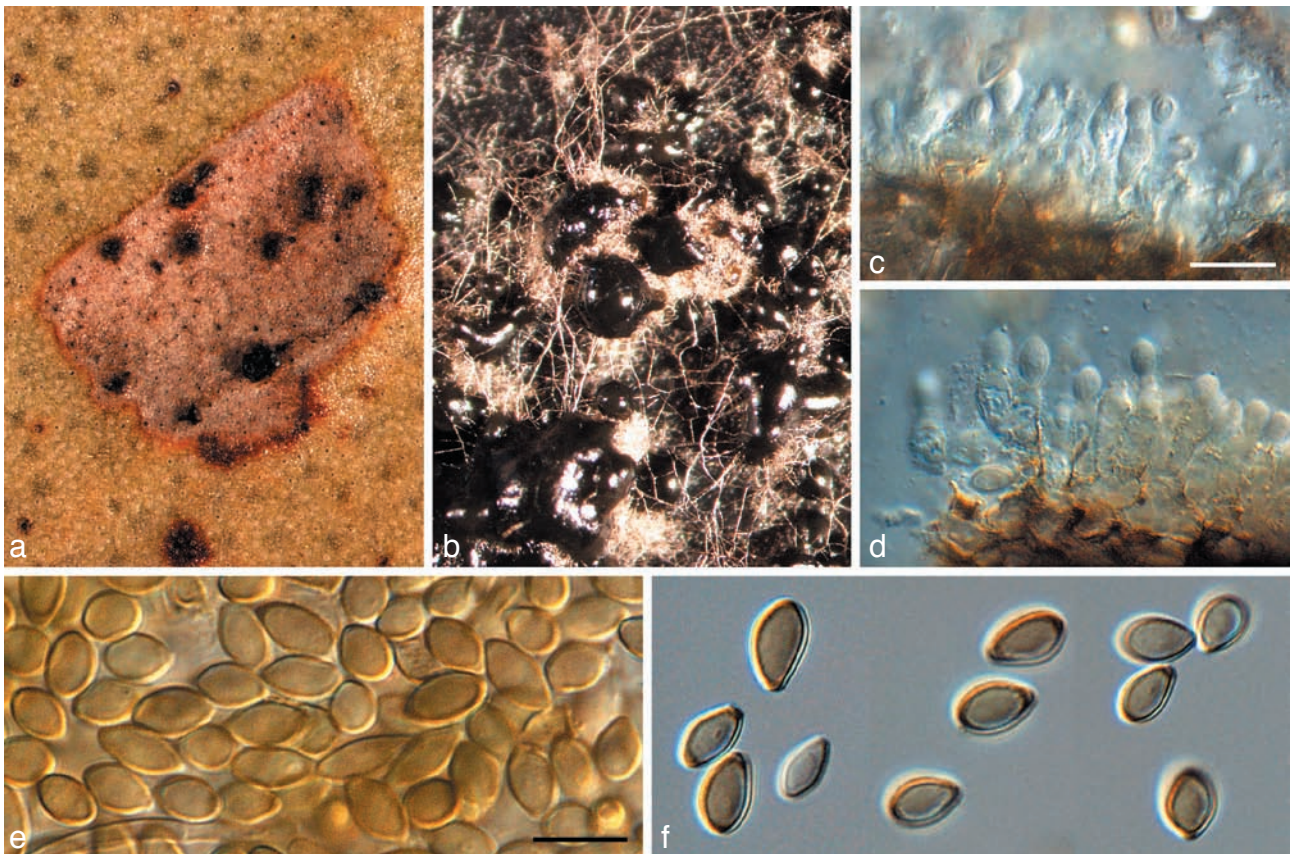
#### **Clade 24: *Readeriella* (incl. *Nothostrasseria*, with *Teratosphaeria*-like teleomorphs, and *Cibiessia* synanamorphs) (*Teratosphaeriaceae*)**

Crous et al. (2007a) used a wider concept for *Readeriella*, and recognised it as being polyphyletic within the *Teratosphaeriaceae*. Furthermore, based on its conidiogenesis that is very similar to that of *Kirramyces*, with conidiogenous cells ranging from mono- to polyphialides with periclinial thickening, to phialides with percurrent proliferation, the two genera were seen as synonymous. However, the present analysis shows that these two clades cluster apart within the *Teratosphaeriaceae* (Fig. 1, part 4). Although they are morphologically similar, *Readeriella* species have conidia that tend to have tapering subtruncate bases, and frequently form *Cibiessia* synanamorphs. In contrast, *Kirramyces* and *Colletogloeopsis* anamorphs have truncate conidial bases, and are never found associated with *Cibiessia* synanamorphs. *Nothostrasseria* (1983) has conidiogenesis similar to that in *Readeriella*, and forms conidia with basal appendages, which can also occur in *Readeriella eucalypti* (Fig. 2, Crous et al. 2007a). The generic name for this clade is the older name, *Readeriella* (1908).





**Fig. 2** *Readeriella eucalypti* (CPC 14950). a. Colony on OA; b–e. conidiogenous cells giving rise to conidia; f–i. conidia with basal appendages; j. conidia. — Scale bars = 10 µm.



**Fig. 3** *Readeriella callista* (CPC 13615). a. Leaf spot with black pycnidia; b. colony on OA; c, d. conidiogenous cells giving rise to conidia; e, f. conidia. — Scale bars = 10 µm.



**Readeriella** Syd. & P. Syd., Ann. Mycol. 6: 484. 1908.Teleomorph. *Teratosphaeria*-like= *Nothotrasseria* Nag Raj, Canad. J. Bot. 61: 23. 1983.= *Cibiessia* Crous, Fung. Diversity 26: 151. 2007.**Readeriella callista** (Syd.) Crous & Summerell, *comb. nov.* — MycoBank MB509719; Fig. 3Basionym. *Coniothyrium callistum* Syd., Ann. Mycol. 35: 358. 1937.= *Microsphaeropsis callista* (Syd.) B. Sutton, Mycol. Pap. 123: 35. 1971.

**Leaf spots** amphigenous, irregular, 2–5 mm diam, pale brown, with a thin, raised, dark brown border; associated with wasp damage in some collections. **Conidiomata** amphigenous, pycnidial, brown, up to 350 µm diam; wall consisting of 3–4 layers of brown *textura angularis*. Description on OA. **Conidiophores** subcylindrical, pale brown, finely verruculose, 0–2-septate, unbranched or branched above, frequently covered in a mucilaginous layer, 10–15 × 3–4 µm. **Conidiogenous cells** pale brown, finely verruculose, aseptate, dolliform to subcylindrical, proliferating percurrently near apex, 5–7 × 3–4 µm. **Conidia** solitary, brown, aseptate, smooth to finely verruculose, ellipsoid to fusoid, thick-walled, apex subobtuse, base subtruncate, apex and base with darker pigmentation, (7–)8–10(–11) × (3–)4–5(–5.5) µm; base 1–2 µm wide. **Microconidiophores** intermixed among macroconidiophores, cylindrical, straight to flexuous, 2 µm wide, variable in length. **Microconidia** ellipsoid, hyaline, smooth, 3–5 × 2 µm, apex obtuse, base subtruncate.

**Culture characteristics** — Colonies on MEA spreading, woolly, with moderate aerial mycelium, erumpent with uneven, catenulate margins; olivaceous-grey on surface, iron-grey in reverse; colonies reaching 50 mm diam after 1 mo; on OA woolly with moderate aerial mycelium, iron-grey with patches of olivaceous-grey, covering the plate after 1 mo; fertile.

**Specimens examined.** AUSTRALIA, New South Wales, Bulli, on leaves of *Eucalyptus haemastoma*, Aug. 1935, F. Fraser, IMI 21230 holotype; New South Wales, Woodford 33°43'30"S, 150°29'25"E, on leaves of *Eucalyptus sclerophylla*, Oct. 2006, coll. B.A. Summerell, CBS H-20246 epitype designated here, isol. P.W. Crous, cultures ex-type CPC 13615 = CBS 124986, CPC13616, 13617; New South Wales, Rylestone, 32°39'31"S, 150°12'30"E, on leaves of *Eucalyptus* sp., Jan. 2006, coll. B.A. Summerell, isol. P.W. Crous, CPC 12727–12729; New South Wales, Rylestone, 32°39'31"S, 150°12'30"E, on leaves of *Eucalyptus deanei*, Jan. 2006, coll. B.A. Summerell, isol. P.W. Crous, CPC 12715–12717; New South Wales, Capertee 33°08'13"S, 150°04'46"E, on leaves of *Eucalyptus cannonii*, Jan. 2006, coll. B.A. Summerell, isol. P.W. Crous, CPC 12841–12843; New South Wales, Faulconbridge 33°40'18"S, 150°32'54"E, on leaves of *Eucalyptus multicaulis*, Oct. 2006, coll. B.A. Summerell, CBS H-20247, isol. P.W. Crous, CPC 13605–13607.

**Notes** — On OA, conidia of *R. callista* are somewhat longer and narrower, (7–)8–10(–11) × (3–)4–5(–5.5) µm, than those observed on host material, 7–8.5 × 4–5.5 µm. The overall conidial shape, thicker appearance of the conidial wall, and pigmentation, are very characteristic for this species.

**Readeriella dendritica** (Crous & Summerell) Crous & Summerell, *comb. nov.* — MycoBank MB509720Basionym. *Mycosphaerella dendritica* Crous & Summerell, Fung. Diversity 26: 161. 2007.Teleomorph. '*Teratosphaeria*' *dendritica* (Crous & Summerell) Crous & U. Braun, Stud. Mycol. 58: 10. 2007.Anamorph. *Spilomyces dendriticus* Hansf., Proc. Linn. Soc. New South Wales 81: 32. 1956.= *Nothotrasseria dendritica* (Hansf.) Nag Raj, Canad. J. Bot. 61: 25. 1983.

**Specimens examined.** AUSTRALIA, New South Wales, Rylestone, 32°39'31"S, 150°12'30"E, on leaves of *Eucalyptus deanei*, Feb. 2006, coll. B.A. Sum-

merell, holotype CBS H-19772, isol. P.W. Crous, cultures ex-type CPC 12709 = CBS 120032, CPC 12710–12711; New South Wales, Laurel Hill, Bago State Forest, research trial, on leaves of *E. nitens*, 22 Dec. 2005, coll. A.J. Carnegie, isol. P.W. Crous, CPC 12820 = CBS 120733; Tasmania, on leaves of *E. globulus*, 31 Aug. 2006, coll. C. Mohammed, isol. P.W. Crous, CPC 13296 = CBS 120734, CPC 13297–13298.

**Notes** — The anamorph genus *Nothotrasseria* was introduced for a single species, *N. dendritica*, having conidia with characteristic basal appendages (Nag Raj 1993). The teleomorph was recently collected by Crous et al. (2007c), and subsequently shown to reside in the *Teratosphaeriaceae* (Crous et al. 2007a). Although the conidiogenesis is similar to that of *Readeriella*, the genus was tentatively retained as separate, as species of *Readeriella* generally lack persistent basal appendages. However, a recent collection of *Readeriella eucalypti* (CPC 14950, Fig. 2), was found to have basal appendages in vivo. Once cultured, conidia were found to frequently retain their basal appendages, similar to those observed in *Harknessia*, where species have appendages of different lengths (see Lee et al. 2004, Summerell et al. 2006). Because some species of *Readeriella* can have basal appendages, and as they cluster in a single well-supported clade (Fig. 1, part 4), there is no reason to retain *Nothotrasseria* as separate from *Readeriella*.

**Readeriella dimorphospora** (Crous & C. Mohammed) Crous, *comb. nov.* — MycoBank MB509721Basionym. *Cibiessia dimorphospora* Crous & C. Mohammed, Fung. Diversity 26: 151. 2007.**Readeriella minutispora** (Crous & Carnegie) Crous & Carnegie, *comb. nov.* — MycoBank MB509722Basionym. *Cibiessia minutispora* Crous & Carnegie, Fung. Diversity 26: 153. 2007.**Readeriella nontingens** (Crous & Summerell) Crous & Summerell, *comb. nov.* — MycoBank MB509723Basionym. *Cibiessia nontingens* Crous & Summerell, Fung. Diversity 26: 154. 2007.**Readeriella patrickii** Crous & Summerell, *sp. nov.* — MycoBank MB509724; Fig. 4

*Readeriellae mirabilis* similis, sed conidiis sine projecturis lateralis, sed conidiis persistente mucilagine vaginatis, (6–)7–8(–9) × (2.5–)3(–3.5) µm.

**Etymology.** Named after Patrick Summerell, who collected this fungus when he accompanied the Council of Heads of Australasian Herbaria on their annual day out in the field after their meeting in Tasmania.

**Leaf spots** amphigenous, subcircular to irregular, pale to medium brown, with a raised, dark brown border, up to 5 mm diam. Description on OA. **Conidiomata** pycnidial, brown, globose, up to 250 µm diam; wall consisting of 2–3 layers of brown *textura angularis*. **Conidiophores** reduced to conidiogenous cells, hyaline to pale brown, smooth to finely verruculose, dolliform, proliferating several times percurrently near apex, 5–7 × 3–4 µm. **Conidia** solitary, medium brown, aseptate, granular, finely verruculose, thick-walled, ellipsoid to obclavate, widest below the obtuse apex, base subtruncate to truncate, 1 µm wide, with inconspicuous marginal frill, (6–)7–8(–9) × (2.5–)3(–3.5) µm; covered in a persistent mucilaginous sheath.

**Culture characteristics** — Colonies on MEA spreading with moderate aerial mycelium and smooth, even margins, surface hazel, reverse amber to chestnut; on OA woolly, spreading with abundant aerial mycelium, and smooth, regular margins, pale olivaceous-grey to olivaceous-grey, covering the dish after 1 mo; colonies fertile on OA.

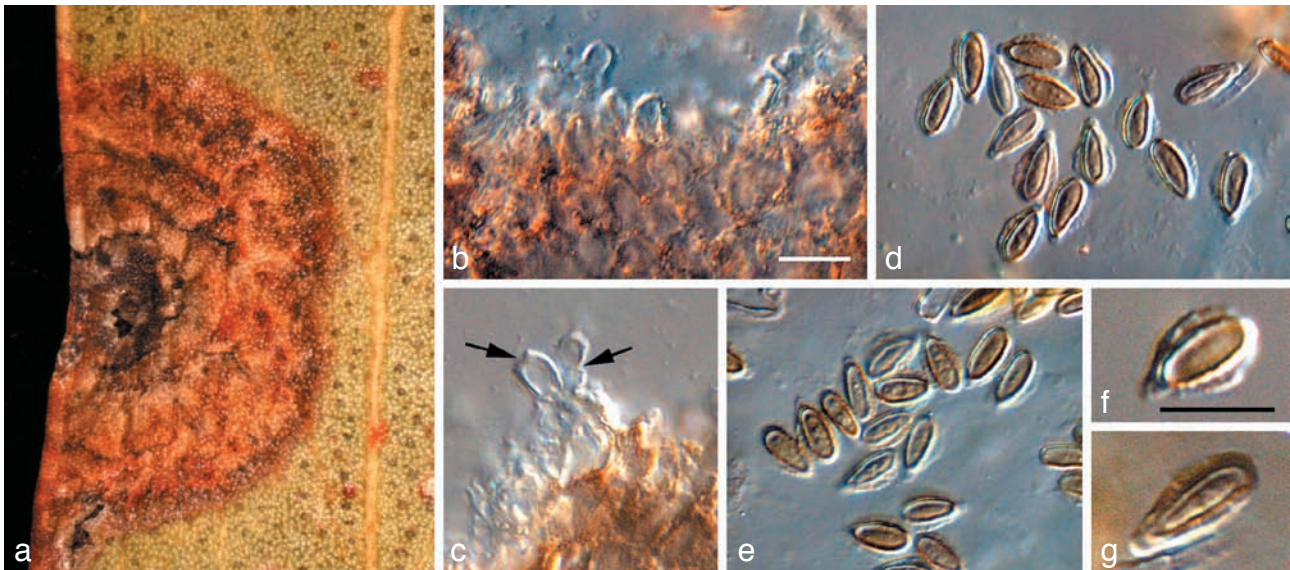


Fig. 4 *Readeriella patrickii* (CPC 13602). a. Leaf spot; b, c. conidiogenous cells giving rise to conidia (arrows denote loci); d–g. conidia with mucoid sheaths. — Scale bars = 10  $\mu$ m.

*Specimen examined.* AUSTRALIA, Tasmania, Tasman Peninsula, 43°11'29.7"S, 147°51'00.7"E, on leaves of *Eucalyptus amygdalina*, 14 Oct. 2006, coll. P. Summerell & B.A. Summerell, CBS H-20248 holotype, isol. P.W. Crous, cultures ex-type CPC 13602 = CBS 124987, CPC 13603, 13604.

**Notes** — The collection on which this species is based sporulates poorly, and only after 1–2 mo were conidiomata observed on OA. *Readeriella patrickii* is distinct in that it has pycnidia, and pigmented, percurrently proliferating conidiogenous cells that give rise to aseptate, brown conidia with a persistent mucilaginous sheath. The latter feature has not been reported previously for any species of *Readeriella*.

#### Clade 25: *Baudoinia* (*Teratosphaeriaceae*)

*Baudoinia*, which is based on *B. compniacensis*, was erected by Scott et al. (2007) for a genus of hyphomycetes occurring on exposed surfaces exposed to substantial temperature and relative humidity shifts, characterised by brown, verrucose chains of conidia. No teleomorph has been reported for this fungus.

#### Clade 27: *Devriesia* (*Teratosphaeriaceae*)

*Devriesia*, which is based on *D. staurophora*, was erected by Seifert et al. (2004) for a heat-tolerant genus of hyphomycetes occurring in soil, with pigmented, catenulate conidia, somewhat darkened scars, and chlamyospores. No teleomorph state has been found.

#### Clades 26, 28, 30: *Catenulostroma* (*Teratosphaeriaceae*)

*Catenulostroma* is morphologically similar to *Trimmatostroma*, though the latter belongs to the *Helotiales* (Crous et al. 2007a). *Trimmatostroma* s.s. 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. However, it is clear that the concept of *Catenulostroma* as proposed by Crous et al. (2007a) is polyphyletic, but before this can be resolved, the type species, *C. protearum*, needs to be recollected.

#### Clade 29: *Phaeothecoidea* (*Teratosphaeriaceae*)

Crous et al. (2007c) established the genus *Phaeothecoidea*, based on *P. eucalypti*, and distinguished it from *Hyphospora* (teleomorph: *Cumminutispora*) and *Phaeotheca*, which both

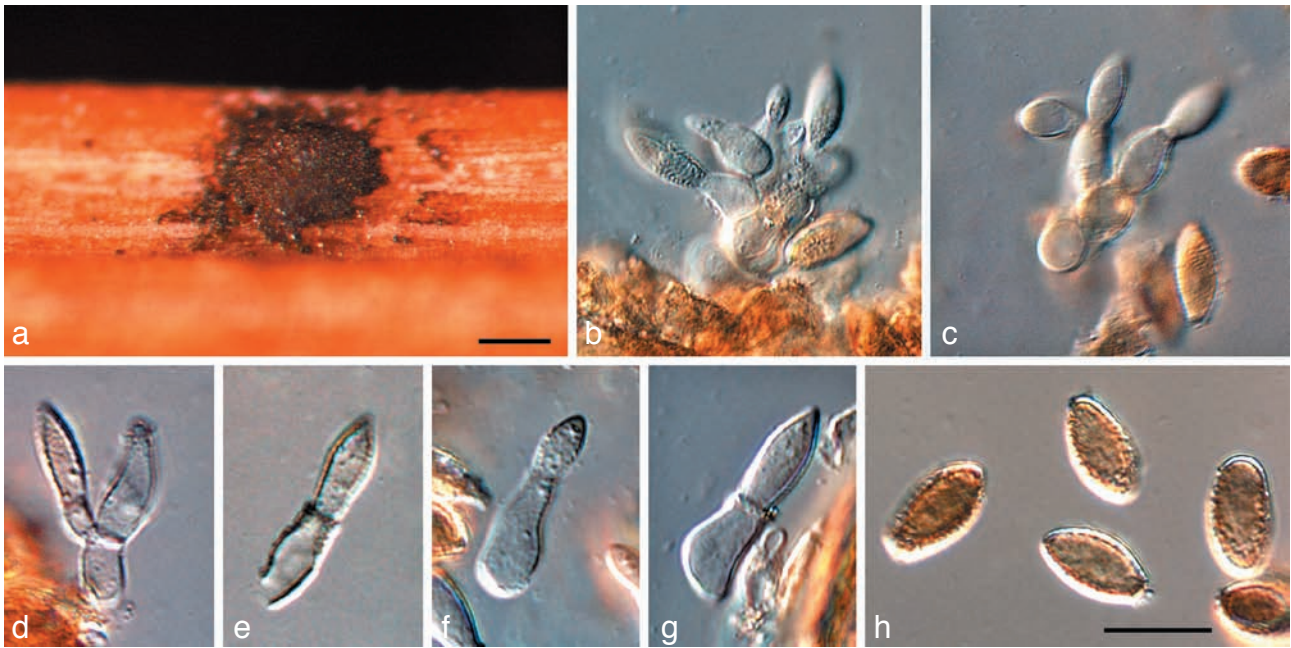
have endoconidia, on the basis of it having more thin-walled conidia, that become pigmented with age (Zalar et al. 1999). Colonies of *Phaeothecoidea* are wet and slimy. No teleomorphs have been reported to date (Crous et al. 2008a).

#### Clade 31: *Teratosphaeria* (with *Kirramyces* and *Colletogloeopsis* anamorphs, and *Batcheloromyces*-like synanamorphs) (*Teratosphaeriaceae*)

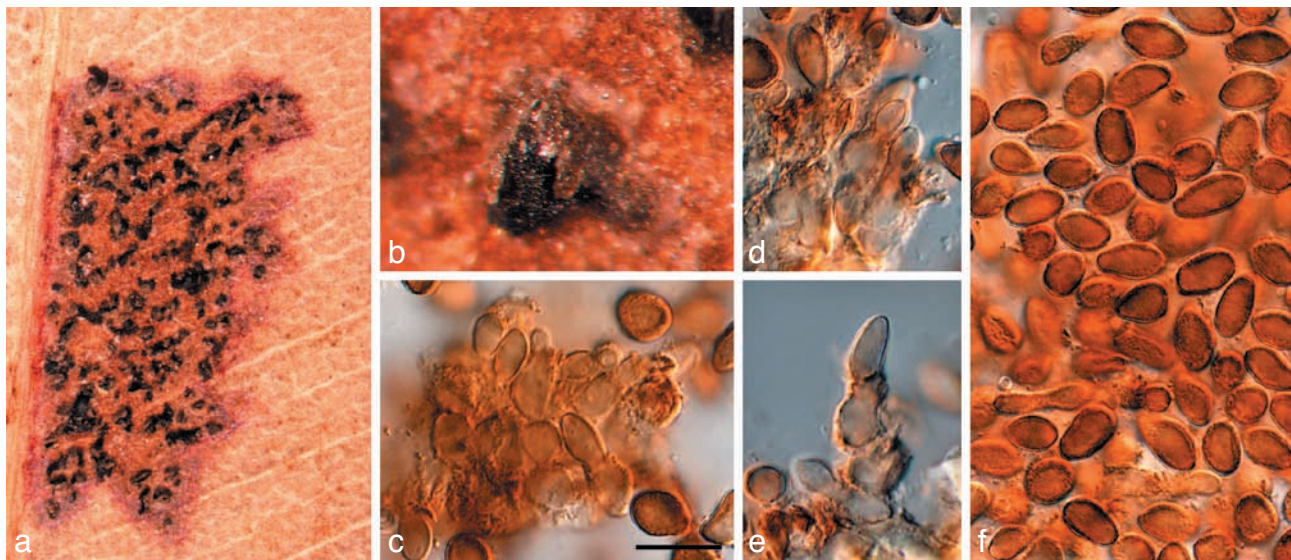
The genus *Kirramyces* (Walker et al. 1992) was established for a group of coelomycetes occurring on *Eucalyptus* with smooth to rough, brown-walled, percurrently proliferating conidiogenous cells, and brown, cylindrical to obclavate conidia with truncate bases and a marginal frill. It was distinguished from *Sonderhenia* on the basis of having distoseptate conidia, and from *Stagonospora*, by having pigmented conidia. Although two series of species were recognised, namely those with pale, finely verrucose conidia, and those with brown, rough conidia, it was decided to place them in a single genus, *Kirramyces* (B. Sutton, pers. comm.). The recollection of the type species of *Phaeophleospora*, namely *P. eugeniae*, showed that it had the same conidiogenesis as *Kirramyces*, leading Crous et al. (1997) to transfer all these taxa to *Phaeophleospora* (1916), which at the time appeared to be the older name for the complex. Crous & Wingfield (1996) introduced *Colletogloeopsis*, characterised by acervuli, and percurrently as well as sympodially proliferating conidiogenous cells, and 0–1-septate conidia. Based on cultural studies, Cortinas et al. (2006) found that species of *Colletogloeopsis* could have pycnidia as well as acervuli, concluding that conidiomatal structure was minimally useful in this group of anamorphic genera.

Employing DNA phylogenetic data, Andjic et al. (2007a) concluded that conidial septation was not informative at the generic level because taxa with aseptate conidia clustered with those having septate conidia. Furthermore, Andjic et al. (2007a) showed that *Phaeophleospora eugeniae*, the type species of *Phaeophleospora* clustered apart from *Kirramyces epicoccoides*, the type species of *Kirramyces*. Although conidia of *P. eugeniae* have an uneven pigmentation (more pale brown at the ends), this feature does not appear to hold up for other species of *Phaeophleospora* s.s. (P.W. Crous, in prep.). Crous et al. (2007a) showed *Phaeophleospora* to reside in the *Mycosphaerellaceae* and *Kirramyces* in the *Teratosphaeriaceae*, respectively. *Phaeophleospora* was retained for *P. eugeniae*





**Fig. 5** *Leptomelanconium allescheri* (WINF 4022). a. Conidioma on pine needle; b–g. conidiogenous cells giving rise to conidia; h. conidia. — Scale bars = 10 µm.



**Fig. 6** *Teratosphaeria australiensis* (IMI 159079a). a. Leaf spot; b. erumpent pycnidium; c–e. conidiogenous cells giving rise to conidia. f. conidia. — Scale bar = 10 µm.

by Andjic et al. (2007a), while other taxa were recombined in *Kirramyces*, with *Colletogloeopsis* treated as synonym. *Kirramyces* was subsequently emended to incorporate conidia that vary from aseptate to euseptate, fusoid to cylindrical to long obclavate to ellipsoidal.

Crous et al. (2007a) placed the *Teratosphaeria* coelomycete anamorphs in *Readeriella* (1908), which they regarded as an older name for the coelomycetes accommodated in *Kirramyces* (1992). However, in the present study (Fig. 1, part 4, 5), we have shown that *Readeriella* is phylogenetically distinct from *Kirramyces* anamorphs. Morphologically, the distinction between *Readeriella* and *Kirramyces* is subtle, and lies in the conidial bases, with conidia of *Readeriella* having tapering subtruncate bases, in contrast to those of *Kirramyces* (= *Colletogloeopsis*) that tend to be more truncate.

Whether *Kirramyces* is the oldest generic name to use for anamorphs in this clade is open to debate. *Phaeoseptoria* (1908) appears to be an anamorph of the *Phaeosphaeriopsis* complex (Arzanlou & Crous 2006), rendering it unavailable

for this group of anamorphs. However, the status of the type species of *Leptomelanconium* (1923) remains unknown (Fig. 5), the species occurring on *Corymbia*, namely *L. australiensis* (Fig. 6), is clearly an anamorph of *Teratosphaeria*. The same is true for several species of ‘*Coniothyrium*’ treated by Sutton (1980) and Crous (1998). *Colletogloeum* (1953) has hitherto been a somewhat confused genus, including many species that appear to belong to *Teratosphaeria*. However, the ITS sequence from DNA extracted from a specimen representative of the type species, *C. sissoo* (IMI 119162) (Fig. 7), clearly revealed *Colletogloeum* to be allied to the *Pseudocercospora* (1910) complex, clustering in the *Mycosphaerellaceae* (data not shown). *Jubispora* (1986) is another interesting candidate genus that predates *Kirramyces*, having conidia partially covered by a mucoid sheath, as observed in *Readeriella patrickii*. The phylogenetic position of *Jubispora* is, however, unknown. Due to the uncertainty surrounding available anamorph names in this clade, we apply a single generic name to this genus. The oldest name, *Teratosphaeria* (1912), was thus selected to apply to all taxa in this clade (Crous et al. 2009a).



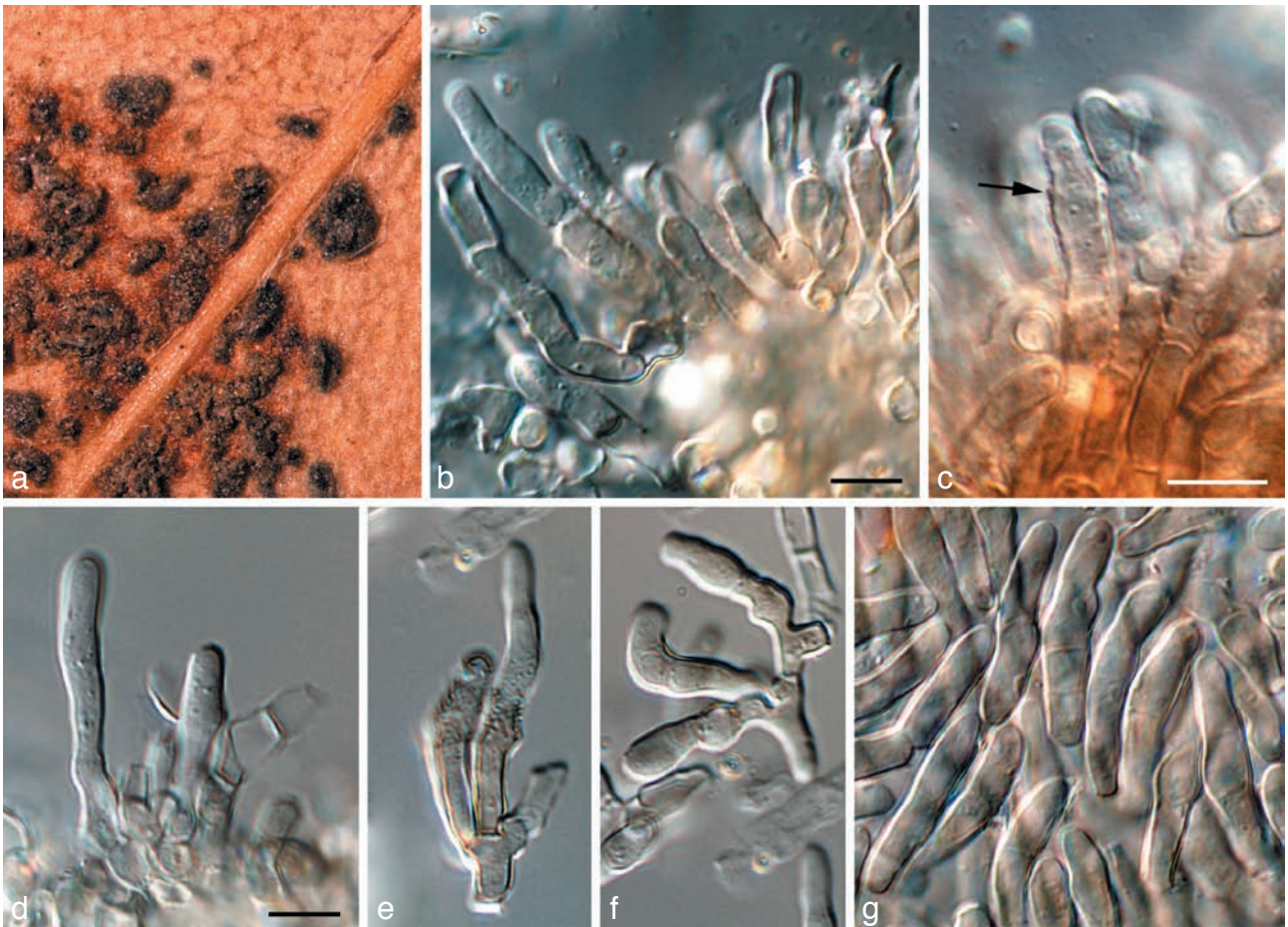


Fig. 7 *Colletogloeum sissoo* (IMI 119162). a. Conidiomata on leaf; b–f. conidiogenous cells giving rise to conidia; g. conidia. — Scale bars = 10 µm.

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

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

Synanamorph. *Batcheloromyces*-like

= *Colletogloeopsis* Crous & M.J. Wingf., Canad. J. Bot. 75: 668. 1997.

***Teratosphaeria alcornii*** Crous, *nom. nov.* — MycoBank MB509725

Basionym. *Stigmata eucalypti* Alcorn, Trans. Brit. Mycol. Soc. 60: 151. 1973.

≡ *Batcheloromyces eucalypti* (Alcorn) Crous & U. Braun, Stud. Mycol. 58: 12. 2007.

Notes — The epithet '*eucalypti*' is already occupied by *Teratosphaeria eucalypti*, based on *Cercospora eucalypti* Cooke & Masee (1889) as shown below.

***Teratosphaeria angophorae*** (Andjic, Carnegie & P.A. Barber) Andjic, Carnegie & P.A. Barber, *comb. nov.* — MycoBank MB509726

Basionym. *Kirramyces angophorae* Andjic, Carnegie & P.A. Barber, Mycol. Res. 111: 1193. 2007.

Notes — *Teratosphaeria angophorae* represents the transition of *Colletogloeopsis* (conidia 0–1-septate) to *Kirramyces* (conidia 3 or more septate). Although the majority of conidia are aseptate, this species provides support for the fact that there is a morphological range in conidial septation from *Colletogloeopsis* to *Kirramyces*.

***Teratosphaeria australiensis*** (B. Sutton) Crous, *comb. nov.* — MycoBank MB509727; Fig. 6

Basionym. *Leptomelanconium australiense* B. Sutton, Nova Hedwigia 25: 163. 1974.

Specimen examined. AUSTRALIA, York, on leaves of *Corymbia ficifolia*, H.L. Harvey, IMI 159079a holotype.

Notes — *Teratosphaeria australiensis* is a typical species of *Teratosphaeria*, not congeneric with *Leptomelanconium al-lescheri*, the type species of *Leptomelanconium*. We examined herbarium material of the latter (WINF 4022, Fig. 5), and found that it was morphologically quite distinct from typical *Colletogloeopsis/Kirramyces* anamorphs, in having conidiophores that can be branched, and pigmented only in the apical conidiogenous region. This species is presently not known from culture.

***Teratosphaeria blakelyi*** (Crous & Summerell) Crous & Summerell, *comb. nov.* — MycoBank MB509728

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

≡ *Readeriella blakelyi* (Crous & Summerell) Crous & U. Braun, Stud. Mycol. 58: 26. 2007.

***Teratosphaeria brunneotingens*** (Crous & Summerell) Crous & Summerell, *comb. nov.* — MycoBank MB509729

Basionym. *Readeriella brunneotingens* Crous & Summerell, Stud. Mycol. 58: 26. 2007.

***Teratosphaeria consideniana*** (Crous & Summerell) Crous & Summerell, *comb. nov.* — MycoBank MB509730

*Basionym.* *Colletogloeopsis consideniana* Crous & Summerell, Fung. Diversity 23: 343. 2006.

≡ *Readeriella consideniana* (Crous & Summerell) Crous & U. Braun, Stud. Mycol. 58: 26. 2007.

***Teratosphaeria corymbiae*** (Carnegie, Andjic & P.A. Barber) Carnegie, Andjic & P.A. Barber, *comb. nov.* — MycoBank MB509731

*Basionym.* *Kirramyces corymbiae* Carnegie, Andjic & P.A. Barber, Mycol. Res. 111: 1193. 2007.

*Specimen examined.* AUSTRALIA, New South Wales, South Grafton, Grafton City Council, Landfill Plantation, 152°54'38"E, 29°46'21"S, on leaves of *Corymbia henryii*, 16 Feb. 2006, coll. A.J. Carnegie, isol. P.W. Crous, cultures CPC 13125 = CBS 124988, CPC 13126, 13127.

***Teratosphaeria destructans*** (M.J. Wingf. & Crous) M.J. Wingf. & Crous, *comb. nov.* — MycoBank MB509732

*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 destructans* (M.J. Wingf. & Crous) Crous & U. Braun, Stud. Mycol. 58: 26. 2007.

***Teratosphaeria eucalypti*** (Cooke & Masee) Crous, *comb. nov.* — MycoBank MB509733

*Basionym.* *Cercospora eucalypti* Cooke & Masee, Grevillea 18: 7. 1889.

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

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

= *Septoria pulcherrima* Gadgil & M.A. Dick, New Zealand J. Bot. 21: 49. 1983.

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

≡ *Readeriella pulcherrima* (Gadgil & M.A. Dick) Crous & U. Braun, Stud. Mycol. 58: 26. 2007.

***Teratosphaeria lilianiae*** (J. Walker, B. Sutton & Pascoe) Crous & Andjic, *comb. nov.* — MycoBank MB509734

*Basionym.* *Kirramyces lilianiae* J. Walker, B. Sutton & Pascoe, Mycol. Res. 96: 921. 1992.

≡ *Phaeophleospora lilianiae* (J. Walker, B. Sutton & Pascoe) Crous, F.A. Ferreira & B. Sutton, S. African J. Bot. 63: 115. 1997.

***Teratosphaeria macowanii*** (Sacc.) Crous, *comb. nov.* — MycoBank MB509735

*Basionym.* *Coniothecium macowanii* Sacc., Syll. Fung. 4: 512. 1886, nom. nov., based on *Coniothecium punctiforme* G. Winter, Hedwigia 24: 33. 1885, non *C. punctiforme* Corda, Icon. Fungorum (Corda) 1: 2. 1837.

≡ *Trimmatostroma macowanii* (Sacc.) M.B. Ellis, More Dematiaceous Hyphomycetes: 29. 1976.

≡ *Catenulostroma macowanii* (Sacc.) Crous & U. Braun, Stud. Mycol. 58: 17. 2007.

***Teratosphaeria multiseptata*** (Carnegie) Carnegie, *comb. nov.* — MycoBank MB509736

*Basionym.* *Mycosphaerella multiseptata* Carnegie, Mycologia 99: 471. 2007.

***Teratosphaeria obscuris*** (P.A. Barber & T.I. Burgess) P.A. Barber & T.I. Burgess, *comb. nov.* — MycoBank MB509737

*Basionym.* *Mycosphaerella obscuris* P.A. Barber & T.I. Burgess, Fung. Diversity 24: 146. 2007.

***Teratosphaeria stellenboschiana*** (Crous) Crous, *comb. nov.* — MycoBank MB509738

*Basionym.* *Colletogloeopsis stellenboschiana* Crous, Stud. Mycol. 55: 110. 2006.

≡ *Readeriella stellenboschiana* (Crous) Crous & U. Braun, Stud. Mycol. 58: 26. 2007.

*Specimens examined.* CORSICA, on leaves of *Eucalyptus* sp., Aug. 2005, coll. J. Dijksterhuis, CBS H-20249, isol. P.W. Crous, cultures CPC 12283–12285. — SOUTH AFRICA, Western Cape Province, Stellenbosch Mountain, on leaves of *Eucalyptus* sp., 4 Dec. 2004, P.W. Crous, CBS H-19688 holotype, culture ex-type CBS 116428 = CPC 10886; Gauteng, Pretoria, on leaves of *Eucalyptus punctata*, 28 Feb. 2007, P.W. Crous, CBS H-20250, CPC 13767 = CBS 124989, CPC 13764–13769.

Notes — Although there are two nucleotide differences between the ex-type strain and these new collections, conidial dimensions of the latter are (6–)7–8(–9) × (3–)4(–4.5) µm, thus being very similar to those of the ex-type strain, (6.5–)7–9(–10) × (3–)3.5(–4) µm (Crous et al. 2006e), suggesting this to be intraspecific variation.

***Teratosphaeria syncarpiae*** (Carnegie & M.J. Wingf.) Carnegie & M.J. Wingf., *comb. nov.* — MycoBank MB509739

*Basionym.* *Mycosphaerella syncarpiae* Carnegie & M.J. Wingf., Mycologia 99: 469. 2007.

***Teratosphaeria viscidus*** (Andjic, P.A. Barber & T.I. Burgess) Andjic, P.A. Barber & T.I. Burgess, *comb. nov.* — MycoBank MB509740

*Basionym.* *Kirramyces viscidus* Andjic, P.A. Barber & T.I. Burgess, Australas. Plant Pathol. 36: 485. 2007.

*Specimen examined.* AUSTRALIA, Queensland, 24 km outside Mareeba Dimbulah, 17°8'21.2"S, 145°14'58.6"E, 503 m, on leaves of *Eucalyptus* sp., 26 Aug. 2006, coll. B.A. Summerell & P.W. Crous, CBS H-20251, isol. P.W. Crous, cultures CPC 13306 = CBS 124992, CPC 13307, 13308.

***Teratosphaeria wingfieldii*** (Crous) Crous, *comb. nov.* — MycoBank MB509741

*Basionym.* *Catenulostroma wingfieldii* Crous, Persoonia 20: 67. 2008.

**DISCUSSION**

In an attempt to delineate natural genera within the *Mycosphaerella* complex, the present study integrates anamorph and teleomorph morphologies with a molecular phylogeny derived from the LSU gene sequences. Because most of these 'morphological genera' have been shown to be poly- and paraphyletic, a generic name (s.s.) can be applied only to the clade in which the type species resides. Furthermore, an attempt has been made to integrate anamorph and teleomorph names, and not introduce further genera. Thus, the oldest available generic name was chosen for each clade (irrespective of anamorph or teleomorph), and the oldest available epithet was chosen for each species, with priority given to teleomorph species epithets for the holomorph. Where a taxon is asexual, but is genetically identical to the teleomorph (thus contains an element of the teleomorph, in this case the DNA), it has been described (or combined) in sexual genera. Likewise, we have described (or combined) sexual taxa in asexual genera only where an asexual genus is available for the clade, and where



it contains the DNA element typical of that anamorph genus. We thus accept the similarity in DNA sequence to be equal in value to the presence of certain morphological features, such as asci and ascospores. Sexual and asexual taxa are treated as equal. Where they are genetically similar, preference has been given to the oldest name (date of publication).

*Mycosphaerella* (1884) sensu Aptroot (2006) is heterogeneous. In the strict sense, *Mycosphaerella* is linked only to *Ramularia* (1833) anamorphs, with preference given to the latter name, due to the confusion surrounding *Mycosphaerella*, as well as date of publication. *Teratosphaeria* (1912) species have *Kirramyces* (1992) (incl. *Colletogloeopsis* 1997) anamorphs, with *Teratosphaeria* used as the generic name for this well-defined clade of foliar pathogens (Crous et al. 2009a). In addition, numerous other genera have been recognised as distinct in the present study, many of which have *Mycosphaerella*-like teleomorphs.

Results of this study have shown that the *Mycosphaerella* complex as it is presently defined in the literature encompasses numerous genera, many of which remain unnamed. Before DNA-based phylogenetic inference was available for this group, these genera were obscured by the fact that the teleomorph morphology, namely a submerged to erumpent ascoma, in most cases without residual hamathelial tissue, with bitunicate asci and 1-celled ascospores, had evolved throughout the order. Due to the unavailability of cultures, these hypotheses could never be tested. The result was that *Mycosphaerella* became known as a genus with up to 30 different anamorph genera (Crous & Braun 2003, Crous et al. 2000, 2001, 2004b, c, 2006a–d, 2007a–c). A further problem arose from the fact that many of these anamorph forms evolved in more than one clade, and they thus occurred in different families, and represent different genera. This phenomenon added to the confusion, and it provided support for a wider generic concept for *Mycosphaerella*. As more taxa and DNA sequence data have become available for study, it has increasingly appeared that the minute features observed among the various anamorphs, were in many cases indicative of different phylogenetic lineages.

Many clades remain unresolved in this study. This is due to the fact that they are poorly populated by taxa, and in some cases the absence of cultures has made it impossible to place them appropriately. These will hopefully be resolved in the future as additional collections are made and cultures and DNA sequence data become available. Nevertheless, the proposed system of a single generic name per clade is infinitely more stable than the one used in the past and in which both the anamorphs and teleomorphs needed to undergo nomenclatural changes. An added advantage of this new taxonomic scheme is that it does not suffer from synanamorphs developing in various places throughout the tree, resulting in a further proliferation of names.

In the title of this paper, we pose the question: 'Do you believe in genera?' In 1943, Bisby & Ainsworth stated that 'Nature may make species, but man has made the genera'. Before the incorporation of DNA sequence-based phylogenies, the Saccardoian system based on spore septation defined numerous artificial boundaries in the *Mycosphaerellaceae* (Crous et al. 2003b). *Mycosphaerella* has until now been used as a convenient receptacle concept to incorporate numerous morphologically diverse anamorphs. A startling fact is that so many solitary lineages and anamorph morphology types remain unresolved in the present phylogeny. This shows that a concerted effort is needed to make collections that will ultimately provide a more robust representation of various morphology types, common ancestors and sister taxa. We now have the ability to use DNA phylogenies to reflect evolutionary history. By integrating the phylogenetic species concept with morphology, we can now

select meaningful break points in lineages which can be attributed to genera.

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Some years ago, Prof. dr DL Hawksworth asked PWC why he regarded Colin Booth as one of his favourite mycologists. From the present paper it is clear that the answer partly lies in his Presidential address (Booth 1978), which continues to inspire to this day.

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