Unravelling *Mycosphaerella*: do you believe in genera?

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**Key words**

Cibissia  
Colletogloeum  
Disoconium  
Kirramyces  
*Mycosphaerella*  
Passalora  
Penidiella  
Phaeophleospora  
Phaeothecoida  
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 share 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*, *Polythrinium*, *Pseudocercospora*, *Ramulispora*, *Septoria* and *SonderHenia*. The genus *Teratosphaeria* accommodates taxa with Kirramyces anamorphs, while other clades supported in the *Teratosphaeraceae* include *Baudoinia*, *Capnobotryella*, *Devriesia*, *Penidiella*, *Phaeothecoida*, *Readeriella*, *Stainwardia* and *Stenella*. The genus *Schizothyrium* with Zygaporia anamorphs is supported as belonging to the *Schizothyriaceae*, while *Disoconium* 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 ascii and 1-septate ascospores, represents numerous genera and several families yet to be defined in future studies.

**Article info**

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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 Schimmelmicroscopie (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 conidialonal 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
Table 1  Details of the isolates for which novel sequences were generated.

| Species | Accession number\(^1\) | GenBank number (28S nrDNA) |
|---------|--------------------------|-----------------------------|
| **Baudoinia compressa** | CBS 123031; DAOM 238773; UAMH 10808 | GQ852580 |
| **Capnobotrya renisipora** | CBS 123032; DAOM 237864; UAMH 10764 | GQ852581 |
| **Cercospora apii** | CBS 118712 | GQ852582 |
| **Cercospora zebrinae** | CBS 118790; IMI 262766; WAC 7973 | GQ852583 |
| **Cercosporella virgaeareae** | CBS 113304 | GQ852584 |
| **Dissoconium acciculare** | CBS 201.89 | GQ852585 |
| **Dissoconium australiensis** | CBS 120729; CPC 13282 | GQ852586 |
| **Dissoconium commune** | CBS 110747; CPC 831 | GQ852587 |
| **Dissoconium dekkeri** | CPC 13098 | GQ852588 |
| **Dothistroma pini** | CBS 116487; CMW 10951 | GQ852589 |
| **Mycosphaerella acaciigena** | CBS 112515; CPC 3837 | GQ852590 |
| **Mycosphaerella africana** | CBS 116154; CMW 4945; CPC 794 | GQ852591 |
| **Mycosphaerella endophytica** | CBS 114662; CPC 1193 | GQ852592 |
| **Mycosphaerella heimi** | CBS 110682; CMW 4942; CPC 760 | GQ852593 |
| **Mycosphaerella heimioides** | CBS 111909; CMW 3046; CPC 1312 | GQ852594 |
| **Mycosphaerella holualoana** | CBS 110699; CPC 2155 | GQ852595 |
| **Mycosphaerella irregularinamoides** | CBS 111211; CPC 1362 | GQ852596 |
| **Mycosphaerella kornei** | CBS 111001; CMW 5147; CPC 1084 | GQ852597 |
| **Mycosphaerella marxii** | CPC 11000 | GQ852598 |
| **Pseudocercospora bixae** | CBS 118711; CPC 2577 | GQ852599 |
| **Pseudocercospora crousii** | CBS 119487; Lynfield 1260 | GQ852600 |
| **Pseudocercospora fijiensis** | CBS 110755; IMI 136770; CPC 4299 | GQ852601 |
| **Pseudocercospora punctata** | CBS 124990; CPC 13492 | GQ852602 |
| **Pseudocercospora schizolobii** | CBS 124996; CPC 12960 | GQ852603 |
| **Pseudocercospora sphaerulinae** | CBS 112621; CPC 4314 | GQ852604 |
| **Ramulispora sorghi** | CBS 110576; CPC 905 | GQ852605 |
| **Readeriella callista** | CBS 124986; CPC 13615 | GQ852606 |
| Mycosphaerella-like genera                  | Accession       | GenBank Accession |
|--------------------------------------------|-----------------|------------------|
| Readeriella eucalypti                      | CPC 13401       | GQ852660         |
| Readeriella mirabilis                      | CPC 12379       | GQ852661         |
| Readeriella nontingens                     | CPC 13611       | GQ852662         |
| Readeriella patrickii                      | CBS 124987; CPC 13602 | GQ852664 |
| Readeriella 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         |
|                                          | CPC 13632       | GQ852673         |
|                                          | CPC 13634       | GQ852674         |
|                                          | CPC 13635       | GQ852675         |
|                                          | CPC 13636       | GQ852676         |
|                                          | CPC 13637       | GQ852677         |
|                                          | CPC 13638       | GQ852678         |
|                                          | CPC 13639       | GQ852679         |
|                                          | CPC 13640       | GQ852680         |
|                                          | CPC 13641       | GQ852681         |
|                                          | CPC 13642       | GQ852682         |
|                                          | CPC 13643       | GQ852683         |
|                                          | CPC 13644       | GQ852684         |
|                                          | CPC 13645       | GQ852685         |
|                                          | CPC 13646       | GQ852686         |
|                                          | CPC 13647       | GQ852687         |
|                                          | CPC 13648       | GQ852688         |
|                                          | CPC 13649       | GQ852689         |
|                                          | CPC 13650       | GQ852690         |
|                                          | CPC 13651       | GQ852691         |
|                                          | CPC 13652       | GQ852692         |
|                                          | CPC 13653       | GQ852693         |
|                                          | CPC 13654       | GQ852694         |
|                                          | CPC 13655       | GQ852695         |
|                                          | CPC 13656       | GQ852696         |
|                                          | CPC 13657       | GQ852697         |
|                                          | CPC 13658       | GQ852698         |
|                                          | CPC 13659       | GQ852699         |
|                                          | CPC 13660       | GQ852700         |
|                                          | CPC 13661       | GQ852701         |
|                                          | CPC 13662       | GQ852702         |
|                                          | CPC 13663       | GQ852703         |
|                                          | CPC 13664       | GQ852704         |
|                                          | CPC 13665       | GQ852705         |
|                                          | CPC 13666       | GQ852706         |
|                                          | CPC 13667       | GQ852707         |
|                                          | CPC 13668       | GQ852708         |
|                                          | CPC 13669       | GQ852709         |
|                                          | CPC 13670       | GQ852710         |
|                                          | CPC 13671       | GQ852711         |
|                                          | CPC 13672       | GQ852712         |
|                                          | CPC 13673       | GQ852713         |
|                                          | CPC 13674       | GQ852714         |
|                                          | CPC 13675       | GQ852715         |
|                                          | CPC 13676       | GQ852716         |
|                                          | CPC 13677       | GQ852717         |
|                                          | CPC 13678       | GQ852718         |
|                                          | CPC 13679       | GQ852719         |
|                                          | CPC 13680       | GQ852720         |
|                                          | CPC 13681       | GQ852721         |
|                                          | CPC 13682       | GQ852722         |
|                                          | CPC 13683       | GQ852723         |
|                                          | CPC 13684       | GQ852724         |
|                                          | CPC 13685       | GQ852725         |
|                                          | CPC 13686       | GQ852726         |
|                                          | CPC 13687       | GQ852727         |
|                                          | CPC 13688       | GQ852728         |
|                                          | CPC 13689       | GQ852729         |
|                                          | CPC 13690       | GQ852730         |
|                                          | CPC 13691       | GQ852731         |
|                                          | CPC 13692       | GQ852732         |
|                                          | CPC 13693       | GQ852733         |
|                                          | CPC 13694       | GQ852734         |
|                                          | CPC 13695       | GQ852735         |
|                                          | CPC 13696       | GQ852736         |

1 CBS: Centraalbureau voor Schimmelcultures, Utrecht, The Netherlands; CMW: Culture Collection of the Forestry and Agricultural Biotechnology Institute (FAABI) 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, Bakeham Lane, UK; MFMN: 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; LrNL: Private culture collection Frank Hill.
genera have been shown as poly- or paraphyletic (Halleen et al. 2004, Lee et al. 2004, Réblova 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 Zygothiala 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 (Zygothiala) 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, Réblova 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 as nouns, and to use teleomorph morphology as a description. 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 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; 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 of 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
(Cymadotpha teleomorph; Mycosphaerellaceae)

Polythrincium trifoli (teleomorph Cymadotpha trifoli), an important foliar pathogen of clover, was recently treated by Simon et al. (2009). The anamorph genus Polythrincium (1817) pre-dates the Mycosphaerella-like teleomorph genus, Cymadotpha (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 B), 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 have been monographed (Braun 1998), representing hyaline hyphomycetes with solitary to fasciculate conidiophores, and asceptate 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 Cercosporella from Ramularia should also be noted here. Based on these observations on Cercosporella centaureicola (CBS 120253) by Kirschner (2009), as well as its phylogenetic placement, C. centaureicola is accepted as a likely synonym of R. nagornyi, 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. L. 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 Kirrmyces 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 Kirrmyces 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: Pseudocercosporella-like (Mycosphaerellaceae)

Taxa residing in this clade have anamorphs and teleomorphs that resemble Pseudocercosporella and Mycosphaerella, respectively. However, the type species of Pseudocercosporella, 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.
**Clade 8: Zasmidium-complex (Mycosphaerella-like and Rastoria 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, convex scars. The identity of Stenella (S. araguata) have plicate scars (David 1993), while those of Zasmidium (Z. cellare) and former Stenella species belonging in the Mycosphaerellaceae are planate, i.e. Circospora-like.

The Zasmidium clade remains poorly resolved (Fig. 1, part 1), and it also includes the type species of Periconiella (P. velutina) and Verrucispora (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 anthuricola** (U. Braun & C.F. Hill) Crous & U. Braun, comb. nov. — MycoBank MB509715

Basionym. Stenella anthuricola U. Braun & C.F. Hill, Fung. Diversity 22: 33. 2006.
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: Cercosporella (Mycosphaerellaceae)
Cercosporella (1880), which is based on C. virgaeae (≡ 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, sclereosporous conidia.
Clade 11: Cercospora (Mycosphaerellaceae)
The genus Cercospora, which is based on Cercospora penicilla (Crous & Braun 2003), contains more than 600 species that are saprobic or pathogenic (Crous & Braun 2003, Groenewald et al. 2005, 2006, Crous et al. 2006a). Conidiophores are solitary, scrobilisporous, obclavate to cylindrical-filiform, acicular, hyaline or subhyaline, mostly pluriseptate, smooth, with thickened, darkened, planate scars. Conidia are predominantly nidiogenous cells, proliferating sympodially, and conspicuously continuous to pluriseptate, subhyaline to pigmented, smooth to fasciculate, arising from internal hyphae or stromata, erect, and occur singly on hyphae in culture, and colonies that form red crystals in agar when cultivated (Crous & Wingfield 1996, Crous and occur singly on hyphae in culture, and colonies that form red crystals in agar when cultivated (Crous & Wingfield 1996, Crous & Wingfield 1996). The genus Cercospora is defined here and is 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, multisepate 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. cyti, 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)

Swar & 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 the complex commonly referred to as the Ps. heimii clade, including species such as Ps. crystallina, Ps. heimi, Ps. heimioides, Ps. konae, Ps. irregulararimosas, 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
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 (*Mycovelllosiella*, based on *M. cajani*) and conidia in chains (*Phaeoramularia*, based on *P. 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 or in superfluous 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 proliferation. Proliferations can be rough and irregular (*Cercostigmina*), or smooth and inconspicuous. Coindia are mostly scolecosporous, smooth or finely roughened, transverse or 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),
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 120028. Thailand, on leaves of Eucalyptus camaldulensis, Oct. 2006, W. Himaman, CPC 13492 = CBS 124990.

Notes — Passalora schizolobi 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 schizolobi 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-genus 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 paraplethyl 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 telemorphs)
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 conidiom-bearing rachis (Hoog 1977). No teleomorph has been linked to the genus. Ramichloridium was accepted as paraplethyl 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 19: Schizothyrium (Zygophiala 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 ascii, and some interasal tissue composed of remnants of stromatal 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: Stainawardha (Teratosphaeriaceae)
Stainawardha 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 synnematous to solitary conidiophores, consisting of a single terminal conidiogenous cell giving rise to several ramosconidia, or a branched apparatus composed of several terminal and sometimes lateral conidiogenous cells giving rise to sequences of ramosconidia. 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 ramosconidia 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 subordinate 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 telemorphs, and Cibissia 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 pericilal 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 Cibissia synanamorphs. In contrast, Kirramyces and Colletogloeopsis anamorphs have truncate conidial bases, and are never found associated with Cibissia 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

≡ Nothostrasserae Nag Raj, Canad. J. Bot. 61: 23. 1983.
≡ Cibisssia Crous, Fung. Diversity 26: 151. 2007.

Readeriella callista (Syd.) Crous & Summerrell, comb. nov. — MycoBank MB509719; Fig. 3

Basionym. Coniothyrium callistum (Syd.) B. Sutton, Mycol. Pap. 123: 35. 1983.

Leaf spots amphigenous, irregular, 2–5 mm diam, pale brown, with a thin, raised, dark brown border; associated with wisp damage in some collections. Conidiodoma 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, asceptate, doliform to subcylindrical, proliferating percurrently near apex, 5–7 × 3–4 µm. Conidia solitary, round, aseptate, smooth to finely verruculose, ellipsoid to fusoid, thick-walled, apex obtuse, base truncate, apex and base with darker pigmentation, (7–)9–10–11 (3–)4–5(–5.5) µm; base 1–2 µm wide. Microconidia intermixed among macroconidiophores, cylindrical, straight to flexuous, 2 µm wide, variable in length. Microconidium ellipsoid, hyaline, smooth, 3–5 × 2 µm, apex obtuse, base truncate.

Culture characteristics — Colonies on MEA spreading with moderate aerial mycelium, erumpent with uneven, catenate 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.

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 & Summerrell) Crous & Summerrell, comb. nov. — MycoBank MB509720

Basionym. Mycosphaerella dendritica Crous & Summerrell, Fung. Diversity 26: 161. 2007.

Teleomorph. "Teratosphaeria" dendritica (Crous & Summerrell) Crous & U. Braun, Stud. Mycol. 58: 10. 2007.

Anamorph. Sclerothyrium dendritica Harkness, Proc. Linn. Soc. New South Wales 81: 32. 1956.
≡ Nothostrassera dendritica (Hansf.) Nag Raj, Canad. J. Bot. 61: 25. 1983.

Leaf spots amphigenous, irregular, 2–5 mm diam, pale brown, with a thin, raised, dark brown border; associated with wisp damage in some collections. Conidiodoma 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, asceptate, doliform to subcylindrical, proliferating percurrently near apex, 5–7 × 3–4 µm. Conidia solitary, round, aseptate, smooth to finely verruculose, ellipsoid to fusoid, thick-walled, apex obtuse, base truncate, apex and base with darker pigmentation, (7–)9–10–11 (3–)4–5(–5.5) µm; base 1–2 µm wide. Microconidia intermixed among macroconidiophores, cylindrical, straight to flexuous, 2 µm wide, variable in length. Microconidium ellipsoid, hyaline, smooth, 3–5 × 2 µm, apex obtuse, base truncate.

Culture characteristics — Colonies on MEA spreading with moderate aerial mycelium, erumpent with uneven, catenate 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.

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 dimorphospora (Crous & C. Mohammed) Crous, comb. nov. — MycoBank MB509721

Basionym. Cibisssia dimorphospora Crous & C. Mohammed, Fung. Diversity 26: 151. 2007.

Readeriella minutispora (Crous & Carnegie) Crous & Carnegie, comb. nov. — MycoBank MB509722

Basionym. Cibisssia minutispora Crous & Carnegie, Fung. Diversity 26: 153. 2007.

Readeriella nontingens (Crous & Summerrell) Crous & Summerrell, comb. nov. — MycoBank MB509723

Basionym. Cibisssia nontingens Crous & Summerrell, Fung. Diversity 26: 154. 2007.

Readeriella patrickii Crous & Summerrell, sp. nov. — MycoBank MB509724; Fig. 4

Readeriellae mirabiliis similis, sed conidios sine projecturis lateralis, sed conidios persistentes multicellularia vaginitis, (6–)7–8–9 × (2.5–)3–3.5 µm.

Etymology. Named after Patrick Summerrell, 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. Conidiodoma 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, doliform, 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 truncate 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 umber 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.
Notes — The collection on which this species is based sporulates poorly, and only after 1–2 mo were conidiomata observed (teleomorph: based on Clade 29: Phaeothecoidea (Teratosphaeriaceae) type species, al. (2007a) is polyphyletic, but before this can be resolved, the they are not associated with leaf spots. However, it is clear of woody plants, or occasionally isolated from leaf litter, i.e., stroma Trimmatostroma Catenulostroma Clades 26, 28, 30: Catenulostroma (Teratosphaeriaceae) has been found. darkened scars, and chlamydospores. No teleomorph state occurring in soil, with pigmented, catenulate conidia, somewhat Seifert et al. (2004) for a heat-tolerant genus of hyphomycetes Devriesia Clade 27: Devriesia (Teratosphaeriaceae) has been reported for this fungus. 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 exposed to substantial temperature and relative humidity shifts, characterised by brown, verrucose chains, and from Stagonospora, by having pigmented conidia. Although two series of species were recognised, namely those with pale, finely verruculosic 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 asceptate conidia clustered with those having septate conidia. Furthermore, Andjic et al. (2007a) showed that Phaeophleospora eugeniae, the type species of Phaeophleospora clustered apart from Kirrmames epicoecidies, the type species of Kirrmames. 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 Myco­ sphaerellaceae and Kirrmames in the Teratosphaeriaceae, respectively. Phaeophleospora was retained for P. eugeniae...
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 oblclavate 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 subtrucate 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).
**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. *Stigmina 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 & Massee (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 allescheri*, 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.

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**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 considenianae (Croux & Summerell) Croux & Summerell, comb. nov. — MycoBank MB509730
Basionym. Colletogloeopsis considenianae Croux & Summerell, Fung. Diversity 23: 343. 2006.
≡ Readeriella considenianae (Croux & Summerell) Croux & U. Braun, Stud. Mycol. 58: 26. 2007.

Teratosphaeria corymbiae (Carnegie, Andjic & P.A. Barber) Carnegie, Andjic & P.A. Barber, comb. nov. — MycoBank MB509731
Basionym. Kirrymes 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 hemsleyi, 16 Feb. 2006, coll. A.J. Carnegie, isol. P.W. Crous, cultures CPC 13125 = CBS 124988, CPC 13126, 13127.

Teratosphaeria destructans (M.J. Wingf. & Croux) M.J. Wingf. & Croux, comb. nov. — MycoBank MB509732
Basionym. Kirrymes destructans M.J. Wingf. & Croux, S. African J. Bot. 62: 325. 1996.
≡ Phaeocephospora destructans (M.J. Wingf. & Croux) Crous, F.A. Ferreira & B. Sutton, S. African J. Bot. 63: 113. 1997.
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Teratosphaeria eucalypti (Cooke & Masssee) Croux, comb. nov. — MycoBank MB509733
Basionym. Cerocospora eucalypti Cooke & Masssee, Grevillea 18: 7. 1889.
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Teratosphaeria lilianiae (J. Walker, B. Sutton & Pascoe) Croux & Andjic, comb. nov. — MycoBank MB509734
Basionym. Kirrymes lilianiae J. Walker, B. Sutton & Pascoe, Mycol. Res. 96: 921. 1992.
≡ Phaeocephospora lilianiae (J. Walker, B. Sutton & Pascoe) Crous, F.A. Ferreira & B. Sutton, S. African J. Bot. 63: 115. 1997.

Teratosphaeria macowanii (Sacc.) Croux, comb. nov. — MycoBank MB509735
Basionym. Coniotheccium macowanii Sacc., Syll. Fung. 4: 512. 1886, nom. nov., based on Coniotheccium punctiforme G. Winter, Hedwigia 24: 33. 1885, non C. punctiforme Corda, Icon. Fungorum (Corda) 1: 2. 1837.
≡ Trimmastospora macowanii (Sacc.) M.B. Ellis, More Dematiaceous Hyphomycetes. 29. 1976.
≡ Catenulostroma macowanii (Sacc.) Crous & U. Braun, Stud. Mycol. 58: 17. 2007.

Teratosphaeria multisepata (Carnegie) Carnegie, comb. nov. — MycoBank MB509736
Basionym. Mycosphearella multisepata Carnegie, Mycologia 99: 471. 2007.

Teratosphaeria obscuris (P.A. Barber & T.I. Burgess) P.A. Barber & T.I. Burgess, comb. nov. — MycoBank MB509737
Basionym. Mycosphearella obscuris P.A. Barber & T.I. Burgess, Fung. Diversity 24: 146. 2007.

Teratosphaeria stellenboschiana (Croux) Croux, comb. nov. — MycoBank MB509738
Basionym. Colletogloeopsis stellenboschiana Croux, Stud. Mycol. 55: 110. 2006.
≡ Readeriella stellenboschiana (Croux) Croux & U. Braun, Stud. Mycol. 58. 26. 2007.

Specimens examined. CORNUCOPIA, on leaves of Eucalyptus sp., Aug. 2005, coll. J. Dijksterhuis, CBS H-20249, isol. P.W. Croux, cultures CPC 12283–12285. — SOUTH AFRICA, Western Cape Province, Stellenbosch Mountain, on leaves of Eucalyptus sp., 4 Dec. 2004, P.W. Croux, CBS H-19688 holotype, culture ex-type CBS 116428 = CPC 10886; Gauteng, Pretoria, on leaves of Eucalyptus punctata, 28 Feb. 2007, P.W. Croux, 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) µm, thus being very similar to those of the ex-type strain, (6.5–7–9–10) 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. Mycosphearella 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. Kirrymes viscidus Andjic, P.A. Barber & T.I. Burgess, Australas. Plant Pathol. 36. 485. 2007.
Specimens 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 (Croux) Croux, 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 ascospores and ascosporae. Sexual and assexual 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 the date of publication. *Teratospaeria* (1912) species have *Kirramyces* (1992) (incl. *Colletogloeopsis* 1997) anamorphs, with *Teratospaeria* 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 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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