Mycosphaerella and Teratosphaeria Diseases of *Eucalyptus*; easily confused with serious consequences

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Abstract The *Mycosphaerella* complex accommodates thousands of taxa. Many of these species are economically important plant pathogens, notably on native and commercially propagated *Eucalyptus* species where they cause a wide range of disease symptoms including leaf spot, leaf blotch, shoot blight and stem cankers. Some of these diseases represent major impediments to sustainable *Eucalyptus* forestry in several countries where infection by *Mycosphaerella* and *Teratosphaeria* species can result in reduction of wood volume and in severe cases tree death. Extensive research has been conducted on these disease complexes over the past 40 years. The incorporation of DNA-based molecular techniques has made it possible to define and to better understand the differences between the *Mycosphaerella* and *Teratosphaeria* species occurring on *Eucalyptus*. These studies have also enabled refinement of anamorph and teleomorph generic concepts for the genera and thus facilitated the more accurate identification of species. They have also promoted a more lucid understanding of the biology, life cycles, population biology and epidemiology of the most important pathogens in the group.

Keywords *Capnodiales*, *Eucalyptus*, *Mycosphaerellaceae*, *Teratosphaeriaceae*, tree diseases, leaf spots

Introduction

Species of *Eucalyptus sensu stricto* (excluding *Corymbia* and *Angophora*) are native to Australia, with only very few species occurring in Indonesia, Papua New Guinea and the Philippines (Ladiges 1997; Potts and Pederick 2000; Turnbull 2000). Many *Eucalyptus* species have been selected and planted as exotics in countries having tropical, sub-tropical and temperate climates and where they are among the favoured tree species for commercial forestry (Poynton 1979; Turnbull 2000). Commercial plantations of *Eucalyptus* spp. are second only to *Pinus* spp. in their deployment and productivity (Old et al. 2003) and over 14 million hectares of *Eucalyptus* spp. and their hybrids are grown in managed plantations (FAO 2007). Other than being suitable for planting in a wide diversity of conditions and climates, *Eucalyptus* spp. offer the advantage of desirable wood and pulp qualities and relatively short rotation periods (Zobel 1993; Turnbull 2000).

Although *Eucalyptus* spp. are favoured for commercial forestry, they are affected by many pests and diseases (Elliott et al. 1998; Keane et al. 2000; Wingfield 2003; Wingfield et al. 2008). A large number of native and non-native fungal pathogens can infect the roots, stems and leaves of *Eucalyptus* spp., often simultaneously (Old and Davison 2000; Park et al. 2000; Old et al. 2003). It is important, therefore, to accurately identify and understand the biology of these pathogens and thus to develop effective management strategies.

Mycosphaerella sensu lato is one of the largest ascomycete genera. Over 3000 taxa are currently accommodated in this generic complex, with species recognised as saprobes, pathogens or endophytes of many plants, or hyperparasites of other fungi (Crous 2009). The sexual structures of *Mycosphaerella* spp. are morphologically conserved, and species are difficult to propagate in culture, making identification difficult (Crous 1998; Crous et al. 1991; 2004). Approximately 30 anamorph genera have been associated with *Mycosphaerella* (Crous et al. 2000; 2004; 2006; Crous 2009; Crous et al. 2009a; b). These anamorph states are morphologically variable and provide greater information for species delineation (Crous and Wingfield 1996; Crous et al. 2000; 2006; Verkley and Priest 2000).

Recent phylogenetic studies have revealed that *Mycosphaerella sensu lato* is polyphyletic. Thus, species formerly accommodated in the genus represent members of the *Mycosphaerellaceae*, *Dissoconiaceae*, *Teratosphaeriaceae* and *Davidiellaceae* (Schoch et al. 2006; Crous et al. 2007a; 2009b). Furthermore, these families consist of numerous genera, some being strictly asexual. In many cases, anamorphs are indicative of the different genera in this complex, with *Mycosphaerella sensu stricto* for example, being restricted to *Ramularia* anamorphs (Verkley et al. 2004). Ultimately, DNA sequence analyses provide the most effective means to ensure accurate identification of *Mycosphaerella* species. Therefore, morphological characteristics, combined with DNA-based methods have served to elucidate species concepts in the genus. As a consequence many *Mycosphaerella* spp., including large numbers associated with *Eucalyptus*, have recently been transferred to the morphologically similar genus *Teratosphaeria* (Crous et al. 2007a).

An extensive body of research on *Mycosphaerella* and *Teratosphaeria* species has been published. However, few published reviews are available for those species of *Mycosphaerella* and *Teratosphaeria* occurring on *Eucalyptus*. The aim of this review is, therefore, to critically analyse the existing research pertaining to outbreaks of *Mycosphaerella* and *Teratosphaeria* diseases on *Eucalyptus* and to highlight differences between the two groups of fungi.

Generic Concepts

More than 3000 taxa, which are characterised as pathogens or saprobes of various vascular and woody hosts, have been accommodated in *Mycosphaerella sensu lato* (von Arx 1983; Corlett 1991; Corlett 1995; Aptroot 2006). *Mycosphaerella sensu lato* does not group within the *Dothideales,* but is rather accommodated in the *Capnodiales* (*Dothideomycetes*) (Schoch et al. 2006). Morphologically, *Mycosphaerella sensu stricto* is characterised by small, spherical, ostiolate, pseudothecial ascomata, 8-spored, bitunicate asci without filamentous paraphyses and 2-celled, hyaline ascospores without appendages (von Arx 1983; Crous et al. 2000; 2007a). The spermatial state of *Mycosphaerella* species is widely accepted to reside in *Asteromella* (von Arx 1983; Crous and Wingfield 1996; Verkley et al. 2004).

Braun (1990) showed that anamorph characters should be used for generic separation within *Mycosphaerella*. This concept was supported by Crous (1998) who evaluated morphological features of *Mycosphaerella* spp. occurring on *Eucalyptus* trees using multiple correspondence analysis (MCA) with their anamorph associations. Accordingly, and supporting the evidence of Braun (1990), species of *Mycosphaerella sensu lato* should be separated into groups reflecting this fact. Crous et al. (2000) recognised 23 anamorph genera for *Mycosphaerella sensu lato,* and separated them based on characters of the mycelium (presence or absence of superficial mycelium), conidiophores (arrangement, branching and pigmentation), conidiogenous cells (placement, proliferation and scar type) and conidia (formation, shape, septation, wall and pigmentation).

Recent studies employing DNA sequence data for the large subunit (LSU) region of the rRNA operon have shown that *Mycosphaerella* is polyphyletic (Crous et al. 2007a; 2009a). From these studies, it became clear that many species accommodated in *Mycosphaerella sensu lato* should reside in the closely related genus *Teratosphaeria*. In addition to sequence data and despite conserved teleomorph morphology, Crous et al. (2007a) were able to identify phylogenetically informative morphological characters which supported the accommodation of various *Mycosphaerella* species in *Teratosphaeria*. These morphological characters for species of *Teratosphaeria* include the presence of superficial stroma linking adjacent ascomata, ascospores that become brown and verruculose in asci, the presence of pseudoparaphysoidal remnants, mucous sheaths surrounding ascospores, multi-layered ascal endotunica, well-developed ostiolar periphyses and different anamorph genera (Crous et al. 2007a).

Several genera have been separated from *Ramularia* (with *Mycosphaerella sensu stricto* teleomorphs; *Mycosphaerellaceae*). These include *Cladosporium* (with *Davidiella* teleomorphs; *Davidiellaceae*) (Braun et al. 2003; Schoch et al. 2006; Schubert et al. 2007; Bensch et al. 2010), *Polytrincium* (with *Cymadothea* teleomorphs) (Simon et al. 2009), *Dissoconium, Ramichloridium* (*Dissoconiaceae*; Crous et al. 2009a), *Cercospora, Cercosporella, Dothistroma* (*Eruptio* teleomorphs), *Lecanosticta, Miuraea, Passalora, Periconiella, Phaeophleospora, Phloeospora, Pseudocercospora*, *Pseudocercosporella, Ramulispora, Rasutoria, Septoria, Sonderhenia, Trochophora, Verrucisporota* and *Zasmidium* (Crous et al. 2009a; b).

Like *Mycosphaerella*, the *Teratosphaeria* complex (*Teratosphaeriaceae*; Crous et al. 2007a; 2009a; b) is far from completely resolved, but several different genera are recognised in the family. These include *Batcheloromyces*, *Baudoinea, Capnobotryella, Catenulostroma, Davisoniella, Devriesia, Hortea*, *Penidiella, Phaeothecoidea, Pseudotaeniolina*, *Readeriella, Staninwardia* and *Stenella* (Crous et al. 2009a).

Sphaerulina is also considered to be closely related to *Mycosphaerella* (von Arx 1983). Although *Sphaerulina* is polyphyletic (Crous et al. 2003), Crous et al. (2011) showed that the type species, *S. myriadea*, represents a distinct lineage in the *Mycosphaerellaceae*.

Comparison of Mycosphaerella and Teratosphaeria diseases

In the past, *Mycosphaerella* spp. occurring on *Eucalyptus* have been broadly treated using the common name Mycosphaerella Leaf Disease (MLD) or Mycosphaerella Leaf Blotch (MLB). More than 150 species of *Mycosphaerella* and *Teratosphaeria* (including their anamorphs) are now recognised as causing or being associated with leaf and stem diseases on *Eucalyptus* spp. (Andjic et al. 2007; 2010; Crous 1998; Crous et al. 2004; 2006; 2007a; 2009a; b; Burgess et al. 2007a; b; Carnegie et al. 2007; Cheewangkoon et al. 2008; 2009; Carnegie et al. 2011). *Mycosphaerella* and *Teratosphaeria* species have been identified from both natural *Eucalyptus* stands and commercial *Eucalyptus* plantations, where they cause a range of symptoms including leaf spots, leaf blotch, twig and stem cankers, premature defoliation, multi-leadered stems, seedling blight and, in severe cases death of young trees (Park and Keane 1982b; Crous 1998; Park et al. 2000; Old et al. 2003). *Eucalyptus* spp. are generally more susceptible to infection by *Mycosphaerella* and *Teratosphaeria* species during their juvenile leaf phase and the leaf infections caused by these fungi reduce the photosynthetic capacity, leading to premature defoliation and stunting of growth (Park and Keane 1982b; Lundquist and Purnell 1987; Carnegie and Ades 2003; Milgate et al. 2005b; Pinkard and Mohammed 2006).

The most common symptom of *Mycosphaerella* or *Teratosphaeria* infection is the development of leaf lesions (Fig. 1, 2). Leaf lesions may vary in shape from circular to irregular (*T. cryptica*, *T. molleriana*, *T. ovata, T. parkii*) (Dick 1982; Crous et al. 1993b; Crous and Alfenas 1995; Crous et al. 1988; Carnegie and Keane 1998;

Maxwell et al. 2003; Crous et al. 2009a), irregular (*T. nubilosa*) (Dick 1982), small and discrete (*M. heimii*) (Crous and Swart 1995), sub-circular to irregular (*T. suttonii*) (Crous and Wingfield 1997b), sub-circular (*T. aurantia*, *M. irregulariramosa*) (Crous and Wingfield 1997b; Maxwell et al. 2003), sub-circular to confluent to angular (*Pseudocercospora eucalyptorum*) (Crous et al. 1989d) and leaf spots may be absent (*M. heimioides*) (Crous and Wingfield 1997b; Crous 1998).

Leaf spots caused by *Mycosphaerella* and *Teratosphaeria* species can vary in colour on leaf surfaces. Leaf spots can be brown (*T. ambiphylla*) (Maxwell et al. 2003), dark brown and corky with a yellow-red margin (*T. suberosa*) (Dick and Dobbie 2001), yellow to brown (*T. nubilosa*) (Crous et al. 1989a; Crous 1998), grey to pale brown (*M. tasmaniensis, P. eucalyptorum*) (Crous et al. 1989a; 1998), pale brown to red-brown [*T. molleriana* (as *M. vespa*)] (Carnegie and Keane 1998), dark purple to black (*T. ovata*) (Crous et al. 1988; Crous et al. 1989a), pale brown surrounded by a red-purple margin (*T. suttonii*) (Crous and Wingfield 1997b) rust-brown (*M. intermedia*) (Dick and Dobbie 2001) or brown with strands of red-brown, spreading hyphae (*T. fimbriata*) (Crous et al. 2007a).

Distinct lesion margins and zones of various colours can also be found. For example, lesions of *M. intermedia* have raised dark brown margins that are surrounded by a red-purple zone (Dick and Dobbie 2001). Lesions caused by *T. eucalypti* (*Kirramyces eucalypti*) are carmine red with yellow margins that become necrotic with red-purple margins while *T. destructans* produces lesions with red-brown margins (Wingfield et al. 1996a; Crous and Wingfield 1997b; Andjic et al. 2007). Lesions caused by *T. suttonii* are surrounded by a distinct purple discolouration (Crous et al. 1989a) while lesions resulting from infection by *T. ambiphylla* are known to be suberised with red margins (Maxwell et al. 2003) and lesions caused by *T. suberosa* are surrounded by red-purple borders (Crous et al. 1993a).

Lesion colour may also vary for a single species of *Teratosphaeria* or *Mycosphaerella* depending on the *Eucalyptus* host. For example, *T. cryptica* causes pale brown to grey-yellow lesions on *E. globulus* and *E. saligna*, but red-brown to grey-brown spots on *E. obliqua* and *E. pilularis*. *Mycosphaerella marksii* causes yellow-brown spots on *E. saligna* and *E. botryoides* but they are red-brown on *E. pilularis*.

Although *Mycosphaerella* and *Teratosphaeria* species produce similar leaf spot symptoms as mentioned above, species of *Teratosphaeria* are associated with subtle yet important differences in disease symptoms when compared to *Mycosphaerella* spp. For example, in addition to leaves, *T. cryptica* can also infect young twigs and stems of *Eucalyptus* species such as *E. obliqua* and *E. globulus* subsp. *globulus* resulting in characteristic cankers (Marks et al. 1982; Park and Keane 1982b; Dick and Gadgil 1983). The development of cankers after infection is also observed for *T. gauchensis* and *T. zuluensis* (Crous et al. 2009a). *T. gauchensis* produces dark brown circular to irregular lesions with red-brown borders on tree trunks and black circular to irregular lesions on *Eucalyptus* twigs (Cortinas et al. 2006c), while *T. zuluensis* initially produces small necrotic lesions which coalesce as they mature to produce larger necrotic swollen cankers producing copious amounts of kino (Wingfield et al. 1996b). Such cankers eventually lead to stem or twig girdling, die-back of young stems, thinning of crowns, tree malformation and in severe cases death of tree tops or entire trees (Cortinas et al. 2006b; c).

Leaf lesions caused by certain species of *Teratosphaeria* can be typical for this genus and different to those observed for *Mycosphaerella* species. Because *T. cryptica* generally infects young expanding leaves, it often causes the leaf lamina to become crinkled and contorted, resulting in a convoluted appearance commonly referred to as "crinkle leaf disease" (Marks et al. 1982; Park and Keane 1982b), while *T. nubilosa* infection is generally characterised by the appearance of leaf blotches (also sometimes referred to as blight) on *Eucalyptus* leaves (Park and Keane 1982a; Park 1988). These species invade large areas of leaf tissue biotrophically before causing death of the area of invaded tissue. Such leaf blotches are a result of several individual *T. nubilosa* lesions that coalesce to form larger spreading blotches over the leaf surface (Perez et al. 2010a). Species of *Teratosphaeria* with *Kirramyces* anamorphs such as *T. destructans*, *T. viscidus* and *T. pseudoeucalypti* are associated with severe blighting of *Eucalyptus* leaves and shoots (Old et al. 2003; Andjic et al. 2007; 2010). In these instances, large areas of the leaf lamina can become blighted and or distorted (Wingfield et al. 1996a; Burgess et al. 2007b; Andjic et al. 2007).

A further character distinguishing infections caused by *Mycosphaerella* spp. and *Teratosphaeria* spp. is that *Mycosphaerella* spp. generally tend to produce smaller and more distinct leaf spots. For example, *Mycosphaerella marksii* produces pale brown circular-irregular amphigenous lesions 3–20 mm diam with a grey adaxial leaf surface, and a yellow to red-brown abaxial leaf surface (Carnegie and Keane 1994; Crous and Wingfield 1996). *Mycosphaerella irregulariramosa* produces amphigenous, subcircular, grey to pale brown lesions 3–15 mm diameter (Crous and Wingfield 1997b). In some instances, leaf spots may appear to be absent with only the presence of pseudothecia as is the case with *Mycosphaerella heimioides* (Crous and Wingfield 1997b). Interestingly, even though species of *Mycosphaerella* produce diverse symptoms on *Eucalyptus*, as yet, no species of *Mycosphaerella* has been reported causing significant damage in plantations or native forests.

The fact that two related but different groups of fungi cause leaf diseases on *Eucalyptus* can result in confusion. This confusion is clearly enhanced by the use of misleading common names. The same fungi can cause different symptoms on different species of *Eucalyptus* and this compounds the problem, which will likely also further increase as new eucalypt hybrids and genetically modified *Eucalyptus* trees emerge in plantations. For this reason, we wish to emphasise the different *Eucalyptus* disease symptoms caused by species of *Mycosphaerella* and *Teratosphaeria*, and to ensure that these differences do not cause confusion. We thus recommend that the common names '*Mycosphaerella* Diseases' and '*Teratosphaeria* Diseases' of *Eucalyptus* are used to define two different groups that have previously been broadly referred to as 'Mycosphaerella Leaf Diseases'.

Geographic Distribution

The known geographic distribution of species of *Mycosphaerella* and *Teratosphaeria* causing diseases of *Eucalyptus* has grown steadily and this trend is likely to continue. These *Eucalyptus* leaf diseases can now be found in virtually all areas where *Eucalyptus* species are grown as non-natives in commercially managed plantations (Table 2). As *Eucalyptus* plantation areas are increased globally to meet the increasing demand for paper and pulp, there will most likely be an increase in the distribution of the *Mycosphaerella* and *Teratosphaeria* spp. causing disease (Wingfield et al. 2008). Because plantations represent large areas of relatively uniform genetic material, they act as magnets for pathogens that are not known in their areas of origin (Wingfield et al. 2010). Hence there will likely be an increase in the number of new *Mycosphaerella* and *Teratosphaeria* taxa being discovered on *Eucalyptus*.

Within Australia

As the overwhelming majority of *Eucalyptus* spp. are endemic to Australia (Poynton 1979) it has been hypothesised that Australia is the centre of origin for most species of *Mycosphaerella* and *Teratosphaeria* occurring as specialised parasites on *Eucalyptus*. Early studies on Mycosphaerella leaf diseases (including those now known to be caused by *Teratosphaeria* spp.) treated collections only from Victoria and New South Wales (Park and Keane 1982a; b). Subsequent to these investigations, studies have reported outbreaks of these fungi from all Australian states including Western Australia (Carnegie et al. 1997; Maxwell et al. 2001; 2003, Jackson et al. 2005; 2008), New South Wales (Summerell et al. 2006; Carnegie 2007a; b; Crous et al. 2007b; Carnegie et al. 2011), South Australia (Park and Keane 1984; Barber et al. 2008), Tasmania (Dungey et al. 1997; Crous et al. 1998; Milgate et al. 2001; Crous et al. 2007b; Smith et al. 2007), Victoria (Carnegie et al. 1994; 1998; Carnegie and Ades 2005) Queensland (Andjic et al. 2007; 2010; Crous et al. 2007b; Carnegie et al. 2011) and offshore islands in the Northern Territory (Burgess et al. 2007b). In the temperate regions of Australia, the most damaging outbreaks have been in Victoria and Tasmania, where *E. globulus*, highly susceptible to *T. nubilosa* and *T. cryptica*, is grown. Outbreaks are not common on *E. globulus* in areas where this species is planted in a more Mediterranean climate (e.g. Western Australia).

In the tropics and subtropics of Australia, species of *Teratosphaeria* with *Kirramyces* anamorphs, e.g. *T. epicoccoides*, *T. pseudoeucalypti* and *T. viscidus*, are the most damaging in *Eucalyptus* plantations (Carnegie 2007b; Andjic et al. 2010a). These species have caused extensive damage in *E. grandis* and *E. grandis* × *E. camaldulensis* plantations, resulting in plantation failure in severe cases, such as occurred to 26 000 ha of *E. grandis* × *E. camaldulensis* in central Queensland (Elders 2010). *T. cryptica* can be damaging to highly susceptible species such as *E. tereticornis* and *E. camaldulensis*, and severe disease is one reason why these species are no longer planted extensively in Queensland (Pegg et al. 2003; Carnegie et al. 2011). *E. globulus* and *E. nitens* are not key plantation species in the tropics and subtropics, and hence *T. cryptica* and *T. nubilosa* (the most damaging species on these hosts) are not key pathogens. This is in comparison to temperate areas in Australia (and worldwide) where *E. globulus* and *E. nitens* predominate and *T. cryptica* and *T. nubilosa* are important pathogens.

Carnegie et al. (2011) identified 28 species of *Teratosphaeria* and *Mycosphaerella* (including *Pseudocercospora* and *Sonderhenia*) from *Eucalyptus* plantations and native forests in New South Wales and Queensland (eastern Australia) based on surveys and published records. *T. cryptica* was by far the most commonly recorded species, being found on at least 30 host species from southern New South Wales to far north Queensland. *M. marksii* was the second most commonly recorded, on 15 hosts from southern NSW to far north Queensland, while *T. nubilosa* had a wide distribution, but restricted host range. *Sonderhenia swartii* is also a common species in Australia with a wide host range (Park and Keane1984; Park et al. 2000), but similar to *M. marksii*, is not considered an important pathogen. Jackson et al. (2008) conducted surveys within a genetics trial in Western Australia and identified 11 *Mycosphaerella* and *Teratosphaeria* species, two (*Pseudocercospora fori*, *M. ellipsoidea*) of which were new records for Australia and two (*M. tasmaniensis*, *M. sutonii*) were new records for Western Australia. Undoubtedly more *Mycosphaerella* and *Teratosphaeria* species will be identified from Australia in the future as additional surveys are undertaken.

In exotic plantations

In New Zealand, where eucalypts are not indigenous, *T. cryptica* was first reported (as *M. nubilosa*) on *E. delegatensis* saplings by Weston (1957) and recorded by Gilmour (1966) as being very common on trees grown in humid conditions. Both *T. cryptica* and *T. nubilosa* are thought to have been present in New Zealand for some time prior to being recognized, becoming prominent during the 1960s when eucalypts were first used in forestry plantations (M. Dick, unpub. data). In 1974, *T. cryptica* reached epidemic proportions in commercial eucalypt plantations (Beresford 1978) and continued to cause epidemics in those forests for many years, affecting over 1000 ha in the Central North Island (Cheah 1977). The most damaging outbreaks, caused by *T. cryptica*, have occurred in highly susceptible species such as *E. delegatensis* and *E. regnans*. *T. eucalypti* has also been associated with severe leaf damage and significant defoliation in *E. nitens* plantations in New Zealand (Gadgil and Dick 1983; Hood et al. 2002; Hood and Alexander 2006).

Large commercial *Eucalyptus* plantations constitute the forestry belt of eastern South Africa, with approximately 565 000 ha planted by 2005, over half of which is *E. nitens* (Rockwood et al. 2008). Commercial *Eucalyptus* forestry has also become important in several other African countries, where *E. globulus* is commonly a dominant species. Several *Mycosphaerella* and *Teratosphaeria* species have been identified in South Africa and can now be found in Kwa-Zulu Natal, Eastern Cape, Mpumalanga and the Limpopo provinces (Crous and Wingfield 1996; Crous 1998; Crous et al. 2004; Hunter et al. 2004a; b). Surveys conducted in other African countries, including Madagascar, Malawi, Mozambique, Tanzania, Kenya, Ethiopia and Zambia, have also revealed species of *Mycosphaerella* and *Teratosphaeria* in *Eucalyptus* plantations (Crous and Swart 1995; Crous 1998; Crous et al. 2004; 2006; Roux et al. 2005; Hunter et al. 2008; Gezahgne et al. 2006). In South Africa, *E. nitens* is the main species affected by leaf diseases caused by *Teratosphaeria* spp., which is different to other African countries where *E. globulus* is the most susceptible species. *T. nubilosa* is the most damaging species on these two hosts. *Teratosphaeria zuluensis* causes a severe canker disease on *E. grandis* clones in South Africa and on *E. camaldulensis* in Ethiopia (Wingfield et al. 1996b; Gezahgne et al. 2003; Cortinas et al. 2010).

Commercial *Eucalyptus* forestry is increasing in European countries with favourable climates. There have consequently also been recent reports of *Mycosphaerella* and *Teratosphaeria* species on *Eucalyptus* in Europe. Early surveys in Europe, especially in Portugal and Spain where *E. globulus* is widely planted, noted the occurrence of *T. nubilosa* in the North West of Spain and the North and South of Portugal (Crous and Wingfield 1997a; Crous et al. 2004; 2006; Hunter et al. 2008). More recent surveys have revealed many more species of *Mycosphaerella* and *Teratosphaeria* and reported significant damage caused by these pathogens in *E. globulus* plantations in both Portugal (Silva et al. 2008; 2009) and Spain (Otero et al. 2007a; b; Tejedor 2007). In these countries *T. nubilosa* has been the predominant species associated with severe damage (Otero et al. 2007a; b). Other European countries where species of *Mycosphaerella* and *Teratosphaeria* have been identified on *Eucalyptus* include Italy and France (Crous et al. 2007b).

South America has some of the largest commercial *Eucalyptus* plantations, utilised for paper and pulp production, with over 3.7 million ha in Brazil, Chile and Argentina alone (Rockwood et al. 2008). Consequently there have also been many *Mycosphaerella* and *Teratosphaeria* species identified from several countries in South

America including Brazil, Colombia, Chile, Mexico, Uruguay and Venezuela (Crous et al. 1993a; b; 2007a; b; Wingfield et al. 1995; Crous 1998; Cortinas et al. 2006c; Perez et al. 2009; Perez et al. 2009; Perez et al. 2010b).

Eucalyptus planting in Asia has expanded substantially in recent years with over 750 000 ha being planted (Old et al. 2003; Rockwood et al. 2008), mostly in the past decade. Recent surveys conducted in Asia have shown that diseases caused by *Teratosphaeria* spp. are common in the area (Old et al. 2003; Zhou et al. 2008; Zhou and Wingfield 2011). These fungi have been reported from China, Indonesia, India, Thailand and Vietnam (Crous and Alfenas 1995; Crous and Wingfield 1997b; Burgess et al. 2006; Crous et al. 2006; Cortinas et al. 2006b; Burgess et al. 2007; Cheewangkoon et al. 2008). While there are various species of *Teratosphaeria* and *Mycosphaerella* causing mainly leaf spot symptoms in these countries, *Teratosphaeria destructans* (Wingfield et al. 1996a) is by far the most important and damaging (Andjic et al. 2011).

In summary, *T. nubilosa* and *T. cryptica* are the most destructive foliar pathogens on *E. nitens* and *E. globulus* planted in temperate climatic zones, while *T. destructans*, *T. pseudoeucalypti* and *T. viscidus* are the most destructive on *E. grandis* and its hybrids in the tropics and subtropics. Furthermore, in the tropics and subtropics *T. zuluensis* causes a major stem disease on *E. grandis*, *E. camaldulensis, E. urophylla* and their hybrids, while in temperate areas, there appears to be no corresponding pathogen-host relationship for stem fungi. Therefore, to avoid large outbreaks, specific site matching should consider the *Eucalyptus* spp. being planted and the dominant *Teratosphaeria* spp. present in that particular climatic zone.

DNA-based techniques for identification

The use of DNA sequence data for taxonomic studies on *Mycosphaerella* and *Teratosphaeria* species infecting *Eucalyptus* is now standard practice. The first studies investigating *Mycosphaerella* species associated with MLD targeted the Internal Transcribed Spacer (ITS) region of the rRNA operon (Crous et al. 1999). These early studies were largely used for species identification and early elucidation of generic concepts for *Mycosphaerella*. However, as more strains of *Mycosphaerella* and *Teratosphaeria* were sequenced, it became evident that certain deeper nodes within the ITS phylogenies were not supported and terminal species complexes proved difficult to resolve (Crous et al. 2000; 2001). Subsequent studies, therefore, used multi-gene loci to investigate generic concepts in *Mycosphaerella* and *Teratosphaeria*. Here, DNA sequence data from more conserved gene regions such as the LSU were used to provide support for deeper nodes and to circumscribe genera within the *Mycosphaerellaceae* and *Teratosphaeriaceae*. More variable and more rapidly evolving nuclear and protein coding gene regions such as actin (ACT), β-tubulin (Bt), calmodulin (CAL) and translation elongation factor 1-alpha (EF1-α) have been used to resolve species complexes (Crous et al. 2004; Hunter et al. 2006b; Crous et al. 2007a, Andjic et al. 2010a). Currently, DNA sequences for several gene regions are used simultaneously in order to produce multi-gene phylogenies of *Mycosphaerellaceae* and *Teratosphaeriaceae*.

Generation of large DNA sequence datasets, predominantly of ITS sequences, have made many sequence targets available for species-specific priming. Likewise, by developing species-specific primers, researchers have been able to effectively identify specific *Mycosphaerella* and *Teratosphaeria* species on *Eucalyptus* (Table 1).

Kularatne et al. (2004) developed species-specific primers for *T. nubilosa* and, by employing restriction endonucleases in combination with specific primers, were able to distinguish between *T. nubilosa*, *T. cryptica*, *M. tasmaniensis* and *M. vespa* through PCR-based Restriction Fragment Length Polymorphisms (RFLP). Maxwell et al. (2005) also targeted the ITS regions, producing species-specific primers to differentiate between *T. cryptica*, *D. dekkeri* (as *M. lateralis*), *M. marksii*, *T. nubilosa* and *T. parva*. Later, Glen et al. (2007) used a nested PCR approach to accurately identify several *Mycosphaerella* and *Teratosphaeria* species from diseased *Eucalyptus* leaf material, thereby considerably facilitating species identification.

Population biology of *Mycosphaerella* and *Teratosphaeria* species

Many *Mycosphaerella* and *Teratosphaeria* species are important pathogens of economically relevant agronomic crops. In the past, most studies of *Mycosphaerella* spp. have focussed on their taxonomy, phylogeny, epidemiology and host associations. Recently, however, the population biology of fungal pathogens, including *Mycosphaerella* spp., has promoted an understanding of the population structure of many important pathogens (McDonald 1997; Hayden et al. 2003a; b; Zhan et al. 2003; Hunter et al. 2008; Perez et al. 2010a). Extensive research into the population biology of several other *Mycosphaerella* spp. such as *Zymoseptoria tritici* (as *Mycosphaerella graminicola*) (Linde et al. 2002; Zhan et al. 2003; Quaedvlieg et al. 2011), *Pseudocercospora fijiensis* (as *Mycosphaerella fijiensis*) (Carlier et al. 1996; Hayden et al. 2003a) and *M. musicola* (Hayden et al. 2003b) have been published in recent years. Results of these studies have led to an increased understanding of the population structure, distribution of genetic diversity, gene flow, centres of origin and mating strategies of *Mycosphaerella* spp. Limited population biology research has, however, been conducted on *Mycosphaerella* and *Teratosphaeria* species occurring on *Eucalyptus*. Thus, knowledge of the population biology of other *Mycosphaerella* pathosystems provides a better understanding that can be used for future population biology studies of *Mycosphaerella* and *Teratosphaeria* species occurring on these trees.

In contrast to species causing disease of agronomic crops, relatively few studies have been undertaken to consider the centres of origin of *Mycosphaerella* or *Teratosphaeria* species on *Eucalyptus*. For example, putative centres of origin have been determined for certain *Mycosphaerella* spp. such as *P. fijiensis* and *Z. tritici*, which are well-characterised pathogens of banana and wheat, respectively. Carlier et al. (1996) determined that populations of *P. fijiensis* from South East Asia had greater allelic and gene diversity than *P. fijiensis* populations from Africa, the Pacific Islands and Latin America. Here, more than 88 % of the alleles detected in the African, Pacific Islands and Latin American populations were also found in the South East Asian *P. fijiensis* population, indicating that South East Asia is most likely the centre of origin of the species. Zhan et al. (2003) investigated the global structure of the wheat pathogen *Z. tritici* by employing data generated from genomic RFLPs and found that populations of the pathogen from the Middle East (Israel and Syria) exhibited higher gene diversity values than populations from America, Australia, Europe or North America. It was, therefore, suggested that *Z. tritici* originates from the Middle East where wheat was also first domesticated (Zhan et al. 2003).

One *Eucalyptus* pathogen that has been intensively studied in terms of its origin is *T. nubilosa*. Hunter et al. (2008) used allele size data from 10 microsatellite markers to show that a population of *T. nubilosa* from eastern

Australia exhibited a higher gene diversity (0.506) and genotypic diversity (76%) than *T. nubilosa* populations from Western Australia and South Africa. This therefore indicated that eastern Australia was most likely the centre of origin for *T. nubilosa*. More recently, Perez et al. (2009; 2010b) has shown that the first outbreak of this pathogen in South America, devastating *E. globulus* in Uruguay and southern Brazil, most likely originated in Spain. The Spanish population has been shown by Hunter et al. (2008) to have originated in South Africa.

The severe damage that *T. zuluensis* and *T. gauchensis* cause to *Eucalyptus* stems, has led to studies to consider the origin of these pathogens. Cortinas et al. (2010) used 11 polymorphic microsatellite markers to examine the genetic diversity of *T. zuluensis* populations from South Africa, Malawi and China and they were able to show that *T. zuluensis* is not native to South Africa as had been previously suggested (Wingfield et al. 1996b). More interesting is the fact that *T. zuluensis* in South Africa, Malawi and China appear to be separate, distinctly evolving populations that have most probably arisen from separate introductions from other source populations. A recent study by Chen et al. (2011) has shown that *T. zuluensis* is genetically diverse in China but this could have arisen due to multiple introductions of the pathogen. Thus the centre of origin of *T. zuluensis* remains uncertain, even though it is not known in Australia, it could have originated there.

Teratosphaeria destructans is sufficiently damaging that studies have begun to consider its possible origin. Initially identified from Northern Sumatra in 1996 (Wingfield et al. 1996a), *T. destructans* has subsequently been found in other South East Asian countries including Thailand, China, Timor, Vietnam and Indonesia. Early hypotheses suggested Indonesia or Australia would be the center of origin for *T. destructans* (Wingfield et al. 1996a). Subsequent studies investigating nucleotide diversity for several genomic loci have found limited diversity, and instead, have relied on microsatellite markers to identify several haplotypes of *T. destructans* from Indonesia while identifying only a single haplotype in the rest of Asia (Andjic et al. 2011). Interestingly, Burgess et al. (2007b) identified *T. destructans* in Australia and showed Australian isolates to be genetically related to those from Asia, suggesting endemism of *T. destructans* in Australia. Future studies incorporating results from more variable genetic markers and larger populations of *T. destructans* from its entire geographic range will undoubtedly clarify the centre of origin of this important *Eucalyptus* pathogen.

Host shifts

For many years, species of *Mycosphaerella* have been thought to represent exclusively host-specific taxa. However, increased sampling has shown that many species of *Mycosphaerella* can be found on a wide range of different host plants. The ability of some *Mycosphaerella* spp. to infect several hosts has been referred to as the "pogo-stick" hypothesis (Crous and Groenewald 2005). This hypothesis suggests that species of *Mycosphaerella* are able to infect alternative hosts on which infection occurs at low levels but provides inoculum for dispersal to their natural host (Crous and Groenewald 2005).

Host shifts are now recognised as important in tree pathogens (Slippers et al. 2005) and also in several *Mycosphaerella* and *Teratosphaeria* species infecting *Eucalyptus*. Several species of *Mycosphaerella* previously thought to be specific to *Eucalyptus* have been identified from other hosts. For example, *Dissoconium commune*, a common species originally identified from *Eucalyptus globulus* in Spain, is now also known to infect *Protea* *magnifica* in Australia and other *Eucalyptus* spp. such as *E. nitens* (South Africa) and *E. globulus* (New Zealand) (Crous et al. 2004). *Mycosphaerella konae* was known only from Hawaii where it infects species of *Banksia* and *Leucospermum*, but has recently been identified from leaves of *E. camaldulensis* in Thailand (Crous et al. 2007b). *Mycosphaerella holualoana* was originally described from leaf spots of *Leucospermum* sp. in Hawaii (Taylor et al. 2001), and has recently been isolated from dead leaves of *Hedychium coronarium* in Hawaii (Crous et al. 2011d). One of the most cosmopolitan *Mycosphaerella* spp. found on *Eucalyptus* is *M. marksii,* which is known from several *Eucalyptus* spp. and different countries. This species is also known to infect *Leucadendron tinctum* (Crous et al. 2008), and is common on *Syncarpia glomulifera* (Myrtaceae) in native forests in eastern Australia (Carnegie 2007a), where it can be intermixed with *E. pilularis* also infected with *M. marksii*. *Mycosphaerella acaciigena* and *M. thailandica* were originally described from leaves of *Acacia mangium* and more recently they have been identified causing lesions on species of *Eucalyptus* species and *Eucalyptus* hybrids (Crous et al. 2007b).

Several species of *Teratosphaeria* are also known to infect various hosts. *Teratosphaeria associata*, originally described from leaves of *Corymbia henryii* in Australia and also known from *C. variegata* and *E. dunnii* has recently been reported from *Protea lepidocarpodendron* (Crous et al. 2007b; 2008). Furthermore, the well-known *Teratosphaeria parva*, a cosmopolitan species on various species of *Eucalyptus* has now been identified from *Protea repens* and *P. nitida* in South Africa (Crous et al. 2007b). *Readeriella minutispora,* originally described from leaves of *Corymbia henryii* in Australia, was subsequently identified from a *Cussonia* sp. in South Africa (Crous et al. 2007b).

The ability of *Mycosphaerella* and *Teratosphaeria* species to infect other hosts is a cause for concern. This is especially true when one considers the ability of these pathogens to infect hosts from different plant orders such as *Myrtales*, *Proteales*, *Fabales* and *Apiales* and different families such as *Myrtaceae* (*Corymbia* spp., *Eucalyptus* spp., *Syncarpia* spp.), *Proteaceae* (*Protea* spp., *Banksia* spp., *Leucospermum* spp., *Leucadendron* spp.), *Fabaceae* (*Acacia* spp.) and *Araliaceae* (*Cussonia* spp.). New records of *Mycosphaerella* and *Teratosphaeria* species occurring in new areas are increasing, indicating that the geographic distribution of many species is significantly larger than previously thought. The apparent ease with which these fungi move between hosts is of concern not only to commercial forestry companies but also in agronomic crops. Quarantine and management strategies for *Mycosphaerella* and *Teratosphaeria* species will, therefore, become increasingly important in the future.

Control and Quarantine

Several authors have discussed management options for those species of *Mycosphaerella* and *Teratosphaeria* causing important diseases of *Eucalyptus* plantations and nurseries (Brown and Ferreira 2000; Gadgil et al. 2000; Old et al. 2003; Carnegie 2007b). These options focus on quarantine, genetic manipulation (tree improvement), site-risk mapping, increasing tree tolerance and recovery as well as chemical control in nurseries. Some of the challenges of disease management in plantations include the large and often disparate areas of plantation where regular surveys and monitoring is difficult, long rotations (5–15 years for pulp and fibre, 15–25 years for solid wood and sawn timber) and a relatively low return on investment.

The movement and spread of fungal pathogens is of primary importance when considering management strategies for their control. This is particularly true for the many species of *Mycosphaerella* and *Teratosphaeria* known to be important pathogens of economically important crop plants. *Mycosphaerella* and *Teratosphaeria* species can be spread to new areas in several ways and thus initiate new epidemics in native and exotic environments. Infected seed or asymptomatic nursery stock may serve as vehicles for the movement of *Mycosphaerella* and *Teratosphaeria* species into non-native environments as has been shown for species of *Mycosphaerella* and *Teratosphaeria* that have been moved from eastern Australia into Western Australia (Maxwell et al. 2003; Jackson et al. 2008). The rapid movement of *T. destructans* throughout South East Asia is ascribed to the movement of infected germplasm (Adjic et al. 2011). Seed that is transferred between countries should thus be tested for pathogen propagules (Boeger et al. 1993). The movement of seed has also been suggested as the possible means by which *T. zuluensis* has moved between countries and around the world where *Eucalyptus* spp. are commercially grown (Cortinas et al. 2006c). Infected seed could also be tested for the presence of *Mycosphaerella* and *Teratosphaeria* species by using species-specific primers that have been developed for several *Mycosphaerella* and *Teratosphaeria* species that infect *Eucalyptus* (Kularatne et al. 2004; Maxwell et al. 2005).

Natural host resistance or tolerance to pathogen infection provides one of the most commonly used means to reduce damage to *Eucalyptus* by species of *Mycosphaerella* and *Teratosphaeria*. Numerous studies have reported wide variation in susceptibility to these pathogens amongst *Eucalyptus* species, provenances and families (Carnegie and Ades 2005; Carnegie et al. 1994; 1998; 2004; Dungey et al. 1997; Hood et al. 2002; Milgate et al. 2005a; Purnell and Lundquist 1986). Thus, *E. globulus* has been replaced with *E. nitens* in high-risk areas in Tasmania, Australia to reduce the impact of MLD (Mohammed et al. 2003). Likewise, *E. nitens* has replaced *E. globulus* in South Africa (Lundquist and Purnell 1987) to avoid damage due to *T. nubilosa*.

Selected hybrids between tree species are known to be more resistant to certain *Mycosphaerella* and *Teratosphaeria* species. Hybrid poplars have for example been used to reduce the impact of *M. populorum* (anamorph: *Septoria musiva*), the causal agent of leaf spot and cankers of various *Populus* spp. (Feau et al. 2005). Likewise, hybrids have been important in reducing the impact of stem canker caused by *T. zuluensis* in South Africa (Wingfield, unpublished). However, clones derived from hybridisation can differ markedly in their resistance to disease. Thus substantial effort must be expended to select appropriate hybrids for planting.

Considering Australia is the origin of most *Eucalyptus* spp. and most likely the centre of diversity for *Mycosphaerella* and *Teratosphaeria* species that occur on these trees, co-evolution between these fungi and their hosts is expected. Therefore, resistant *Eucalyptus* spp. can be sourced from Australia to reduce the impact caused by *Mycosphaerella* and *Teratosphaeria* species. In many countries where *Eucalyptus* spp. have been grown as exotics, natural hybridisation has occurred between species and this has led to the emergence of land races from which resistance to species of *Mycosphaerella* and *Teratosphaeria* can be found (Wingfield et al. 2001; 2008).

The movement of infected *Eucalyptus* plant material between countries and continents appears to be increasing (Wingfield et al. 2001; 2008). There is good evidence that this is leading to the emergence of many fungal pathogens of *Eucalyptus* in new environments (Wingfield 1999; Wingfield et al. 2008, Andjic et al. 2011). Through human mediated dispersal, propagules of *Mycosphaerella* and *Teratosphaeria* species will most likely increasingly be transferred within and between countries and continents. Quarantine measures should consequently be strictly implemented and updated to reduce the risk of fungal pathogens being introduced into non-native environments.

Future prospects

Phylogenetic studies based on DNA sequence data from several gene regions have shown a very large group of *Eucalyptus* pathogens treated as *Mycosphaerella sensu lato* are now better placed in two distinct genera, namely *Mycosphaerella* and *Teratosphaeria* (Crous et al. 2007a). The most damaging *Eucalyptus* pathogens appear to be species of *Teratosphaeria* including *T. cryptica*, *T. nubilosa*, *T. destructans*, *T. pseudoeucalypti*, *T. gauchensis*, *T. viscidus* and *T. zuluensis* (Wingfield et al. 1996a; Crous 1998; Cortinas et al. 2006b; c; Andjic et al. 2007; Hunter et al. 2009; Andjic et al. 2010a). However, based on experience with other crops, those in *Mycosphaerella* occurring on *Eucalyptus* should not be ignored and they could become important in the future.

Accurate diagnosis of *Eucalyptus* diseases caused by species of *Teratosphaeria* is now possible due to advances in DNA-based molecular techniques such as PCR and DNA sequencing. In this regard, real-time amplification technologies offer an attractive method for *Mycosphaerella* and *Teratosphaeria* species identification. Extensive datasets of gene sequences from several loci have been generated for those species of *Mycosphaerella* and *Teratosphaeria* associated with *Eucalyptus* and these data can now be targeted for species identification. Species-specific oligonucleotides can easily be generated and combined with specific probes and several real-time techniques to be used in identification and quantification. This has already occurred for other "*Mycosphaerella"* pathogens such as *P. fijiensis*, *P. musicola* and *P. eumusae* on banana (Arzanlou et al. 2007) and *Z. tritici* on wheat (Gou et al. 2006; Abd-Elsalam et al. 2011). These techniques are geared to high-throughput, speed and accuracy, and can be used to detect the causal organism *in vitro* and to monitor disease progression as well as aid in disease forecasting for fungicide applications.

Very little is known regarding the population genetics of the most important *Teratosphaeria* species. This is in contrast to some of the *Mycosphaerella* pathogens on agricultural crops such as wheat (Zhan et al. 2003; Zhan and McDonald 2004). However, in recent years, several polymorphic markers have been developed for important *Teratosphaeria* spp. occurring on *Eucalyptus* such as *T. nubilosa* (Hunter et al. 2006a), *T. zuluensis* (Cortinas et al. 2006a) and *T. destructans* (Andjic et al. 2011). These markers have allowed for an increased understanding into the genetic diversities of some of the most important *Teratosphaeria* spp. causing disease on *Eucalyptus*. However, there are other important *Teratosphaeria* spp., such as *T. cryptica*, for which little is known regarding its population structure, although microsatellite primers have now been developed for *T. cryptica* (Taylor et al. 2011). It will be important to develop informative DNA-based molecular markers to further understand and elucidate the epidemiology of these pathogens on *Eucalyptus*.

Genome sequencing is rapidly becoming affordable for scientific investigations. This is also true for fungal pathogens of important crops where many genomes have already been sequenced, including species of *Mycosphaerella* and *Teratosphaeria* such as *Z. tritici* (*M. graminicola)* and *P. fijiensis*. Through the Mycosphaerella Genome Consortium several more *Mycosphaerella* and *Teratosphaeria* species including *T. nubilosa* will be sequenced in the near future. Once these data become available, researchers will be able to select phylogenetically informative markers that, in combination with existing markers or on their own, will increase genetic resolution for several complexes within *Mycosphaerella* and *Teratosphaeria*. These genomes will also make it possible to better understand many aspects of the pathogenicity of these fungi

Mycosphaerella and *Teratosphaeria* species are difficult to culture. It is not unreasonable to expect that there are at least as many *Mycosphaerella* and or *Teratosphaeria* species infecting *Eucalyptus* spp. as there are *Eucalyptus* species. Thus, there is still much to discover in terms of *Mycosphaerella* and *Teratosphaeria* biodiversity on *Eucalyptus*. Metagenomics provides a powerful approach to explore and catalogue the biodiversity of these species either on leaf material or in cankers on *Eucalyptus*. Specific universal loci such as the ITS region can be targeted and used in a metagenomics approach to isolate sequences that will further populate the *Mycosphaerella* and *Teratosphaeria* phylogeny. Although these novel sequences will not be linked back to specimens, researchers will gain an increased understanding of *Mycosphaerella* biodiversity, and undoubtedly new sequence types and or lineages within *Mycosphaerella* and *Teratosphaeria* will be identified.

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Table 1 Species-specific primers developed for selected species of *Mycosphaerella* and *Teratosphaeria*

Species	Primer name	Sequence (5'– 3')	Annealing Temp	Amplicon size (bp.)	Reference
Teratosphaeria cryptica	MCF	TTTTCCAACCATGTTGCC	45	267	Kularatne et al. 2004
	MCR	TGTAATGACGCTCGAACAG			
	MC2F	CCCGCCCGACCTCCAACC	58	-	Maxwell et al. 2005
	MC2R	CGGTCCCGGAAGCGAAACAG			
	McrypF	CATCTITGCGTCTGAGTGATAACG	-	331	Glen et al. 2007
	McrypR	GGGGGTIGACGGCGCGAC			
Teratosphaeria nubilosa	MNF	CGTCGGAGTAATACAACC	50	199	Kularatne et al. 2004
	MNR	AGGCTGGAGTGGTGAAATG			
	MN1F	GCGCCAGCCCGACCTCC	57	-	Maxwell et al. 2005
	MN1R	GGTCCCCGTCAGCGAAACAGT	56		
	MnubF	CAACCCCATGTTTTCCCACCACG	-	395	Glen et al. 2007
	MnubR	CGCCAGACCGGTCCCCGTC			
Mycosphaerella lateralis	ML1F	AAACGCCGGGGCCTTCG	54	-	Maxwell et al. 2005
	ML1R	CGACGTCTCCGCCGATGTTTTCC	61		
Mycosphaerella marksii	MM1F	CGGCCCGACCTCCAACC	57	-	Maxwell et al. 2005
	MM1R	GATGCCACAACGCTCGGAGA	55		
Mycosphaerella parva	MP1F	CCTCCGGGCTCGACCTCCA	60	-	Maxwell et al. 2005
	MP1R	TCTCGCAAGCGGATGATTAAACC	55		
	MgpF	CCCATIGTATICCGACCTCTIG		359	Glen et al. 2007
	MgpR	CGCTIAGAGACAGTIGGCTCAG			
Mycosphaerella tasmaniensis	MtasF	GTCACGCGGCCGACCGC		298	Glen et al. 2007
	MtasR	CATIAGGGCACGCGGGCTG			

Table 2 Species of *Mycosphaerella* and *Teratosphaeria* and their anamorphs occurring on *Eucalyptus*.

Epithet	Genus	Geographic Distribution	Hosts	Reference
acaciigena	*Pseudocercospora*	Australia, Venezuela	*Eucalyptus sp., E. camaldulensis × E. urophylla*	Crous et al. 2007b
acerosa	*Pseudocercospora*	New Zealand	*E. baxteri, E. nitens*	Braun and Dick 2002
aerohyalinosporum	*Zasmidium*	Australia	*E. tectifica*	Crous et al. 2009c
africana	*Teratosphaeria*	Colombia, Portugal, South Africa, Zambia	*E. deanei, E. globulus, E. grandis, E. radiata, E. viminalis*	Crous and Wingfield 1996

				Crous 1998
alboconidia	*Teratosphaeria*	Australia	*E. miniata*	Crous et al. 2009c
ambiphylla	*Mycosphaerella*	Australia	*E. globulus*	Maxwell et al. 2003
angustia	*Readeriella*	Australia	*E. delegatensis, E. regnans*	Crous et al. 2009c
associata	*Teratosphaeria*	Australia	*E. dunnii, Corymbia henryii, C. variegata*	Carnegie 2007a Crous et al. 2007b Carnegie et al. 2011
aurantia	*Mycosphaerella*	Australia	*E. globulus*	Maxwell et al. 2003
aurantia	*Teratosphaeria*	Australia, Uruguay	*E. dunnii, E. grandis*	Perez et al. 2009 Andjic et al. 2010b
australiensis	*Teratosphaeria*	Australia	*C. ficifolia*	Crous et al. 2009d
basitruncata	*Pseudocercospora*	Colombia	*Eucalyptus sp., E. grandis*	Crous 1998
basiramifera	*Pseudocercospora*	Thailand	*E. camaldulensis, E. pellita*	Crous 1998
biformis	*Teratosphaeria*	Australia	*E. globulus*	Andjic et al. 2010b
blakelyi	*Teratosphaeria*	Australia	*E. blakelyi*	Taylor et al. 2011
brunneotingens	*Readeriella*	Australia	*E. tereticornis*	Crous et al. 2007a
callista	*Readeriella*	Australia	*Eucalyptus sp., E. cannonii, E. deanei, E. haemastroma, E. multicaulis, E. sclerophylla*	Crous et al. 2009d
chiangmaiensis	*Pseudocercospora*	Thailand	*E. camaldulensis*	Cheewangkoon et al. 2008
colombiensis	*Pseudocercospora*	Colombia	*E. urophylla*	Crous 1998
complicata	*Teratosphaeria*	Australia	*E. miniata*	Crous et al. 2009c
considenianae	*Readeriella*	Australia	*E. consideniana*	Taylor et al. 2011
coolabuniensis	*Teratosphaeria*	Australia	*C. torelliana × C. variegate*	Carnegie et al. 2011
corymbia	*Penidiella*	Australia	*C. foelscheana*	Cheewangkoon et al. 2009
crispata	*Teratosphaeria*	Australia	*E. bridgesiana*	Carnegie et al. 2011
crousii	*Pseudocercospora*	Australia, New Zealand	*E. delegatensis, E. dendromorpha, E. fastigata, E. muelleriana, E. obliqua, E. oreades, E. pilularis, E. regnans, E. regnans × E. obliqua, E. stenostoma*	Braun and Dick 2002 Carnegie et al. 2007
cryptica	*Teratosphaeria*	Australia, New Zealand	*E. acmenoides, E. alba, E. bridgesiana, E. camaldulensis, E. cinerea, E. cloeziana, E. consideniana, E. cordata, E. crenulata, E. delegatensis, E. diversicolor, E. dunnii, E. fastigata, E. fraxinoides, E.*	Dick 1982 Cheah and Hartill 1987 Carnegie et al. 1997 Crous 1998 Carnegie and Ades 2002

			globulus, E. globulus × E. nitens, E. grandis, E. grandis × E. camaldulensis, E. grandis × E. urophylla, E. gunnii, E. laevopinea, E. longirostrata, E. marginata E. micrantha, E. microcorys, E. moluccana, E. nitens, E. nova-anglica, E. obliqua, E. ovata, E. patens, E. parvula, E. pellita, E. pilularis, E. propinqua, E. pulverulenta, E. punctata, E. regnans, E. saligna, E. saligna × E. tereticornis, E. scorparia, E. tereticornis, E. urophylla	Barber et al. 2003 Jackson et al. 2005 Carnegie 2007a Carnegie et al. 2011
crystallina	*Pseudocercospora*	South Africa	*E. bicostata, E. grandis × E. camaldulensis*	Crous and Wingfield 1996
cubae	*Pseudocercospora*	Cuba	*Eucalyptus sp.*	Crous 1998
davisoniellae	*Mycosphaerella*	Australia	*E. marginata*	Crous et al. 2006
deglupta	*Pseudocercospora*	Malaysia, Papua New Guinea	*E. deglupta, E. delegatensis*	Crous 1998 Braun 2001 Braun and Dick 2002
delegatensis	*Kirramyces*	Australia	*E. delegatensis, E. obliqua*	Park and Keane 1984
dendritica	*Teratosphaeria*	Australia	*E. deanei, E. globulus, E. nitens*	Crous et al. 2007b
denticulate	*Pseudocercospora*	Dominican Republic, Japan	*Eucalyptus sp., E. globulus.*	Crous 1998 Braun and Dick 2002
destructans	*Kirramyces*	Australia, China, Indonesia	*Eucalyptus spp., E. camaldulensis, E. grandis × urophylla, E. urophylla*	Wingfield et al. 1996a Burgess et al. 2007b Zhou and Wingfield 2011
dimorpha	*Teratosphaeria*	Australia	*Eucalyptus sp., E. caesia, E. nitens*	Crous et al. 2009a
dimorphospora	*Readeriella*	Australia	*E. nitens*	Crous et al. 2007b
ellipsoidea	*Mycosphaerella*	Australia, South Africa	*E. cladocalyx, E. globulus, E. nitens*	Crous and Wingfield 1996 Hunter et al. 2004b Jackson et al. 2008

elongata	*Mycosphaerella*	Venezuela	*E. camaldulensis × E. urophylla*	Crous et al. 2007b
endophytica	*Mycosphaerella*	South Africa	*Eucalyptus sp., E. grandis, E. nitens*	Crous 1998
epispermogonia	*Pseudocercospora*	South Africa	*E. grandis × E. saligna*	Crous and Wingfield 1996 Braun and Dick 2002
eucalypti	*Mycosphaerella*	Australia	*Eucalyptus sp.*	Park and Keane 1984 Crous 1998 Carnegie et al. 2011
eucalypti	*Passalora*	Brazil	*E. saligna*	Crous 1998
eucalypti	*Penidiella*	Thailand	*E. camaldulensis*	Cheewangkoon et al. 2008
eucalypti	*Ramularia*	Australia, Italy	*Eucalyptus sp., E. grandiflora*	Crous et al. 2007b
eucalypti	*Readeriella*	Australia	*E. dunnii, E. globulus, E. grandis, E. grandis × E. camaldulensis, E. gunnii, E. haemastoma, E. microcorys, E. pilularis, E. parvula, E. saligna*	Barber et al. 2003 Carnegie 2007a
eucalypti	*Teratosphaeria*	Argentina, Australia, Brazil, India, Italy, Peru, Paraguay, New Zealand, Taiwan, Zaire	*E. aggregata, E. alba, E. albens, E. amygdalina, E. blakelyi, E. bosistoana, E. botryoides, E. bridgesiana, E. camaldulensis, E. camphora, E. cephalocarpa, E. cinerea, E. crebra, E. cypellocarpa, E. dalrympleana, E. fasitgata, C. ficifolia, E. gardneri, E. globulus, E. gomphocephala, E. goniantha, E. goniocalyx, E. grandis, E. gunnii, E. largiflorens, E. leucoxylon, E. longiflora, E. melliodora, E. moluccana, E. nitens, E. nutans, E. obliqua, E. occidentalis, E. oreades, E. ovata, E. paniculata, E. pauciflora, E. paulistana, E. perriniana, E. platypus, E. ployanthemos, E. populnea, E. pulchella, E. punctata, E. regnans, E. resinifera, E. robusta,*	Gadgil and Dick 1983 Crous 1998 Crous et al. 2007a

			E. rostrata, E. rubida, E. rudis, E. saligna, E sideroxylon, E. stellulata, E. stenostoma, E. tereticornis, E. trabutii, E. viminlais	
eucalypti	*Zasmidium*	Australia	*E. tereticornis*	Crous et al. 2007b
eucalyptigena	*Pseudocercospora*	Australia	*C. citriodora*	Braun 2001
eucalyptigena	*Readeriella*	Australia	*E. dives*	Crous et al. 2009c
eucalyptorum	*Catenulostroma*	Australia	*E. laevopinea*	Crous et al. 2011b
eucalyptorum	*Mycosphaerella*	Indonesia	*Eucalyptus sp.*	Crous et al. 2006
eucalyptorum	*Pseudocercospora*	Germany, Italy, Madagascar, New Zealand, Portugal, South Africa	*E. aggregata, E. alba, E. albens, E. amygdalina, E. bicolour, E. blakelyi, E. bosistoana, E. botryoides, E. bridgesiana, E. camaldulensis, E. camphora, E. cinerea, E. crebra, E. dalrympleana, E. globulus, E. gomphocephala, E. goniocalyx, E. grandis, E. gunnii, E. melliodora, E. nitens, E. occidentalis, E. ovata, E. paniculata, E. ployanthemos, E. populnea, E. punctata, E. resinifera, E. robusta, E. rubida, E. rudis, E. saligna, E. scoparia, E sideroxylon, E. stellulata, E. tereticornis, E. trabutii, E. viminlais*	Crous 1998 Crous et al. 1989d Braun and Dick 2002
eucalyptorum	*Septoria*	India	*Eucalyptus sp.*	Crous et al. 2006
eucalyptorum	*Sonderhenia*	Australia, New Zealand	*E. cameronii, E. coccifera, E. delegatensis, E. dives, E. elata, E. fastigata, E. globoidea, E. leucoxylon, E. nitens, E. obliqua, E. agglomerata, E. amygdalina, E. baxteri, E. consideniana, E. dalrympleana, E. fastigata, E. fraxinoides, E. grandis, E. johnstonii, E. melliodora, E. muellerana, E. pauciflora, E. phaeotricha, E. radiata, E. regnans, E. sieberi, E. smithii, E.*	Dick 1982 Park and Keane 1984 Crous 1998 Carnegie 2000

			tereticornis	
excentrica	*Teratosphaeria*	Australia	*E. agglomerata, C. torelliana x C. variegata, C. variegata*	Crous et al. 2007b Carnegie 2007a Carnegie et al. 2011
fimbriata	*Teratosphaeria*	Australia	*Corymbia sp., C. claksoniana*	Crous et al. 2007b Carnegie et al. 2011
flavomarginata	*Pseudocercospora*	Thailand	*E. camaldulensis*	Hunter et al. 2006b
flexuosa	*Teratosphaeria*	Colombia	*E. globulus*	Crous 1998
foliensis	*Teratosphaeria*	Australia	*E. globulus*	Andjic et al. 2010b
fori	*Pseudocercospora*	Australia, South Africa	*E. globulus, E. grandis*	Hunter et al. 2004b Jackson et al. 2008
gamsii	*Teratosphaeria*	India	*Eucalyptus sp.*	Crous et al. 2006
gauchensis	*Teratosphaeria*	Uruguay	*E. grandis, E. globulus, E. maidenii, E. tereticornis*	Cortinas et al. 2006c Perez et al. 2009
gracilis	*Pseudocercospora*	Indonesia	*E. urophylla*	Crous and Alfenas 1995
gregaria	*Mycosphaerella*	Australia	*E. botryoides, E. globulus, E. grandis, E. saligna, C. maculata*	Carnegie and Keane 1997 Maxwell et al. 2003
heimii	*Pseudocercospora*	Australia, Madagascar, Thailand, Uruguay, Venezuela	*E. camaldulensis, E. dunnii, E. obliqua, E. platyphylla, E. urophylla*	Crous 1998 Whyte et al. 2005 Crous et al. 2007b Perez et al. 2009
heimioides	*Pseudocercospora*	Indonesia	*Eucalyptus sp.*	Crous and Wingfield 1997b Crous 1998
hortaea	*Teratosphaeria*	Madagascar	*E. camaldulensis*	Crous et al. 2009e
intermedia	*Mycosphaerella*	New Zealand	*E. saligna*	Dick and Dobbie 2001
intermedia	*Passalora*	Madagascar	*E. camaldulensis*	Crous et al. 2009e
irregulari	*Mycosphaerella*	Thailand	*Eucalyptus sp.*	Cheewangkoon et al. 2008
irregulariramosa	*Pseudocercospora*	South Africa	*E. grandis, E. saligna*	Crous and Wingfield 1996 Hunter et al. 2004b
irregularis	*Pseudocercospora*	Peru	*Eucalyptus sp.*	Crous 1998
juvenalis	*Teratosphaeria*	South Africa	*E. cladocalyx*	Crous et al. 2009a
keanei	*Teratosphaeria*	Australia	*E. globulus* × *E. camaldulensis*	Carnegie et al. 2011
keniensis	*Mycosphaerella*	Kenya	*E. grandis*	Crous 1998
konae	*Mycosphaerella*	Thailand	*E. camaldulensis*	Crous et al. 2007b
leptophlebiae	*Passalora*	Brazil	*E. leptophlebia*	Crous et al. 2011a

lilianiae	*Teratosphaeria*	Australia	*E. eximia*	Walker et al. 1992
longibasalis	*Mycosphaerella*	Colombia	*E. grandis*	Crous 1998
madagascariensis	*Pseudocercospora*	Madagascar	*E. camaldulensis*	Crous et al. 2009e
madeirae	*Mycosphaerella*	Madeira, Portugal, Spain	*E. globulus*	Crous et al. 2004 Otero et al. 2007a Silva et al. 2009
majorizuluensis	*Teratosphaeria*	Australia	*E. botryoides*	Crous et al. 2009c
mareebensis	*Teratosphaeria*	Australia	*E. alba*	Crous et al. 2011c
marksii	*Mycosphaerella*	Australia, China, Ethiopia, Indonesia, Madagascar, Portugal, South Africa, Uruguay	*Eucalyptus sp., E. bicostata, E. botryoides, E. camaldulensis, E. cloeziana, E. diversicolor, E. dunnii, E. fraxinoides, E. grandis, E. grandis × E. camaldulensis, E. grandis × E. resinifera, E. grandis × E. saligna, E. globulus, E. globulus × E. camaldulensis, E. longirostrata, E. maidenii, E. nitens, E. pellita, E. pilularis, E. propinqua, E. quadrangulata, E. resinifera, E. rudis, E. saligna, E. scias, E. smithii, E. tereticornis, C. maculate, C. torelliana × C. variegata*	Carnegie and Keane 1994 Crous and Wingfield 1996 Crous 1998 Hunter et al. 2004b Jackson et al. 2005 Gezaghne et al. 2006 Carnegie 2007a Perez et al. 2009 Carnegie et al. 2011 Zhou and Wingfield 2011
medusae	*Mycosphaerella*	Australia	*E. alba*	Carnegie et al. 2011
menaiensis	*Readeriella*	Australia	*E. oblonga*	Crous et al. 2009c
mexicana	*Teratosphaeria*	Australia, USA, Mexico	*Eucalyptus sp., E. globulus*	Crous 1998 Maxwell et al. 2003 Crous et al. 2007b
micromaculata	*Teratosphaeria*	Australia	*E. globulus*	Andjic et al. 2010b
miniata	*Teratosphaeria*	Australia	*E. miniata*	Crous et al. 2009c
minutispora	*Readeriella*	Australia, South Africa	*Cussonia sp., C. henryii*	Crous et al. 2007b
mirabilis	*Readeriella*	Australia	*E. capitellata, E. cinerea, E. globulus, E. nicholii, E. pilularis*	Barber et al. 2003 Carnegie 2007a Crous et al. 2009c
molleriana	*Teratosphaeria*	Portugal, Uruguay	*E. globulus*	Crous et al. 2007b Perez et al. 2009
multiseptata	*Teratosphaeria*	Australia	*A. costata, A. subvelutina*	Carnegie et al. 2007
nabiacense	*Zasmidium*	Australia	*Eucalyptus sp.*	Crous et al. 2009c
natalensis	*Pseudocercospora*	South Africa	*E. nitens*	Crous 1998
nootherensis	*Mycosphaerella*	Australia	*C. intermedia*	Carnegie et al. 2011
nontingens	*Readeriella*	Australia	*E. molucanna, E. tereticornis*	Crous et al. 2007b

norchiensis	*Pseudocercospora*	Italy, Uruguay	*Eucalyptus sp., E. grandis, E. globulus*	Crous et al. 2007b Perez et al. 2009
novezelandiae	*Readeriella*	New Zealand	*E. botryoides*	Crous et al. 2004
nubilosa	*Teratosphaeria*	Australia, Brazil, Ethiopia, Kenya, New Zealand, Portugal, South Africa, Spain, Tanzania, Uruguay, Zambia	*Eucalyptus sp., E. bicostata, E. botryoides, E. bridgesiana, E. camaldulensis, E. cypellocarpa, E. dalrympleana, E. dunnii, E. globulus, E. grandis, E. grandis × E. nitens, E. grandis × E. resinifera, E. macarthurii, E. maidenii, E. nitens, E. nova-anglica, E. quadrangulata, E. saligna, E. smithii, E. stuarrtiana, E. tereticornis, E. urophylla × E. globulus, E. viminalis*	Dick 1982 Crous et al. 1989a Crous 1998 Maxwell et al. 2001 Crous et al. 2004 Hunter et al. 2004b Jackson et al. 2005 Carnegie 2007a Gezaghne et al. 2006 Perez et al. 2009a
obscuris	*Teratosphaeria*	Indonesia, Vietnam	*Eucalyptus sp., E. pellita*	Burgess et al. 2007a
ohnowa	*Teratosphaeria*	Australia, South Africa, Uruguay	*E. dunnii, E. grandis, E. smithii, E. viminalis*	Crous et al. 2004 Crous et al. 2007b Perez et al. 2009
ovata	*Teratosphaeria*	Australia, South Africa, New Zealand	*E. cladocalyx, E. dives, E. lehmannii, E. dives, E. leucoxylon, E. maqcrohyncha, E. melliodora, E. obliqua, E. phoenicea, E. regnans*	Crous et al. 1989 Crous 1998 Crous et al. 2009a
paraguayensis	*Pseudocercospora*	Brazil, Israel, Paraguay, Taiwan	*Eucalyptus sp., E. globulus, E. nitens*	Crous 1998
parkii	*Zasmidium*	Brazil, Colombia, Indonesia	*E. globulus, E. grandis, E. saligna*	Crous and Alfenas 1995
parkiiaffinis	*Teratosphaeria*	Venezuela	*E. urophylla*	Crous et al. 2007b
parva	*Teratosphaeria*	Australia, Ethiopia, Portugal, South Africa, Spain	*E. agglomerata, E. botryoides, E. cypellocarpa, E. delegatensis, E. dunnii, E. grandis × E. camaldulensis, E. globulus, E. globulus ×E. urophylla, E. grandis, E. grandis × E. camaldulensis, E. moluccana, E. nitens, E. oblique, E. pellita, E. pilularis, E. regnans, E. saligna*	Park and Keane 1982a Carnegie 2000 Maxwell et al. 2003 Jackson et al. 2005 Gezaghne et al. 2006 Carnegie 2007a Otero et al. 2007a Crous et al. 2008 Silva et al. 2009 Carnegie et al. 2011
patrickii	*Readeriella*	Australia	*E. amygdalina*	Crous et al. 2009d

perpendicularis	*Teratosphaeria*	Colombia	*E. eurograndis*	Crous et al. 2006 Crous et al. 2007a
pluritubularis	*Teratosphaeria*	Australia, Spain, Uruguay	*E. globulus*	Crous et al. 2006 Perez et al. 2009 Carnegie et al. 2011
praelongispora	*Teratosphaeria*	Australia	*Eucalyptus sp., E. dives, E. dunnii*	Carnegie et al. 2011
profusa	*Teratosphaeria*	Australia	*E. nitens*	Crous et al. 2009c
provencialis	*Septoria*	France	*Eucalyptus sp.*	Crous et al. 2006
pseudafricana	*Teratosphaeria*	Zambia	*E. globulus*	Crous et al. 2006
pseudobasitruncata	*Pseudocercospora*	New Zealand	*E. nitens*	Braun and Dick 2002
pseudocallista	*Readeriella*	Australia	*E. prominula*	Crous et al. 2009c
pseudocryptica	*Teratosphaeria*	New Zealand	*Eucalyptus sp.*	Crous et al. 2006
pseudoendophytica	*Mycosphaerella*	South Africa	*E. nitens*	Crous et al. 2006
pseudoeucalypti	*Teratosphaeria*	Australia	*E. grandis × E. camaldulensis*	Andjic et al. 2010a
pseudoeucalyptorum	*Pseudocercospora*	Australia, Spain, China, New Zealand	*Eucalyptus sp., E. globulus*	Crous et al.2004 Carnegie et al. 2011
pseudomarksii	*Mycosphaerella*	Thailand	*Eucalyptus sp.*	Cheewangkoon et al. 2008
pseudoparkii	*Zasmidium*	Colombia	*Eucalyptus sp.*	Crous et al. 2006
pseudosuberosa	*Teratosphaeria*	Uruguay	*Eucalyptus sp.*	Crous et al. 2006
pseudotasmaniensis	*Penidiella*	Australia	*E. globulus*	Crous et al. 2009c
pseudovespa	*Mycosphaerella*	Australia	*E. biturbinata*	Carnegie et al. 2007
quasicercospora	*Teratosphaeria*	Tanzania	*E. maidenii*	Crous et al. 2006
quasiparkii	*Mycosphaerella*	Thailand	*Eucalyptus sp.*	Cheewangkoon et al. 2008
readeriellophora	*Teratosphaeria*	Spain	*E. globulus*	Crous et al. 2004
robusta	*Pseudocercospora*	Malaysia	*E. robusta*	Crous 1998
schizolobii	*Pseudocercospora*	Thailand	*E. camaldulensis*	Crous et al. 2009d
scytalidii	*Mycosphaerella*	Colombia, Uruguay	*E. dunnii, E. grandis, E. urophylla*	Crous et al. 2006 Perez et al. 2009
secundaria	*Teratosphaeria*	Brazil, Colombia	*Eucalyptus sp.*	Crous et al. 2006
sphaerulinae	*Pseudocercospora*	Chile	*E. globulus, E. nitens*	Crous et al. 2003
stonei	*Phaeophleospora*	Australia	*Eucalyptus sp.*	Crous et al. 2007b
stramenti	*Mycosphaerella*	Brazil	*Eucalyptus sp.*	Crous et al. 2006
stramenticola	*Teratosphaeria*	Brazil	*Eucalyptus sp.*	Crous et al. 2006
stellenboschiana	*Readeriella*	South Africa	*Eucalyptus sp., E. punctata*	Crous et al. 2006 Crous et al. 2009d
suberosa	*Teratosphaeria*	Australia, Brazil, Colombia, Indonesia, New Zealand	*E. agglomerata, E. cloeziana, E. dunnii, E. globulus, E. grandis, E. grandis × E. camaldulensis, E.*	Crous et al. 1993a Carnegie et al. 1997 Carnegie 2007a

			laevopinea, E. moluccana, E. nitens, E. nitens × E. nobilis, E. muelleriana, E. punctata, E. saligna, E. tereticornis, E. viminalis	Dick and Dobbie 2001
subulata	*Pseudocercospora*	Australia, New Zealand	*E. botryoides*	Crous et al. 2006 Carnegie et al. 2007
sumatrensis	*Mycosphaerella*	Indonesia	*Eucalyptus sp.*	Crous et al. 2006
suttonii	*Teratosphaeria*	Argentina, Australia, Bhutan, Brazil, China, Ethiopia, Hong Kong, India, Indonesia, Italy, Madagascar, Malawi, Myanmar, New Zealand, Philippines, South Africa, Taiwan, Tanzania, USA, Zambia	*E. amplifolia, E. camaldulensis, C. citriodora, E. cladocalyx, E. crebra, E. dealbata, E. delegatensis, E. drepanophylla, E. dunnii, E. exserta, E. globulus, E. grandis, E. longifolia, E. macarthurii, C. maculata, E. major, E. microcorys, E. nitens, E. nova-anglica, E. pellita, E. platypus, E. punctata, E. quadrangulata, E. radiata, E. resinifera, E. robusta, E. rostrata, E. saligna, E sideroxylon, E. tereticornis, E. urophylla, E. viminalis*	Crous et al. 1998 Carnegie 2007a Jackson et al. 2008 Zhou and Wingfield 2011
syncarpiae	*Teratosphaeria*	Australia	*S. glomulifera*	Carnegie et al. 2007
tasmanica	*Readeriella*	Australia	*E. delegatensis*	Crous et al. 2009c
tasmaniensis	*Mycosphaerella*	Australia	*E. globulus, E. nitens*	Crous et al. 1998 Jackson et al. 2008
tenuiramis	*Penidiella*	Australia	*E. tenuiramis*	Crous et al. 2009c
tereticornis	*Pseudocercospora*	Australia	*E. nitens, E. tereticornis*	Crous et al. 2009c
thailandica	*Pseudocercospora*	Thailand	*E. camaldulensis*	Crous et al. 2007b
tinara	*Teratosphaeria*	Australia	*Corymbia sp.*	Andjic et al. 2010b
toledana	*Teratosphaeria*	Spain	*Eucalyptus sp.*	Crous et al. 2004
tumulosa	*Mycosphaerella*	Australia	*C. variegata, Eucalyptus sp., E. acmeniodes, E. amplifolia, E. melanophloia, E. moluccana, E. seeana, E. tereticornis*	Carnegie 2007a Carnegie et al. 2007
veloci	*Teratosphaeria*	Australia	*E. miniata*	Crous et al. 2009a
verrucosa	*Teratosphaeria*	South Africa	*Eucalyptus sp., E. cladocalyx*	Crous et al. 2009a
verrucosiafricana	*Mycosphaerella*	Australia, Indonesia	*Eucalyptus sp., E. tereticornis*	Crous et al. 2006 Carnegie et al. 2011
vietnamensis	*Mycosphaerella*	Vietnam	*E. camaldulensis, E. grandis*	Burgess et al. 2007a

viscidus	*Teratosphaeria*	Australia	*Eucalyptus sp., E. grandis, E. grandis × E. camaldulensis*	Andjic et al. 2007 Crous et al. 2009d
walkeri	*Sonderhenia*	Australia, Chile, Colombia, Ecuador, New Zealand, Portugal	*E. globulus, E. globoidea, Eucalyptus sp., E. cladocalyx, E. gomphocephala, E. nitens, E. polyanthemos*	Park and Keane 1984 Crous 1998 Carnegie 2000
xenocryptica	*Teratosphaeria*	Chile	*Eucalyptus sp.*	Crous et al. 2009c
xenoparkii	*Zasmidium*	Indonesia	*E. grandis*	Crous et al. 2006
yunnanensis	*Mycosphaerella*	China	*E. urophylla*	Burgess et al. 2007a
zambiae	*Passalora*	Zambia	*E. globulus*	Crous et al. 2004
zuluensis	*Teratosphaeria*	China, Malawi, South Africa	*E. grandis* *E. urophylla*	Wingfield et al. 1996b Cortinas et al. 2010 Chen et al. 2011

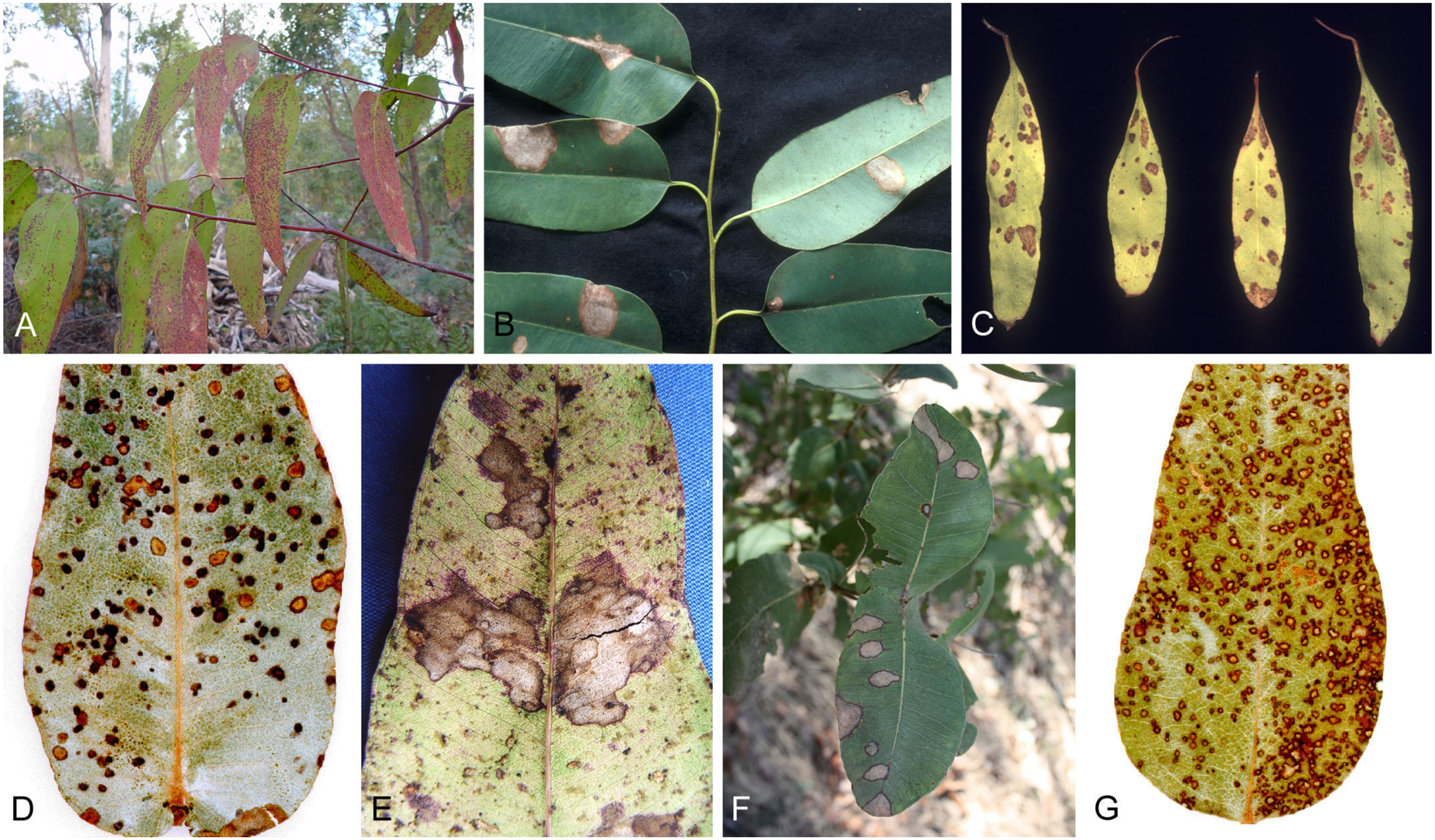

Fig. 1 Characteristic leaf spot symptoms caused by selected species of *Mycosphaerella* and their anamorphs on *Eucalyptus*. **A**. *Sonderhenia swartii* on *E. sieneri*. **B**. *Zasmidium parkii*. **C**. *Mycosphaerella africana*. **D**. *Sonderhenia walkeri*. **E**. *Mycosphaerella marksii*. **F**. *Mycosphaerella marksii*. **G**. *Sonderhenia swartii*

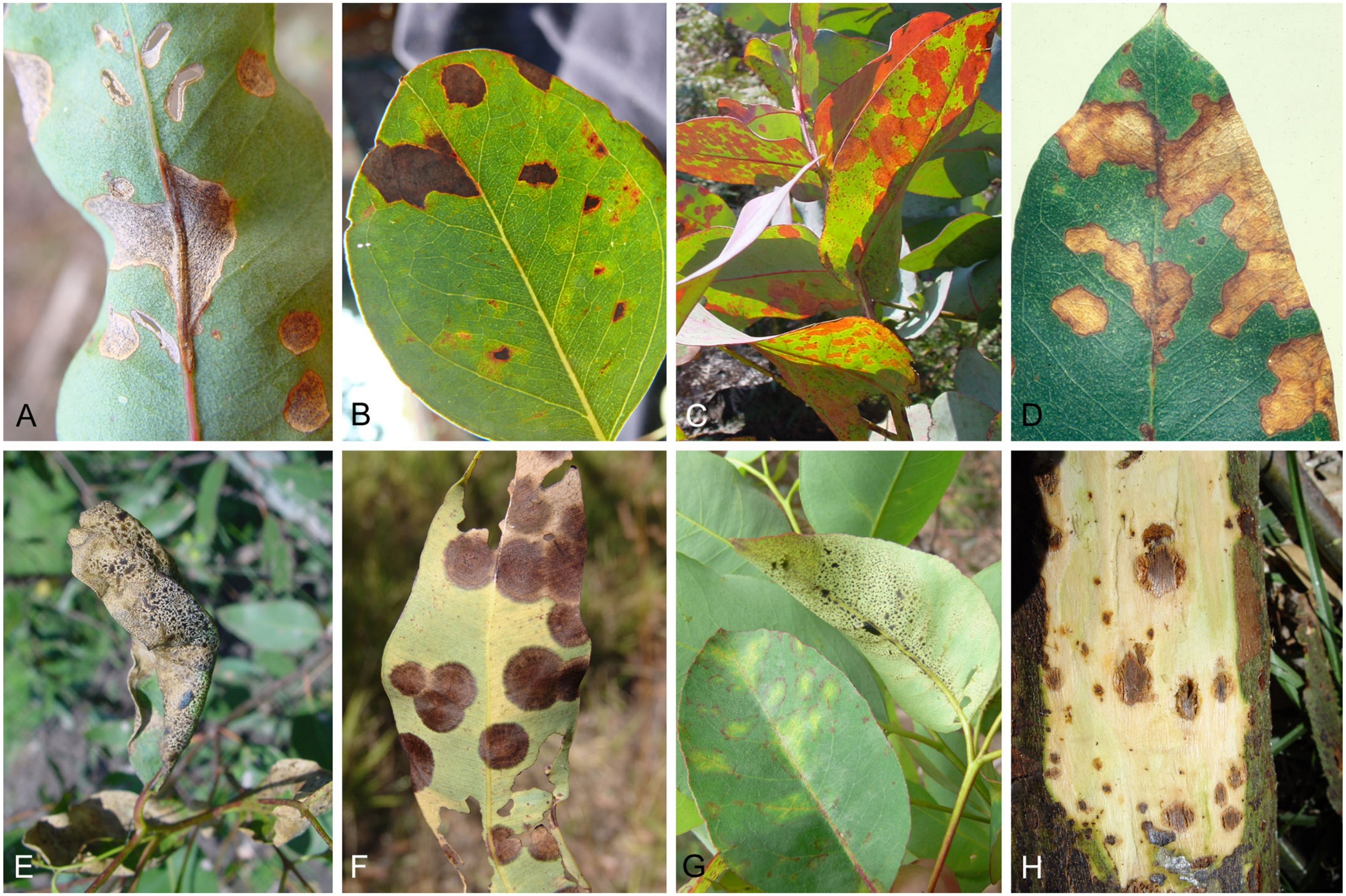

Fig. 2 Characteristic symptoms caused by selected species of *Teratosphaeria* on *Eucalyptus*. **A**. *Teratosphaeria cryptica* on *E. globulus*. **B**. Mixed infection of *T. juvenalis* and *T. verrucosa*. **C**. *T. eucalypti*. **D**. *T. nubilosa* on *E. globulus*. **E**. *T. pseudoeucalypti*. **F**. *T. fimbriata*. **G**. *T. destructans*. **H**. *T. gauchensis*